The alteration of biotic interactions in fragmented tropical forests

WILLIAM F. LAURANCE

Smithsonian Tropical Research Institute and National Institute for Amazonian Research (INPA)

Introduction

Tropical rainforests are renowned for their ecological complexity and the seeming ubiquity of coevolved relationships among species (Janzen 1969; Gilbert 1980). Unfortunately, these forests are being destroyed and fragmented at alarming rates, to the extent that many tropical protected areas are becoming virtual islands in a sea of heavily degraded land (Laurance & Bierregaard 1997; DeFries *et al.* 2002). The future of tropical biodiversity will be largely determined by the extent to which natural ecological processes and communities can be maintained in isolated fragments of forest.

Here I summarize available information on the alteration of biotic interactions, such as predation and key symbioses like pollination and seed dispersal, in fragmented tropical forests. This review is necessarily preliminary, given the great diversity of species and ecological interactions in the tropics and the fact that the alteration of biotic linkages is among the most poorly understood consequences of habitat fragmentation.

Initial impacts of fragmentation

Forest fragmentation leads to the reduction and isolation of remnant forest patches. Although each fragmented landscape is unique, a common pattern is that most forest fragments in human-dominated landscapes are small, ranging in size from a hectare or less to a few hundred hectares (Gascon *et al.* 2000; Cochrane & Laurance 2002). The biota of such small forest patches are expected to be vulnerable to edge effects and many other negative consequences of fragmentation (e.g. Laurance *et al.* 1998, 2002).

As forest-clearing proceeds, some species that are initially present in a landscape may be completely extirpated by habitat loss, and others may persist in tiny numbers in fragments, especially if they are rare or patchily distributed (termed the sample effect; Wilcox 1980). Forest-dependent species will be demographically and genetically isolated to varying degrees in fragments, depending on
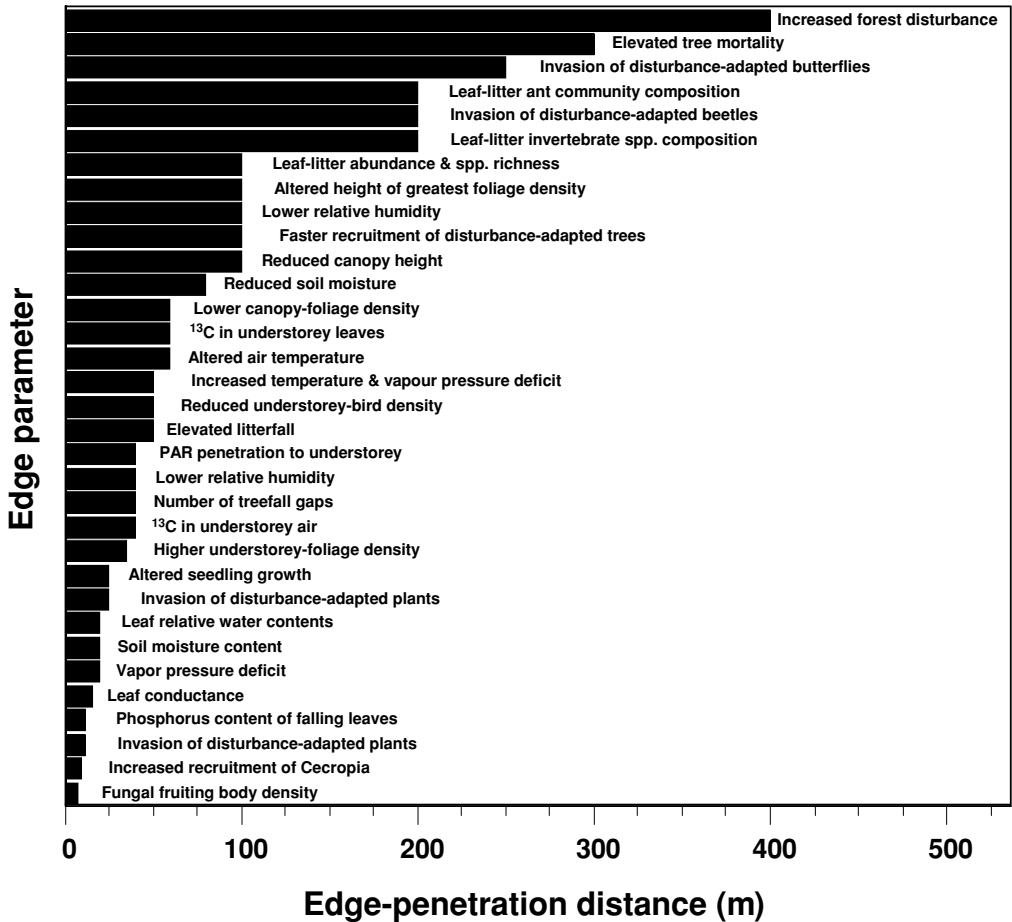
Figure 18.1 Penetration distances of different edge effects into Amazonian forest remnants (after Laurance *et al.* 2002). The distances shown here are typical; landscape factors such as edge age and the type of modified vegetation adjoining fragments can also have a significant influence on the intensity and penetration of edge effects.

their intrinsic characteristics (such as their mobility and tolerance of degraded habitats; Diamond *et al.* 1987; Laurance 1991) as well as attributes of the particular landscape (such as the degree to which the fragment is isolated from other forests and the types of degraded lands surrounding the fragment). When isolated, small populations (< 100 individuals) are vulnerable to local extinction from random demographic and genetic effects, frequently exacerbated by environmental variations and local catastrophes (Leigh 1981; Shafer 1981; Lande 1988).

In addition to physical isolation, an important driver of ecological change in forest fragments is edge effects (Fig. 18.1) – diverse physical and biotic alterations associated with the abrupt, artificial margins of habitat fragments (Janzen 1986;

Lovejoy *et al*. 1986; Murcia 1995; Laurance *et al*. 2002). Fragmented tropical forests often have sharply elevated tree mortality, a proliferation of disturbance-adapted trees and vines (Viana *et al*. 1997; Laurance *et al*. 1998), and hotter, drier conditions near forest boundaries (Kapos 1989). Most edge effects penetrate anywhere from a few metres to a few hundred metres into fragments, although some phenomena (such as surface fires and certain invading species) can penetrate as far as 2–10 km into forests (Laurance 2000). As a result of such changes, some forest-dependent species decline near fragment margins whereas disturbance-adapted and generalist species increase, sometimes dramatically (Lovejoy *et al*. 1986; Restrepo *et al*. 1999; Laurance *et al*. 2002).

