Gordon Brent Ingram, Ph.D.
Department of Forest Resources Management,
270 - 2357 Main Mall, University of British Columbia,
Vancouver V6T 1W5 CANADA -
tel. (604)228-5271,
fax. (604)228-6394

Proyek EMDI, Kantor Menteri Negara,
Kependudukan dan Lingkungan Hidup, Jalan
Medan Merdeka Barat 15,
10110 Jakarta INDONESIA –
tel. (62)(21)380-7566, fax. (62)(21)380-2183

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Fragmentation:
Towards an expanded model of the vulnerability of forest habitats on islands

abstract

Archipelagoes have had a central place in the development of modern concepts of biogeography and fragmentation. While the vulnerability to further fragmentation and other forms of human-induced disturbance is recognized, the variables which determine how local biological diversity will fare under proposed disturbance whether from industrial logging, expanded agriculture, expanded roads or more subtle alterations of the landscapes have been poorly explored. Without such a framework, it is difficult to formulate a range of mitigation measures as part of comprehensive land use planning. This paper proposes an approach which emphasizes concepts from the emerging field of landscape ecology along with cause-effect linkages as related to particular human-induced disturbances. An assessment methodology is described which considers:

1. island size;
2. isolation, rates of colonization and island age;
3. terrain and other physical parameters;
4. ecosystem structure;
5. pre-human disturbance regimens;
6. patterns of endemism, rarity and intra-specific variation;
7. requirements of vulnerable organisms and the viability of particular populations; and
8. traditional cultural factors and the potential impacts of particular technologies .

The data and modelling requirements for each set of factors and their inter-relationships are explored. Some applications for land use planning on the remaining "wilderness" islands with forest in the Pacific Rim are considered. Three examples are described: Siberut, Mentawai Islands,

Sumatera Barat, Indonesia; Fergusson Island, D'Entrecasteaux Islands, Milne Bay Province, Papua New Guinea; and Burnaby Island, *Skwa-ikungwa-i,* Haida Gwaii (Queen Charlotte Islands), Canada.

Introduction:
Archipelagoes and the development of modern concepts of biogeography and fragmentation

The concept of "fragmentation" (Lovejoy et al. 1984, Temple and Wilcox 1985, Wilcove et al. 1986) - the loss of species in areas with formerly contiguous mosaics of habitats - has taken on a central position in conservation biology theory, particularly on islands and in landscapes dominated by forest. The emerging concerns for biological diversity - and in particular the minimizing of the loss of heritable variation and the ecological and biogeographical processes that sustain it (Ehrlich 1988) - have provided a more general forum for the implications of the loss and isolation of habitat.

We are living in a time where virtually all of the habitats and landscapes on Earth are threatened with some form of fragmentation. But does the cumulative fragmentation of a natural landscape necessarily lead to loss of species? No, loss of habitat that provides the requirements that a species has for survival, along with new threats from diverse factors such as increased competition and degradation of the regional environment, lead to extirpation and extinctions. In order to make land use planning and management decisions (including reserve design) the types and interactions of fragmentation processes must be considered.

An understanding of the specific processes which constitute fragmentation has been slow in coming and the theory of island biogeography still comprises a contentious set of theories. Island biogeography theory emerged from information on land masses isolated by water (MacArthur and Wilson 1967) and this in turn has too often been over-generalized for other settings. Processes of fragmentation have, so far, been rarely verified empirically nor quantified (Case and Cody 1987). In response to this problem, this paper speculates on the variables of a very particular set of fragmentation processes: those marine islands which still have landscapes dominated by primary rainforest.

Much of the theory of island biogeography emerged from the work of Diamond on island avifaunas (Diamond 1971, 1972, 1975). Some of the obvious relationships between isolate size, isolation, time factors and species compositions are undeniable. But in many other cases, a divergence of interpretations becomes apparent - differences that represent both gaps in the general theory and an understanding of the cumulative impacts (Dickert and Tuttle 1985), and inadequate information on particular organisms, biophysical settings and human-induced changes.