Fragmented forests are not merely reduced and isolated; they also face additional threats from hunting, logging, surface fires, pollution, and climatic and atmospheric change (e.g. Peres 2001; Weathers *et al*. 2001; Cochrane & Laurance 2002; Milner-Gulland *et al*. 2003; Laurance 2004). The impacts of such ancillary threats on fragmented populations are poorly understood, in part because they vary greatly in intensity among different landscapes and regions, complicating efforts to develop simple generalizations. However, because hunting is nearly ubiquitous and can have important impacts on tropical vertebrates and their ecological roles in fragmented forests (Cullen *et al*. 2000; Peres 2001), its effects will be considered briefly here.

Many species are highly vulnerable in fragmented and hunted tropical landscapes, including large predators and herbivores, many understorey birds, some primates, a variety of insects and various plant species (Lovejoy *et al*. 1986; Didham *et al.* 1998; Restrepo *et al*. 1999; Laurance *et al*. 2002). Clearly, the diverse changes in species composition, species abundances, forest dynamics and physical environment alter some – and possibly many – biotic interactions in tropical forest fragments. As discussed below, what is far more poorly understood is the degree to which these altered interactions accelerate local species extinctions or disrupt key ecological processes in fragmented forests, especially over longer time scales ranging from centuries to millennia (e.g. Kellman *et al.* 1996; Corlett & Turner 1997).

Pollination

Most tropical plants are pollinated by insects, birds or bats, and rely on pollinators to maintain genetic diversity through outcrossing (Bawa 1990; Ricklets & Renner 1994; Momose *et al*. 1998). Recent analyses confirm that inbreeding depression in small, isolated populations of plants can reduce seed set, germination, survival and resistance to stress; and that populations with reduced genetic variation can experience reduced growth and increased extinction rates (cf. Keller and Waller 2002 and references therein).

Three factors largely determine the vulnerability of a plant species to the loss of its pollinators in fragmented forests. The first is the degree to which the plant is reliant on pollinators for reproduction. Many tropical plants are obligate

outbreeders, being either dioecious or self-incompatible, or possess mixed mating systems that are highly outcrossed through various mechanisms that select for non-self pollen or outcrossed seed (Bawa & Opler 1975; Renner & Ricklefs 1995; Kenta *et al*. 2002). Many species are also rare, with effective populations often encompassing hundreds to many thousands of hectares (Murawski & Hamrick 1991; Chase *et al*. 1996; Stacy *et al*. 1996; Nason *et al*. 1998), and they frequently have clumped distributions, and thus can be vulnerable to population isolation and an erosion of genetic diversity. Hence, for most tropical plants, animal pollinators are critical.

The second factor is the degree to which the plant depends on specific pollinator species. Plants that rely on just one or a few pollinator species may be more vulnerable to habitat disturbance than are those can utilize a suit of different pollinators (but see Aizen *et al*. 2002). Only a relatively small number of plant species, such as orchids and figs, have obligate relationships with a single bee or wasp pollinator (Bawa 1990). A restricted suite of pollinators is also common on faunally depauperate islands, where a number of plants rely on specific birds (Cox 1983) or flying foxes (Cox *et al*. 1991; Rainey *et al*. 1995) for pollination and seed dispersal. The majority of other plant species, however, have a higher degree of redundancy in their pollinators (e.g. Horvitz & Schemske 1990). Notably, most tropical trees rely on insects and are pollination generalists (Ashton 1969; Bawa & Opler 1975; Stacy *et al*. 1996; Momose *et al*. 1998).

The third factor is the impact of habitat fragmentation on the pollinators. At present, only a few generalizations can be made about the responses to fragmentation of pollinators, as species respond to habitat fragmentation in individualistic ways depending on their tolerance of edge and degraded habitats, population density, trophic position and other factors (Terborgh 1974; Laurance 1991; Didham *et al*. 1998). Among Amazonian butterflies, for example, a number of forest-interior species (especially in the Ithomiinae) decline in forest fragments, whereas light-loving generalist species increase (Brown & Hutchings 1997). Of 12 euglossine-bee species studied by Powell & Powell (1987), four declined in abundance in recently isolated Amazonian forest fragments but other euglossines increased in the modified habitats surrounding the fragments (see also Becker *et al.* 1991). Larger pollinators, such as many hummingbirds (Aizen & Feinsinger 1994a; Stouffer & Bierregaard 1995; Aldrich & Hamrick 1998) and nectar- and fruit-eating bats (Kalko 1998; Law & Lean 1999; Sampaio 2000), appear relatively resilient to habitat fragmentation and can often traverse the degraded lands surrounding fragments (Steffan-Dewenter & Tscharntke 1999). When subjected to both fragmentation and hunting, however, flying foxes have often declined precipitously, especially on oceanic islands (Cox *et al*. 1991; Rainey *et al*. 1995). Even when pollinators do not decline markedly in fragmented forests, changes in the distribution of resources can alter pollinator foraging behaviour with

respect to flower fidelity and foraging distance, which affects the quality and quantity of pollen arriving at the plant (Aizen & Feinsinger 1994a; Aldrich & Hamrick 1998; Ghazoul & McLeish 2001).

To date, only a few studies have provided unequivocal evidence of reduced plant reproduction in response to fragmentation-induced changes in pollinators. One of the most important studies is that of Aizen and Feinsinger (1994a), who worked not in tropical rainforest but in dry subtropical forest in the Argentinian Chaco. Among 16 plant species they studied (most of which were mainly bee-pollinated), 13 had reduced seed production in forest fragments. Moreover, among three self-compatible species, plants in fragments appeared to receive most pollen from themselves or from closely related neighbours, suggesting that pollinators were unable to transport pollen between different fragments (Aizen & Feinsinger 1994a).

Other evidence of negative fragmentation effects is more anecdotal. In the central Amazon, Dick (2001a) observed an absence of small beetles and stingless bees on mass-flowering trees in cattle pastures, and suggested that plants that are pollinated exclusively by small beetles, such as those in the nutmeg family (Myristicaceae), could be especially vulnerable to fragmentation. In Costa Rican forest fragments, Ghazoul and McLeish (2001) found no decrease in the abundance of *Trigona* bee pollinators for the widespread tree *Anacardium excelsum*, but observed that pollination success and seed production was positively correlated with fragment size. They proposed that *Trigona* bees rarely move among fragments, reducing genetic variability, fertilization and seed set among trees in small fragments. Aldrich and Hamrick (1998) found that reproduction of the bat-dispersed tree *Symphonia globulifera* in forest fragments in Costa Rica was dominated by a few large, isolated trees in pastures that had high rates of selfing, suggesting that fragmentation might eventually cause a genetic bottleneck in the population. Finally, Murren (2002, 2003) found that epiphytic orchids (*Catasetum viridiflavum*) on small man-made islands in Lake Gatun, Panama had lower seed set than did plants in nearby mainland areas, suggesting that pollination by euglossine bees was reduced on islands, although there was no evidence of reduced gene flow among island populations.

A collapse of plant–pollinator mutualisms has also been observed on oceanic islands, which are somewhat analogous to habitat fragments in being isolated and having relatively depauperate biotas. In Hawaii, the loss or severe decline of native sphingid-moth pollinators has been implicated in the very low fruit set of endemic *Brighamia* (Campanulaceae). Moreover, Hawaiian plants like *Stenogyne kanehoana* (Lamiaceae) have not set seeds for many years because their honeycreeper pollinators have been extirpated (Renner 1998). The decimation of flying foxes on many Pacific islands has also led to reduced reproduction in endemic plants that rely on these large bats for pollination (Cox *et al*. 1991; Rainey *et al*. 1995).

In other cases, however, fragmentation has had little effect on plant reproduction because native pollinators are unaffected or recover quickly from population declines. Two species of hummingbird-pollinated plants in the Argentinian Chaco actually had stable or increased reproduction, evidently because hummingbirds preferred the flower-rich fragments and readily moved among them (Aizen & Feinsinger 1994a). After being decimated by a hurricane, populations of fig wasps recovered quickly (within 5–16 months) because the wasps were able to disperse at least 60 km from other forests that were unaffected by the hurricane (Bronstein & Hossaert-McKey 1995). Harrison (2003) inferred that some fig-wasp species in an isolated forest fragment (4500 ha) in Borneo had arrived by dispersing from forests at least 30 km away, although wasps that pollinated dioecious figs were poorly represented and appeared to be much more dispersal-limited than monoecious-fig wasp species. Nason and Hamrick (1997) found that small populations of the neotropical tree *Spondias mombin* in forest fragments actually had higher rates of pollen immigration than did trees in intact forests, suggesting that fragmentation did not result in genetic isolation of populations. Indeed, studies of genetic markers suggest that small fragments and isolated trees in pastures can act as important stepping stones for many pollinators (Boshier *et al.* 1995; Chase *et al.* 1996; Stacy *et al.* 1996; Dick 2001b; White *et al.* 2002; Dick *et al.* 2003; Murren 2003). Finally, Murcia (1996) found no effect of fragment size or edge effects on pollination of 16 plant species in Colombian cloud forests.

In some fragmented landscapes, plant reproduction and gene flow have been maintained despite severe declines of natural pollinators, when exotic animal species take over the pollination duties. Isolated canopy trees (*Dinizia excelsa*) in Amazonian pastures were genetically 'rescued' by abundant Africanized honeybees (*Apis mellifera scutellata*), which more than compensated for the decline of native insect pollinators and contributed to an increase in the production of outcrossed seeds in pasture trees, relative to those in intact forest (Dick 2001a, 2001b; Dick *et al.* 2003). Similarly, in the Argentinian Chaco, the proportion of flower visits by Africanized honeybees increased in forest fragments relative to intact forest (Aizen & Feinsinger 1994b). In Hawaii, a number of endemic plant species that formerly relied on honeycreepers for pollination are now being pollinated by introduced bird species (Renner 1998). Although exotic pollinators help to maintain plant reproduction in some cases, it is possible that they may displace native pollinators and thereby contribute to the breakdown of natural plant–pollinator interactions.

In summary, habitat fragmentation and related disturbances alter many plant–pollinator interactions, but the effects of these changes on plant reproduction vary considerably among different studies and landscapes. In some cases, ecological redundancy of pollinators and exotic pollinators limit the impact of declining native pollinators, but in many other cases plant fecundity is clearly being reduced. In general, pollen movement among the most isolated fragments

is more likely to be mediated by large pollinators, such as birds, bats and large bees, than by small insects (Steffan-Dewenter & Tscharntke 1999). Surprisingly, self-compatible and self-incompatible plants may show little overall difference in their vulnerable to fragmentation, despite the latter being more reliant on animal pollinators (Aizen *et al.* 2002). However, canopy trees, which are typically pollination generalists, could be less vulnerable to fragmentation than are understorey plants, which rely on fewer pollinator species (Aizen & Feinsinger 1994a; Momose *et al.* 1998; Renner 1998). Plant–pollinator relationships are often asymmetrical, with the pollinator being more specialized on the host plant than vice versa (as in some solitary bees; Renner 1998), and thus host-specific pollinators could be vulnerable in fragmented forests if their host plants decline.

Seed dispersal, seed predation and herbivory

Although some tropical plants rely on wind, gravity or water to disperse their propagules, the bulk of species have animal-dispersed fruits or seeds. Birds and bats are the main dispersers for smaller-seeded plants, whereas terrestrial and arboreal mammals disperse larger-seeded species (Levey *et al.* 1994). A distinction can be drawn between primary dispersers (such as monkeys) that remove fruit or seeds directly from tree crowns, and secondary dispersers (such as terrestrial mammals) that remove fallen fruit and seeds (Wright 2003).