Area-specific descriptions and better-tailored predictive models for quanitification of such relationships will provide a better basis for reserve design. Unfortunately, for most parts of the world, adequate data sets are decades away. Still be questions must be posed, inventorying and monitoring organized, and partial, qualified answers devised **now**.

In the next two decades, nearly all of the primary rainforest on the Earth's islands are scheduled for cutting by logging concessions or will be cleared for agriculture and tourist facilities. There is currently a tremendous economic incentive to loglowland rainforest. Most of this timber is exported to affluent or newly industrialized countries such as Japan and South Korea and then is exported to the rest of the world as part of or as packing for various products. Islands have often been attractive for logging because of the relative ease of marine transport to metropolitan centres. But export-oriented logging is capital-intensive and because of the higher costs in establishment of operations on islands, there are pressures to maximize the short-term extraction of timber in order to generate profit.

This paper is concerned with the few islands left with large tracts of primary rainforest and considers how networks of protected areas and well-managed buffers can be designed in the coming decade. All of these areas have some conservation programmes though research on island ecology is necessary for effective land management for conservation, tourism and where appropriate, extractive uses which are highly regulated and monitored.

This paper is not to make new island / rainforest-wide generalizations but rather is for development of a method of landscape ecology analysis - for the factors that determine the sites, species and severity of the vulnerability to fragmentation. I use three examples to illustrate environmental conditions and research questions. All three islands have relatively high degrees of endemism, in terms of their respective regions, and are or were under pressures for logging. The islands are:

Burnaby Island, Skwa-ikungwai-i, Queen Charlotte Islands, British Columbia, Canada (temperate Nearctic, unstable low-lying mountains, post-glacial (< 10,000 year old) low diversity but endemics and disjuncts associated with glacial refugia and more recent climatic fluctuations, a traditional social economy largely under 10,000 years in age that was marine oriented with only modest alteration of the forest);

Siberut Island, Sumatera Barat, Indonesia (tropical Indo-Malayan, low-lying and swampy with high rates of tropical weathering, a continental island increasingly isolated, geologically, from the Asian mainland, extremely high species diversity and endemism associated with island isolation and possible Pleistocene ever-moist refugia, possibly a fairly recent period of human occupation with intensive use of riverine corridors for garden agriculture and intensive exploitation of forest plant and animal resources); and

Fergusson Island, Milne Bay Province, Papua New Guinea (tropical Australasian, extremely steep with rapid and on-going uplift and high rates of tropical weathering, volcanism, highly diverse forest communities including dry forest, island endemics and extremely rare and evolutionarily distinct vertebrates, a traditional system of lowland gardens and low levels of exploitation of forest resources).

All three islands have been subjects of conservation-related research (Ingram 1989) and extensive monitoring and modelling will be necessary. More site-specific planning (Ingram in press) as well as adaptive management is necessary in order to forge a framework for "sustainable" conservation of local biological diversity. Development of island-specific research programmes to better understand fragmentation are increasingly being recognized as necessary as the basis for on-going conservation interventions.

Human-induced change on islands with large tracts of primary rainforest

The ecology of islands, or rather progressive interpretations of their ecologies, have played a key role in the development of community biology as a whole (Berry 1983). Since the advent of island biogeography theory there have been numerous applications to the management of habitat isolates (Gorman 1979).

The world's remaining islands with large tracts of remaining primary rainforest are some of the most diverse areas, in terms of habitat mosaics and species numbers, both in their respective regions and in the world. This is particularly the case in the humid tropics where there are adjacent coral reefs. Such islands, therefore, constitute a particular global resource - one that is relatively vulnerable and neglected. Given that most of these islands are in the Pacific Rim and that the pressures for extractive development are intensifying, such islands should be high priorities for careful planning of reserves, buffers and tourism as well as for intensive monitoring.

The modern alterations of island landscapes are producing changes which are often not comparable to those of natural processes nor impacts from traditional societies. The scales (Noss and Harris 1986, Meentemeyer and Box 1987) and rates and spatial magnitudes of change often greatly different. Various technologies, the almost complete intrusion of the global economy with reduction of peripheral areas to resource extraction, and greater human populations have all exacerbated more natural extirpation and extinction processes.

The conservationism and preservationism dichotomy in biological conservation is not always workable on small islands. There is not enough room for areas of "pure" conservation nor anything but the most carefully considered and monitored use of the land and adjacent shallow areas (Dahl 1985b).

Models for prediction of loss of elements of local biological diversity from fragmentation

It may be possible to predict the vulnerability to fragmentation in terms of:

sizes of islands;
ecosystem and community types;
landform types;
frequencies and sizes of natural patches and gaps;
typologies of vulnerability for communities and species; and

in terms of patterns of social factors such as:

traditional and semi-permanent modification of ecosystems;
particular technologies on particular sites and over particular areas and with particular intensities with;
almost inevitable species introductions (Carlquist 1974, Vitousek 1988); and
demands for non-consumptive recreation.

Unfortunately, the only cohesive bodies of theory that have so far emerged have emphasized island size (MacArthur and Wilson 1967, Diamond 1972, Cole 1981) and age and isolation (Diamond 1971, Wilcox 1978, Faeth and Connor 1979).

There are discussions in the field of landscape ecology on patches (Pickett and Thompson

1978, Brokaw 1985), gaps (Denslow 1980) and successional mosaics (Forman 1982, Ewel 1983, Merriam 1988). There are discourses from which less generalizations can arise involving disturbance and ecotones (Raney et al. 1981, Schonewald-Cox and Bayless 1986, Hansen et al. 1988, Wiens et al. 1988) and the impacts of land use on adjacent fragments of protected habitat(Giacomini and Romani 1978, Janzen 1983).

We are in an age quite different from that from which island biogeography theory arose in the mid-1960s. The magnitudes of habitat alteration and conversion have increased well beyond what had been expected for some areas - particularly for isolated areas of the Pacific and with the advent of the strength of the Yen. The technologies to monitor and interactively model environmental impacts have made quantum leaps with satellite imagery and with the latest wave of computerized geographic information systems. Perhaps more importantly our current "paradigms" (Kuhn 1970) in biology and land use planning better allow for interactive frameworks for ascertaining biological requirements in nature conservation and for defining acceptable impacts of economic and social development (Golley 1983, Sachs 1984).

Given the pervasiveness of modern land use factors that induce fragmentation at various scales and intensities, the lack of a theoretical framework beyond island size and age is dangerous - both in contributing to the lack of expertise for precise decision-making in land use and in threatening the credibility of conservation efforts. What should we know for predicting vulnerability to fragmentation for a particular island or archipelago? And how should these inevitably long progressions of questions be linked in hierarchical and spatial models?

Identification of key variables in an expanded model of habitat fragmentation on islands for impact assessment

What should a new theory of island biogeography consist of? Certainly, none of the early concerns are not important but their significance varies due to a range of other factors that follow.

1. island size

Bigger islands do tend to support more species and greater habitat diversity over time. But how much diversity can a protected area be expected to sustain over time is less a function of area and more that of maintenance of strategically arranged mosaics with full ranges of local habitat types and prescribed amplitudes of disturbance regimens over extended periods.

Points of super-saturation (Diamond 1971 and 1972) and consequent loss of diversity (Diamond 1972) as related to species numbers and area of forest fragments are probably determined as much from rates of colonization and isolation in conjunction with intensifying rates of disturbance driven by forces external to reserves. And as was proposed by Diamond (1975), the shape of fragments of mosaics of habitats in conjunction with the shape of particular habitat isolates within these natural landscapes may have as much of a bearing in the extent of species loss as the total area in protection.

2. isolation, rates of colonization and island age

The island biogeography model was based on a simplistic notion of isolation which emphasized distance. While this is probably much of the case, between marine islands, there are additional variables beyond distance, isolation and time as originally described by MacArthur and Wilson (1967). Older islands, particularly those which have been more stable ecologically, do tend to support more species - both non-endemic and endemic. Most forest fragments on islands are destined to be fairly unstable entities both in terms of size, boundaries and disturbance regimens and all of these factors retard recolonization processes especially as source areas of other natural habitat in the district dwindle and isolation increases.