Many seed-dispersing animals are also seed predators, although different species vary greatly in the degree to which they consume seeds; for example, peccaries and white-tailed deer are almost exclusively predators of large seeds, whereas tapirs act primarily as large-seed dispersers and agoutis are major seed predators but aid plant recruitment by caching and burying seeds (Brewer *et al.* 1997). Insects (notably bruchid beetles) are usually seed predators (Janzen 1970). Seed dispersal can provide a critical escape from severe density-dependent seed predation, seedling herbivory and pathogen attack near parent plants (Janzen 1970; Connell 1971), and there is a strong indication that some tree species would be unable to recruit without mammalian dispersers (Augspurger 1984; Chapman & Chapman 1995).

How does forest fragmentation affect dispersal and predation of plant propagules? At least on small man-made islands, these processes appear to be profoundly disrupted. On tiny (< 1 ha) islands created in the late 1980s in Venezuela, predators of vertebrates have disappeared and some of their prey, including rodents, howler monkeys, iguanas and leaf-cutter ants, have increased 10- to 100-fold in density. As a consequence, seedlings and saplings of canopy trees are severely reduced, providing evidence of a trophic cascade that is ramifying throughout the animal and plant communities (Terborgh *et al.* 2001). On equally small (< 2 ha) but older (*c.* 80-year-old) islands in Lake Gatun, Panama, most mammals have disappeared but rats (*Proechimys semispinosus*) have increased sharply in abundance, and predation on large seeds is sharply elevated relative

to mainland forest (Asquith *et al.* 1997). On Lake Gatun islands that are too small to support any mammals, tree communities are dominated by a few large-seeded species (Putz *et al.* 1990; Leigh *et al.* 1993) that may out-compete smaller-seeded trees when key predators of large seeds, such as agouti and paca, are absent (Terborgh 1992).

It is unclear, however, whether such trends are typical of 'real' forest fragments, which are surrounded by a matrix of modified land and subjected to varying levels of hunting pressure. Fragmented forests in Los Tuxtlas, Mexico, have experienced sharply reduced grazing pressure and increased plant regeneration, leading to dense monospecific carpets of seedlings on the forest floor (Dirzo & Miranda 1991). As discussed by Asquith *et al.* (1997), this may arise from defaunation of larger (>1 kg) predatory and herbivorous mammals by hunters and, perhaps more importantly, from suppression of small-rodent populations by abundant vipers (*Bothrops* spp.). The net effect is that plant recruitment at Los Tuxtlas is very different from that observed on small islands.

Plant recruitment is often altered in fragmented forests. In Costa Rican fragments, Guariguata *et al.* (2002) found higher seed predation by small rodents, and reduced dispersal, for one canopy tree species (*Dipterix panamensis*) but not for a second species (*Carapa guianensis*). Tabarelli *et al.* (1999) found that small (<15 ha) forest fragments of Brazilian Atlantic forest isolated for over 50 years had more abiotically dispersed trees and shrubs, and fewer animal-dispersed trees, than did larger (370–7900 ha) fragments, probably because of large-scale declines of frugivores in small fragments. In Tanzania, a number of tree species in small (<9 ha) forest fragments show reduced recruitment, apparently because of sharp declines in frugivorous birds and primates in the fragments (Cordeiro & Howe 2001, 2003).

In at least two studies, fragmentation reduced plant recruitment by promoting an influx of seed predators from surrounding degraded habitats. In a national park in Indonesian Borneo, large influxes of vertebrate seed predators from adjoining degraded lands led to a dramatic collapse in recruitment of dipterocarp canopy trees during a major masting event (Curran *et al.* 1999). Similar patterns were observed at Pasoh Forest Reserve in Peninsular Malaysia, where pigs (*Sus scrofa*) achieved abnormally high population densities by feeding on oil palms surrounding the reserve and then severely damaged the understorey vegetation (Ickes *et al.* 2001) and dipterocarp recruitment within the reserve. Moreover, when the surrounding oil palms were felled in 2001, pig populations crashed and dipterocarp recruitment in the reserve recovered following a general flowering event the following year (S. J. Wright, personal communication).

Some evidence suggests that large-seeded plants may be more vulnerable than small-seeded species in fragmented landscapes because the large vertebrates on which they rely for dispersal, such as ungulates and primates, are often sharply

reduced in abundance by the combined effects of hunting and fragmentation (Fuentes 2000; Peres 2001). In central Panama, hunting and fragmentation had negative effects on long-distance recruitment of the large-seeded palm *Attalea butyraceae* (Wright & Duber 2001). Seed predation and dispersal of seeds away from presumptive parent trees were reduced on small islands and in areas subjected to heavy hunting pressure, relative to lightly hunted and intact-forest sites. Seedling densities were highest around parent trees on islands and in heavily poached sites, suggesting that human disruption of mammal communities may eventually reduce local tree diversity by disrupting natural density-dependent seed predation (Wright & Duber 2001). Small-seeded plants can also be vulnerable if their key dispersers respond negatively to fragmentation, as occurs in some species dispersed by birds (e.g. Cordeiro & Howe 2001, 2003) or by dung beetles (e.g. Chapman *et al.* 2003).

Forest fragmentation can also affect rates of leaf herbivory, although this phenomenon has been relatively little studied in the tropics. As discussed above, Terborgh *et al.* (2001) found intense herbivory on seedlings and saplings on small man-made islands in Venezuela, following population explosions of leaf-cutting ants and other herbivores on the islands. Forest fragments in the Amazon and Brazilian Atlantic region also show atypically high densities of leaf-cutting ants, especially near fragment margins, which could increase mortality and turnover of young trees (Vasconcelos & Cherrett 1995; Laurance 2003). Herbivorous insects generally increase near the margins of Amazonian forest fragments, possibly in response to increased leaf flush there (Lovejoy *et al.* 1986; Didham 1997). Herbivory from mammals (mainly rodents) on seedlings and saplings was evidently greater on small islands than on large islands and mainland areas in Panama (Asquith *et al.* 1997). With the exception of Benitez-Malvido *et al.* (1999), who found little difference in insect damage to leaves between fragmented and intact Amazonian forests, most studies have found increased herbivory in forest fragments. The decline of many predators in fragments (see below), and the concomitant increases in herbivorous vertebrates and insects, may partially explain this pattern.