The isolation of forest fragments over a terrestrial area can vary greatly depending on the type of land use and disturbance in the non-protected areas. For example, areas where forest has been converted to grassland usually pose more severe barriers and therefore are more isolating, than carefully managed areas of selective logging. But even here the possibility of making spatial generalizations breaks down. Rates of loss and recolonization are related to the spatial requirements of particular species and assemblages of species in relation to population size and available habitat features. Changes in competition and predation involve an additional dimension.

Besides becoming isolated, a protected fragment of forest may become degraded by such factors as recreational use, intensification of tradition use or regional environmental change. This brings the discussion back to the rather amorphous notion presented by Giacomini and Romani (1978) of networks of protected areas as "open systems".

3. terrain and other physical parameters

Fragmentation processes may differ radically depending on the landform and the size and shape of an island. Mountainous islands often support a diversity of habitat types that are particularly diverse and are therefore often small and limited to certain elevations and micro-climates. The odds of fragmenting these habitat units to the point where a species can not persist are often higher than for flat islands. Likewise, areas with diverse mosaics of soil types, especially with species associated with one or a small number of soil types are particularly prone to losses.

Boundaries that allow for a full balance of habitat types represented in protected areas are necessary to avert losses. Because of island size, shape and isolation some island systems may already be much closer to some sort of super-saturation than others. Such vulnerable island systems should probably be the first candidates for land use planning emphasizing such non-consumptive uses as "eco-tourism" and research areas.

4. ecosystem structure

The first set of variables in consideration of ecosystem structure, in terms of vulnerability to fragmentation, involve the extent of the terrestrial / marine interface. What are the extents of terrestrial / shallow marine ecosystems (Johannes 1986, Ray 1988) such as mangrove and saltmarsh? Are there species in the upper trophic levels dependent on both marine and terrestrial food webs that involve small areas? What are the shapes and sizes of the "purely" terrestrial and freshwater ecosystems? Certainly the biological diversity of highly diverse tropical forest and coral reef coastal systems are problematic to maintain under anything but traditional or highly regulated land tenure (Dahl 1985b, Hodgson 1988, Hodgson and Dixon 1988).

A second set of variables involves basic ecosystem functions resulting from temperatures, rainfall and humidity and daily and seasonal fluctuations. There are radical differences between moist forest types in tropical and temperate settings but there are significant differences between ever-wet and seasonal forest types (Richards 1952) that are at the same latitudes. On mountainous islands, elevation with implications for temperature and precipitation can be a key variable.

A third set of variables related to structure result from biogeographical factors such as the presence and roles of certain groups of plant and animal species. For example, the ecosystem structures on Australasian and Indo-Malayan islands may be quite divergent especially in terms of the niches of forest-dwelling mammals. And similarly, islands which have certain predators may be quite distinct in structure from similar mainland areas which do have those species.

5. pre-human disturbance regimens

The intensity and frequency of natural disturbance regimens (Brady and Hanley 1984) and indeed the shifts associated with the Pleistocene give some indication of the resilience of ecosystems and what may be required to maintain certain habitats, edges and species. We can no longer make generalizations about stability, disturbance and biodiversity for island and rainforest ecosystems. Even in the most disturbance-intensive successional mosaics and landscape edges, there are relatively stability-dependent species. Similarly, the micro-scale gaps in relatively stable primary rainforests are key for the persistence of certain organisms.

The concept of ecological amplitude is useful here. The species that have more specific requirments and limited tolerances are often more vulnerable to disappearance in a fragmented landscape - whether certain disturbances increase or decrease in terms of frequency, intensity or spatial coverage.

6. patterns of endemism, rarity and intra-specific variation

Older islands tend to have higher levels of endemism than more recent ones. On more isolated islands, higher portions of overall species numbers often involve some form of endemism. Vacant niches, such as those on young islands, can often support rapid speciation - even in diversity-poor areas. Islands that have not been as effected by the Pleistocene fluctuations in precipitation, temperatures and sea levels may well support higher levels of endemism though this have not yet been carefully reviewed.

Areas of relatively high degrees of endemism are difficult to predict and locate. Identification of the distributions of the endemics and possible "centres" diversity for certain groups and phylla is key and may determine priority areas for conservation. For example, the high levels of tree endemism in Sri Lanka (Gunatilleke and Gunatillete 1984) suggest a relatively narrow membrane of foothill forest, the preservation of which is strategic for the maintenance of key elements of the island's biological diversity. Similarly, the spatial structure (Gilpin 1987) of the populations of species which occur in low densities or which are rare can play a key role in identification of the key tracks of mosaics of natural habitat.

7. requirements of vulnerable organisms and the viability of particular populations

Each population of each species involves a unique matrix of viability and vulnerability as based on heritable, ecological and human factors. Some natural populations, even of the same species, are more vulnerable to disappearance than others. In such cases, modest fragmentation of respective habitat isolates could be devastating. The population viability analysis could contain a component for rating the prospects of the persistence of a population under certain impacts associated with fragmentation. Certain island populations are probably so fragmented that they probably cannot survive additional types of perterbations.

The requirements for the in situ conservation of populations of wild plants with genetic resources have still been only poorly considered especially for the forests of southeast Asia (Ingram 1987). Likewise is true for animals though more models are available for the resilience and fitness of vertebrate populations. In order to conserve much of the alleles of a particularly diverse populations and species, maintenance of larger populations under a wider range of biophysical factors may be necessary.

8. traditional cultural factors and the potential impacts of particular technologies

Even the most remote islands with large tracts of rainforest are still very much cultural landscapes that may be, in part, the result of relatively sustainable patterns of traditional resource tenure (Johannes 1982) and, in part, types of land use that can radically alter mosaics of natural habitat (Rambo 1982). The spatial distributions of human-induced disturbance regimens, no matter how subtle, should be carefully considered (Balser et al. 1981).

Certain types of technologies may be virtually incompatible with certain island ecosystems. For example, roads, road-building equipment and logging practices that induce erosion are a threat to some species in adjacent coral reefs. But every operation and activity involves various steps and technologies and only certain aspects of these change factors are devastating to certain requirements of certain species.

When particularly deleterious relationships can be identified, there is a potential for determining mitigation measures involving either alternative technologies or more limited use. The more synergistic and cumulative linkages between technologies and the status of certain populations under fragmentation are difficult to quantify.

Modelling and cause-effect linkages

Each island and system of islands requires a unique framework for analysis of vulnerability to fragmentation. The relative importance of the preceeding sets of questions will vary as based on: 1. the biota; 2. the structure and spatial mosaics of ecosystems; and 3. the knowledge base - particularly for the more elusive species.

The analysis framework can then be used to first identify the most critical forest and marine fragments for conservation. Secondly, the key cause-effect linkages related to regional environmental change and sensitive habitat can be modelled to identify adjacent buffers and regulatory constraints on adjacent land use which will be necessary for long-term maintenance of local biological diversity (Ingram 1989).

Examples and discussion

Siberut, Mentawai Islands, Sumatera Barat, Indonesia

The Mentawai Islands are off the Indian Ocean coast of Sumatra. Siberut is the largest and most northerly of the four Mentawi Islands (see figure 1). The vegetation of Siberut consists of various types of tropical rainforest and, in particular, primary dipterocarp types (see figure 5). The Mentawai islands have some of the highest levels of island species endemism on Earth.

The total land mass of the Mentawais is roughly 7,000 square kilometres. The islands first became isolated from Sumatra about about 4 million years ago but was connected intermittently until probably 500,000 years ago. The the last time that Siberut was connected to the island of Sipora to the south was about 20,000 years before present.

The levels of species diversity in Indo-Malesian rainforest vary markedly with successional conditions, edaphic and climatic variations, and patterns of reproduction and dispersal. There is sometimes an inverse correlation between soil fertility and plant species diversity because of shorter regeneration cycles and the greater representation of species characteristic of the gap phase. Other discussions of the Sahul Shelf region have attributed the diversity of plant species to various factors related to fruit dispersal and patterns of seedling establishment.

The proportion of mammal endemism to area in the Mentawai Islands is one of the highest on Earth. The high degree of mammalian endemism, including four primate species, and the absence of large predators has been the source of extended scientific interest.