It must be emphasized that the effects of habitat fragmentation on plant recruitment and survival are often context specific, depending on the nature of the fragmented landscape, its constituent fauna and the relative impact of hunting on predatory and herbivorous mammals. As proposed by Wright (2003), the indirect effects of hunting on plant communities could depend on whether large carnivores are being hunted (such as for the fur trade) or whether hunting is principally for food, in which case agoutis, deer and other herbivorous mammals are mainly taken. In the former case, abundances of larger-bodied seed predators and herbivores may actually increase, whereas in the latter case they are likely to decline.

Predation

Large predators such as jaguars, tigers and some raptors are more vulnerable to local extinction in fragmented forests than are species at lower trophic levels, because predators require large home ranges and are frequently persecuted by humans. The disappearance of large predators may have important ecological impacts in fragmented landscapes, especially if top-down regulation of prey species is common (Terborgh 1992). The phenomenon of 'mesopredator release' was coined to describe population explosions of medium-sized omnivores (e.g. agoutis, coati mundis, opossums, raccoons, coyotes) in fragmented habitats where large predators have disappeared (Soulé *et al.* 1988; Terborgh 1992; Crooks & Soulé 1999).

Mesopredator release has been documented in fragmented temperate habitats (Soulé *et al.* 1988; Crooks & Soulé 1999) but its importance in the tropics is uncertain. The near extirpation of jaguars, pumas and harpy eagles on Barro Colorado Island, Panama might have led to unusually high densities of medium-sized mammals such as agoutis, coati mundis, sloths and howler monkeys (Glanz 1982; Terborgh 1992), which could account for elevated nest predation on the island (Loiselle & Hoppes 1983; Sieving 1992). It is unclear, however, whether medium-sized mammals are actually hyper-abundant on Barro Colorado Island or merely appear to be so, as they are habituated to humans and therefore conspicuous to researchers on the island (Wright *et al.* 1994). In tropical Australia, atypically high abundances of native rodents in fragmented rainforests may result from the loss of larger rainforest-dependent predators, although edge-related forest disturbances could also favour rodents (Laurance 1994, 1997).

Another potential impact of forest fragmentation is that generalist omnivores, seed predators and brood parasites may flood into fragments from surrounding degraded lands (Curran *et al.* 1999; Ickes *et al.* 2001), causing negative impacts on nesting birds, other small vertebrates and plant communities, especially near forest edges. This phenomenon has been demonstrated in many fragmented temperate and boreal forests (e.g. Gates & Gysel 1978; Wilcove 1985; Paton 1994), but relatively few such studies have been conducted in the tropics. Experimental studies provided no evidence of increased nest or seed predation near forest edges in central Amazonia (Meyer 1999; Bruna 2002) and tropical Australia (Laurance *et al.* 1993; Laurance & Grant 1994; Harrington *et al.* 1997), although Lindell (2000) found increased predation on quail eggs near forest edges in Costa Rica.

It is clear, nevertheless, that important changes in predator and insectivore communities do occur in fragmented forests. In the central Amazon, predation on understorey invertebrates may be reduced because insectivorous bats, understorey birds and army ants all decline sharply (Laurance *et al.* 2002). In tropical Australia, larger rainforest-dependent predators, such as spotted-tailed quolls (Fig. 18.2), rufous owls and larger pythons, decline sharply in forest fragments and are replaced by smaller, generalist predators like barn owls, red-bellied

Figure 18.2 The decline in fragmented landscapes of forest-dependent predators, such as this spotted-tailed quoll (*Dasyurus maculatus*) from tropical Australia, may lead to population explosions of omnivorous mammals that in turn prey on nesting birds, invertebrates, seeds and other rainforest species (photo by S. E. Williams).

blacksnakes and white-tailed rats (Laurance 1997). As discussed above, at least on small man-made islands, striking trophic cascades have been observed following the disappearance of large predators (Terborgh *et al*. 1997, 2001). Such wholesale changes in predator communities must alter predation pressure on different groups of vertebrates and invertebrates.

Other ecological interactions

Fragmentation could potentially alter a great diversity of ecological interactions. For example, army ants require extensive areas for foraging and disappear from small forest fragments in the Amazon and East Africa; in turn, obligate ant-following birds, which prey on insects that flee the marauding ants, also frequently disappear (Harper 1989; Bierregaard *et al*. 1992; Peters & Kramer 2003). The disappearance of collared peccaries (*Tayassu pecari*) from Amazonian forest fragments leads to declines of several frog species that require the muddy pools created by wallowing peccaries, for reproduction (Zimmerman & Bierregaard 1986). The decline of dung beetles in fragmented forests could have large effects on the phoretic mites that rely on these beetles for dispersal (Klein 1989). Altered

levels of insect herbivory in fragments could potentially affect the vulnerability of rainforest plants to infection by fungal pathogens (Benitez-Malvido *et al.* 1999).

It is apparent that these and a great many other ecological interactions are being altered by habitat fragmentation. For some phenomena, such as population explosions of leaf-cutting ants along forest-fragment margins (Vasconcelos & Cherrett 1995; Laurance 2003) that could negatively affect plant recruitment, we have some inkling of their potential impacts on forest ecosystems. For many others – such as the potential effects of fragmentation on disease and parasite dynamics, and on ecological interactions that occur belowground or in the forest canopy – very little is known. In the future, researchers should continue to document the remarkably varied impacts of habitat fragmentation on biotic interactions, but we must also attempt to determine the effects of these alterations on species survival and key ecological processes, and their generality across a range of fragmented landscapes.

Acknowledgements

References

Aizen, M. A., Ashworth, L. & Galetto, L. (2002) Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *Journal of Vegetation Science* **13**, 885–892.