The Mentawai Islands are remarkable in the cultural isolation which extended into the Twentieth Century. This, "enabled the people to retain many cultural practices once common throughout archaic Indonesia"(Mitchell and Tilson 1986). There was a New Stone Age level of development and an economy based on sago, taro, fishing, pig-raising and the hunting of primates.

The traditional religion of the Mentawai is centred on a belief in "internal harmony in the environment" and fostered a system of rituals and taboos which "kept people and forest resources in an equilibrium" (Mitchell and Tilson 1986). Hunting, gathering and agriculture require various observances and ceremonies for the maintenance of "balance". Taboos and extensive knowledge of local ecosystems and populations contributed to relatively sustainable patterns of natural resource use. There is a cultural landscape consisting of communal village lands and outlying swidden horticulture, ladang. These formerly modest gaps may well be threaten certain populations as widths increase (figure 6).

By 1980, 4 logging companies were logging, with selective methods, on the islands and their concessions included all of the island except for the nature reserve, the cultivated land and settlements. A breakdown of land disturbance categories as of 1982 showed 13 % of the total area of the island had been logged. Another 1 or 2 % was probably disturbed for roads, camps and other aspects of operation.

There is compelling evidence that even careful, selective logging can alter forest environments to the extent that certain species can no longer survive in previously hospitable areas (Johns 1983). As many as 70 % of the mammals and birds of Siberut may be dependent on "intact primary lowland forest" for at least one point in their life histories. A major impact of logging and forest clearing is the decline in food availability and nesting sites.

Research for a conservation master plan for Siberut was begun in 1976 (WWF - Indonesia 1980)and there was a subsequent proposal for management (Mitchell 1982). Three categories of use zones were proposed:

Development Zones (logging areas, settlements, rattan collecting, areas with the best potential for sustainable logging and agriculture);

Traditional Use Zones (wildlife reserve, buffer zone, village forest and strict protection forest); and

Nature Reserve Zone (Forest fruit collection was for human consumption and no for sale. Hunting, ladang clearings and new villages were to be prohibited.)

A large portion of the Mentawai population has cooperated with the conservation proposals and has moved into or become more dependent on the traditional use zones. But the government squeezing of these traditional peoples into narrow coastal areas along with the lack of respect for the reserve boundaries by the logging operations could jeopardize the precarious balance. Since the management plan was approved (Mitchell 1982), there has been little implementation. Logging has expanded and there has been little monitoring. There has yet to be an analysis of the logging technologies and mitigation measures that are necessary especially as related to the impact of road building and roads.

The two major contributors to fragmentation on Siberut are selective logging and expansion of village agricultural and gathering areas. Both types of processes are comparatively subtle. But for significant periods of time, the lack of mature forest structures for vertebrates and the change in microclimate and nutrient availability limit the distributions and movement of some vulnerable species. To understand key fragmentation processes and to model the viability of possible conservation strategies, it will be necessary to monitor the successional mosaics at the micro-scale within the complex, upper regions of watersheds.

Fergusson Island, D'Entrecasteaux Islands, Milne Bay Province, Papua New Guinea

Fergusson Island is the largest island in the D'Entrecasteaux Archipelago and one of the largest islands off of eastern New Guinea. It has an area of 1340 square kilometres with mountains which rise to 1830 metres (see figure 2). The island is particularly significant as as it has or rather had, until 1988, one of the most pristine mosaics of primary rainforest (see figure 8) and shallow marine ecosystems for a relatively large, mountainous island of anywhere on Earth (see figure 7).

The structures of terrestrial ecosystems of the off-shore islands of New Guinea are poorly understood. Certainly, the relative lack of mammalian diversity allows for more niches to be occuppied by birds. In this part of the northeastern Australasian continental mass, large tracts of ever-wet tropical forests may have been a comparatively recent development.

The area has a poorly understood blend of Australian and Asian plants and animals. Data on the D'Entrecasteaux Islands was key in Diamond's original (1971, 1972) assertion of the dynamics of "saturation" in island biogeography (with its implication for reserve design). Diamond inferred from tentative data that the D'Entrecasteaux islands have been one land mass in periods of the Pleistocene, that had never been part of the New Guinea mainland. However, there have been divergent geological interpretations in recent years (Ingram 1989).