Aizen, M. A. & Feinsinger, P. (1994a) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest. *Ecology* **75**, 330–351.

(1994b) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano'. *Ecological Applications* **4**, 378–392.

Aldrich, P. R. & Hamrick, J. L. (1998) Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science* **281**, 103–105.

Ashton, P. S. (1969) Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* **1**, 155–196.

Asquith, N. M., Wright, S. J. & Clauss, M. J. (1997) Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* **78**, 941–946.

Augspurger, C. K. (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology* **65**, 1705–1712.

Bawa, K. S. (1990) Plant–pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* **21**, 399–422.

Bawa, K. S. & Opler, P. A. (1975) Dioecism in tropical forest trees. *Evolution* **29**, 167–179.

Becker, P., Moure, J. B. & Peralta, F. (1991) More about euglossine bees in Amazonian forest fragments. *Biotropica* **23**, 586–591.

Benitez-Malvido, J., Garcia-Guzman, G. & Kossman-Ferraz, I. (1999) Leaf-fungal incidence and herbivory on tree seedlings in tropical rainforest fragments: an

experimental study. *Biological Conservation* **91**, 143–150.

Bierregaard, R. O., Lovejoy, T. E., Kapos, V., dos Santos, A. & Hutchings, R. (1992) The biological dynamics of tropical rainforest fragments. *BioScience* **42**, 859–866.

Boshier, D. H., Chase, M. R. & Bawa, K. S. (1995) Population genetics of *Cordia alliodora* (Boraginaceae), a neotropical tree. III. Gene flow, neighborhood, and population structure. *American Journal of Botany* **82**, 484–490.

Brewer, S. W., Rejmanek, M., Johnstone, E. & Caro, T. (1997) Top-down control in tropical forests. *Biotropica* **29**, 364–367.

Bronstein, J. L. & Hossaert-McKey, M. (1995) Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. *Biotropica* **27**, 373–381.

Brown, K. S. Jr & Hutchings, R. W. (1997) Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (ed. W. F. Laurance & R. O. Bierregaard). Chicago: University of Chicago Press, pp. 91–110.

Bruna, E. M. (2002) Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia* **132**, 235–243.

Chapman, C. A. & Chapman, L. J. (1995) Survival without dispersers: seedling recruitment under parents. *Conservation Biology* **9**, 675–678.

Chapman, C. A., Chapman, L. J., Vulinec, K., Zanne, A. & Lawes, M. J. (2003) Fragmentation and alteration of seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* **35**, 382–393.

Chase, M. R. Moller, C., Kesseli, R. & Bawa, K. S. (1996) Distant gene flow in tropical trees. *Nature* **383**, 398–399.

Cochrane, M. A. & Laurance, W. F. (2002) Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* **18**, 311–325.

Connell, J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations* (ed. P. den Boer & G. Gradwell). Wageningen: Centre for Agricultural Publishing and Documentation, pp. 298–313.

Cordeiro, N. J. & Howe, H. F. (2001) Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* **15**, 1733–1741.

(2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences* **100**, 14052–14056.

Corlett, R. T. & Turner, I. M. (1997) Long-term survival in tropical forest remnants in Singapore and Hong Kong. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (ed. W. F. Laurance & R. O. Bierregaard). Chicago: University of Chicago Press, pp. 333–346.

Cox, P. A. (1983) Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, *Freycinetia arborea*. *Oikos* **41**, 195–199.

Cox, P. A., Elmquist, T., Pierson, E. D. & Rainey, W. E. (1991) Flying foxes as strong interactions in South Pacific island ecosystems: a conservation hypothesis. *Conservation Biology* **5**, 448–454.

Crooks, K. R. & Soulé, M. E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**, 563–566.

Cullen, L., Bodmer, R. E. & Padua, C. V. (2000) Effects of hunting in habitat fragments of the Atlantic forest, Brazil. *Biological Conservation* **95**, 49–56.

Curran, L. M., Caniago, I., Paoli, G. *et al.* (1999) Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**, 2184–2188.

DeFries, R. S., Houghton, R. A., Hansen, M. C., Field, C. B., Skole, D. & Townsend, J. (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. *Proceedings of the National Academy of Sciences* **99**, 14256–14261.

Diamond, J. M., Bishop, K. D. & van Balen, S. (1987) Bird survival in an isolated Javan island or mirror? *Conservation Biology* **1**, 132–142.

Dick, C. W. (2001a) Habitat change, African honeybees and fecundity in the Amazonian tree *Dinizia excelsa* (Fabaceae). In *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest* (ed. R. O. Bierregaard, C. Gascon, T. Lovejoy & R. Mesquita). New Haven: Yale University Press, pp. 146–157.

  (2001b) Genetic rescue of remnant tropical trees by an alien pollinator. *Proceedings of the Royal Society of London B* **268**, 2391–2396.

Dick, C. W., Etchelecu, G. & Austerlitz, F. (2003) Pollen dispersal of tropical trees (*Dinizia excelsa*: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest. *Molecular Ecology* **12**, 753–764.

Didham, R. K. (1997) The influence of edge effects and forest fragmentation on leaf-litter invertebrates in central Amazonia. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (ed. W. F. Laurance & R. O. Bierregaard). Chicago: University of Chicago Press, pp. 55–70.

Didham, R. K., Lawton, J. H., Hammond, P. M. & Eggleton, P. (1998) Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society of London B* **353**, 437–451.

Dirzo, R. & Miranda, A. (1991) Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (ed. P. Price, T. Lewinsohn, G. Fernandes & W. Benson). New York: John Wiley & Sons, pp. 273–287.

Fuentes, M. (2000) Frugivory, seed dispersal and plant community ecology. *Trends in Ecology and Evolution* **15**, 487–488.

Gascon, C., Williamson, G. B. & Fonseca, G. A. B. (2000) Receding edges and vanishing reserves. *Science* **288**, 1356–1358.

Gates, J. E. & Gysel, L. W. (1978) Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**, 871–883.

Ghazoul, J. & McLeish, M. (2001) Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. *Plant Ecology* **153**, 335–345.

Gilbert, L. E. (1980) Food web organization and the conservation of neotropical diversity. In *Conservation Biology: An Evolutionary–Ecological Perspective* (ed. M. E. Soulé & B. A. Wilcox). Sunderland, MA: Sinauer Associates, pp. 11–33.

Glanz, W. E. (1982) The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. In *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (ed. E. G. Leigh, A. S. Rand & D. Windsor). Washington DC: Smithsonian Institution Press, pp. 455–468.

Guariguata, M. R., Arias-Le Claire, H. & Jones, G. (2002) Tree seed fate in a logged and fragmented forest landscape, northeastern Costa Rica. *Biotropica* **34**, 405–415.

Harper, L. H. (1989) The persistence of ant-following birds in small Amazonian forest fragments. *Acta Amazônica* **19**, 249–263.

Harrington, G. N., Irvine, A. K., Crome, F. H. J. & Moore, L. A. (1997) Regeneration of

large-seeded trees in Australian rainforest fragments: a study of higher-order interactions. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (ed. W. F. Laurance & R. O. Bierregaard). Chicago: University of Chicago Press.

Harrison, R. D. (2003) Fig wasp dispersal and the stability of a keystone plant resource in Borneo. *Proceedings of the Royal Society of London B* **270**, 576–579.

Horvitz, C. C. & Schemske, D. W. (1990) Spatiotemporal variation in insect mutualists of a neotropical herb. *Ecology* **71**, 1085–1097.

Ickes, K., DeWalt, S. J. & Appanah, S. (2001) Effects of native pigs (*Sus scrofa*) on the understory vegetation in a Malaysian lowland rain forest: an exclosure study. *Journal of Tropical Ecology* **17**, 191–206.

Janzen, D. H. (1969) Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. *Ecology* **50**, 147–153.

  (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**, 501–528.

  (1986) The eternal external threat. In *Conservation Biology: An Evolutionary-Ecological Perspective* (ed. M. E. Soulé & B. A. Wilcox). Sunderland, MA: Sinauer Associates, pp. 286–303.

Kalko, E. K. V. (1998) Organization and diversity of tropical bat communities through space and time. *Zoology: Analysis of Complex Systems* **101**, 281–297.

Kapos, V. (1989) Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* **5**, 173–185.

Keller, F. K. & Waller, D. M. (2002) Inbreeding effects in wild populations. *Trends in Ecology and Evolution* **17**, 230–241.

Kellman, M., Tackaberry, R. & Meave, J. (1996) The consequences of prolonged

fragmentation: lessons from tropical gallery forests. In *Forest Patches in Tropical Landscapes* (ed. J. Schelhas & R. Greenberg). Washington, DC: Island Press, pp. 37–59.

Kenta, T., Shimuzu, K., Nagagawa, M., Okada, K., Hamid, A. & Nakashizuka, T. (2002) Multiple factors contribute to outcrossing in a tropical emergent *Dipterocarpus tempehes*, including a new pollen tube guidance mechanism for self-incompatability. *American Journal of Botany* **89**, 60–66.

Klein, B. C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* **70**, 1715–1725.

Lande, R. (1988) Genetics and demography in biological conservation. *Science* **241**, 1455–1460.

Laurance, W. F. (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* **5**, 79–89.

  (1994) Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation* **69**, 23–32.

  (1997) Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. *Wildlife Research* **24**, 603–612.

  (2000) Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* **15**, 134–135.

  (2003) Rainforests at risk from altered ant ecology. News feature, *BioMedNet* (www.bmn.com), 17 March.

  (2004) Forest–climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society of London B* **359**, 345–352.

Laurance, W. F. & Bierregaard, R. O., eds. (1997) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities.* Chicago: University of Chicago Press.

Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. & Laurance, S. G. (1998) Rain

forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79**, 2032–2040.

Laurance, W. F., Garesche, J. & Payne, C. W. (1993) Avian nest predation in modified and natural habitats in tropical Queensland: an experimental study. *Wildlife Research* **20**, 711–723.

Laurance, W. F. & Grant, J. D. (1994) Photographic identification of ground-nest predators in Australian tropical rainforest. *Wildlife Research* **21**, 241–248.

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L. *et al.* (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* **16**, 605–618.

Law, B. S. & Lean, M. (1999) Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. *Biological Conservation* **91**, 201–212.

Leigh, E. G. (1981) The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* **90**, 213–239.

Leigh, E. G., Wright, S. J., Herre, E. A. & Putz, F. E. (1993) The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology* **7**, 76–102.

Levey, D. J., Moermond, T. C. & Denslow, J. S. (1994) Frugivory: an overview. In *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (ed. L. McDade, K. S. Bawa, H. Hespenheide & G. Hartshorn). Chicago: University of Chicago Press, pp. 282–294.

Lindell, C. (2000) Egg type influences predation rates in artificial nest experiment. *Journal of Field Ornithology* **71**, 16–21.

Loiselle, B. A. & Hoppes, W. G. (1983) Nest predation in insular and mainland lowland rain forest in Panama. *Condor* **85**, 93–95.

Lovejoy, T. E., Bierregaard, R. O., Rylands, A. *et al.* (1986) Edge and other effects of isolation on Amazon forest fragments. In *Conservation Biology: The Science of Scarcity and Diversity* (ed. M. E. Soulé). Sunderland, MA: Sinauer, pp. 257–285.

Meyer, J. (1999) Efeitos da fragmentação de floresta sobre predação em ovos de aves e remoção de sementes. Unpublished M.Sc. thesis. Manaus, Brazil: National Institute for Amazonian Research (INPA).

Milner-Gulland, E. J., Bennett, E. L. & Society for Conservation Biology 2002 Annual Meeting Wild Meat Group (2003) Wild meat: the bigger picture. *Trends in Ecology and Evolution* **18**, 351–357.

Momose, K., Yunoto, T., Nagamitsu, T. *et al.* (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollination community in a lowland dipterocarp forest. *American Journal of Botany* **85**, 1477–1501.

Murawski, D. A. & Hamrick, J. L. (1991) The effect of the density of flowering individuals on the mating systems of nine tropical tree species. *Journal of Heredity* **67**, 167–174.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**, 58–62.

(1996) Forest fragmentation and the pollination of neotropical plants. In *Forest Patches in Tropical Landscapes* (ed. J. Schelhas & R. Greenberg). Washington DC: Island Press, pp. 19–36.

Murren, C. J. (2002) Effects of habitat fragmentation on pollination: pollinators, pollinia viability and reproductive success. *Journal of Ecology* **90**, 100–107.

(2003) Spatial and demographic population genetic structure in *Catasetum viridiflavum* across a human-dominated habitat. *Journal of Evolutionary Biology* **13**, 333–340.

Nason, J. D. & Hamrick, J. L. (1997) Reproductive and genetic consequences of forest fragmentation: two case studies of neotropical canopy trees. *Journal of Heredity* **88**, 264–276.

Nason, J. D., Herre, E. A. & Hamrick, J. L. (1998) The breeding structure of a tropical keystone plant resource. *Nature* **391**, 685–687.

Paton, P. W. C. (1994) The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**, 17–26.

Peres, C. A. (2001) Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* **15**, 1490–1505.

Peters, M. & Kramer, M. (2003) Vulnerability of driver ants and ant-following birds in fragmented forests in Kenya. Published abstract, *Annual Meeting of the Association for Tropical Biology and Conservation*, Aberdeen, Scotland.

Powell, A. H. & Powell, G. V. V. (1987) Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica* **19**, 176–179.

Putz, F. E., Leigh, E. G. & Wright, S. J. (1990) The arboreal vegetation on 70-year-old islands in the Panama Canal. *Garden* **14**, 18–23.

Rainey, W. E., Pierson, E. D., Elmqvist, T. & Cox, P. A. (1995) The role of flying foxes (Pteropodidae) in oceanic island ecosystems of the Pacific. In *Ecology, Evolution and Behavior of Bats* (ed. P. A. Racey & S. H. Swift). London: Symposia of the Zoological Society of London, vol. **67**, pp. 47–62.

Renner, S. S. (1998) Effects of habitat fragmentation on plant pollinator interactions in the tropics. In *Dynamics of Tropical Communities* (ed. D. M. Newberry, H. Prins & N. D. Brown). London: 37th Symposium of the British Ecological Society, pp. 339–358.

Renner, S. S. & Ricklefs, R. E. (1995) Dioecy and its correlates in the flowering plants. *American Journal of Botany* **82**, 596–606.

Restrepo, C., Gomez, N. & Heredia, S. (1999) Anthropogenic edges, treefall gaps, and fruit–frugivore interactions in a neotropical montane forest. *Ecology* **80**, 668–685.

Ricklefs, R. E. & Renner, S. S. (1994) Species richness within families of flowering plants. *Evolution* **48**, 1619–1636.

Sampaio, E. (2000) The effects of fragmentation on structure and diversity of bat communities in a central Amazonian tropical rain forest. Unpublished Ph.D. thesis, University of Tuebingen.

Shafer, M. L. (1981) Minimum population sizes for species conservation. *BioScience* **31**, 131–134.

Sieving, K. E. (1992) Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology* **73**, 2310–2328.

Soulé, M. E., Bolger, D. T., Alberts, A., Wright, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2**, 75–92.

Stacy, E. A., Hamrick, J. L., Nason, J. D., Hubbell, S. P., Foster, R. B. & Condit, R. (1996) Pollen dispersal in low-density populations of three neotropical tree species. *American Naturalist* **148**, 275–298.

Steffan-Dewenter, I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia* **121**, 432–440.

Stouffer, P. C. & Bierregaard, R. O. (1995) Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* **9**, 1085–1094.

Tabarelli, M., Mantovani, W. & Peres, C. A. (1999) Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* **91**, 119–128.

Terborgh, J. (1974) Faunal equilibria and the design of wildlife preserves. In *Tropical Ecological Systems* (ed. F. B. Golley &

E. Medina). New York: Springer-Verlag, pp. 369–380.

(1992) Maintenance of diversity in tropical forests. *Biotropica* **24**, 283–292.

Terborgh, J., Lopez, L., Nuñez V. *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926.

Terborgh, J., Lopez, L., Tello, J., Yu, D. & Bruni, A. (1997) Transitory states in relaxing ecosystems of tropical land-bridge islands. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (ed. W. F. Laurance & R. O. Bierregaard). Chicago: University of Chicago Press, pp. 256–274.

Vasconcelos, H. L. & Cherrett, J. M. (1995) Changes in leaf-cutting ant populations (Formicidae: Attini) after the clearing of mature forest in Brazilian Amazonia. *Studies on Neotropical Fauna and Environment* **30**, 107–113.

Viana, V. M., Tabanez, A. & Batista, J. (1997) Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (ed. W. F. Laurance & R. O. Bierregaard). Chicago: University of Chicago Press, pp. 351–365.

Weathers, K. C., Cadenasso, M. L. & Pickett, S. T. A. (2001) Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology* **15**, 1506–1514.

White, G. M., Boshier, D. & Powell, W. (2002) Increased pollen flow counteracts fragmentation in a tropical dry forest: an example from *Swietenia humilis* Zuccarini. *Proceedings of the National Academy of Sciences* **99**, 2038–2042.

Wilcove, D. S. (1985) Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**, 1211–1214.

Wilcox, B. A. (1980) Insular ecology and conservation. In *Conservation Biology: An Evolutionary–Ecological Perspective* (ed. M. E. Soulé & B. A. Wilcox). Sunderland, MA: Sinauer Associates, pp. 95–117.

Wright, S. J. (2003) The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology, Evolution and Systematics* **6**, 73–86.

Wright, S. J. & Duber, H. C. (2001) Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* **33**, 583–595.

Wright, S. J., Gompper, M. E. & DeLeon, B. (1994) Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* **71**, 279–294.

Zimmerman, B. L. & Bierregaard, R. O. (1986) Relevance of the equilibrium theory of island biogeography and species–area relations to conservation with a case from Amazonia. *Journal of Biogeography* **13**, 133–143.