The societies of the area are extremely diverse and it is difficult to generalize. Land is held by local household units. The subsistence economy is still viable. There is reliance on a wide array of wild species, population pressures are still low and political power is decentralized. The traditional systems of swidden farming and management of resulting successional mosaics are relatively intact (see figure 9). There is even a locally initiated wildlife management area in a remote part of the centre of the island.

A relatively high portion of the bird species on the island have characteristics which make them particularly vulnerable to logging, roads and expansion of the swidden gardens - especially below 1500 meters elevation (Ingram 1989). The large remaining areas of primary forest that are left constitute strategic tracts for the southeastern New Guinea region (Beehler 1985). There pare potential linkages to marine areas which are also extremely rich, biologically.

Burnaby Island, *Skwa-ikungwa-i*, Haida Gwaii (Queen Charlotte Islands), Canada

Skwa-ikungwa-i is a North American example with relatively low species and habitat diversity, some island endemics (Foster 1984), slow-growing "old growth" forest (Franklin 1981) (see figure 10), and a highly productive terrestrial / marine interface (see figure 12). The Queen Charlotte Islands lie to the west of the northern coast of British Columbia and to the south of southeastern Alaska. The Burnaby Island area is on the east coast of the South Moresby (see figure 3). There are complex mosaics of various shore, islet (see figure 11), lowland coniferous forest and sub-alpine habitats at various successional phases. Much of the forest is in relatively mature phases though there is on-going gap generation (Brady and Hanley 1984). Since the 1950s, the forests have been transformed by the introduced black-tailed deer, Odocoileus hemionus sitkensis, which, without natural predators on the Queen Charlotte Islands, is literally browsing to stuble much of the shrub layer.

The indigenous peoples, the Haida, probably have occupied the area since soon after the last glacial retreat around 10,000 years b. p. and these communities adapted to the ecological transitions from tundra to boreal to "warmer" coniferous forest and then to the cooler type of "rainforest" that exists today. Settlements in the Gwaii Haanas area were well-established and so too were culturally influenced landscapes. Haida villages were situated along shore areas as was much gathering and fishing. There was gathering in forest interiors, particularly western red cedar, Thuja plicata. Much of the berry gathering, of Vaccinium spp. , Rubus spp. , Ribes spp. and Viberum sp. was in culturally modified edges and gaps in landscapes dominated by forest.

Since the 1950s, clearcut logging taken place on the north Pacific coast of North America and the size of cuts and the speed of old-growth removal has increased progressively. Concerns for the protection of the terrestrial and marine environments of the Queen Charlotte islands, and of the biological resources of particular interest to the Haida has intensified since the early 1970s. The Burnaby Island area is now part of a large terrestrial and marine, "National Park Reserve" which will eventually be managed by the Haida.

Given that clearcut logging is no longer a possibility in the South Moresby, many of the problems of the fragmentation of temperate forests (Harris 1985) are no longer threats. However, intensive and poor siting of non-consumptive recreation, especially in relatively small shore strips with rare species (Ingram 1989), along with additional species introductions (Vitousek 1988) could be devastating. The fencing of mature forest to exclude the introduced deer and to therefore sustain fragments of forest with an intact shrub layer and fuller assemblages of the fruit-producing plants - the temperate equivalents of "keystone mutualists."

Comparisons of the islands in terms of the variables of the model

1. island size

Of the three examples, Burnaby Island is the smallest and with the least diversity of overall species numbers but while Siberut is larger than Fergusson Island (Figure 4) but there is not yet enough inventory data to confirm a species/area relationship. Fergusson Island may well have more species due to its dramatic elevational gradients along with a range of factors related to diversity of climatic, micro-climatic and landform types. Even though Fergusson is the largest island, it may well be the most vulnerable to fragmentation if Diamond's postulated saturation is at work. But in contrast, many of the habitat isolates on Burnaby Island are relatively small, as a function of landform and climate, and because of this, some populations of plants and animals appear to be especially vulnerable to any loss of area or alteration of habitat.

2. isolation, rates of colonization and island age

Of the three islands, within their respective archipelagoes, Siberut is the most isolated spatially but the waters separating the island from the island of Sipora to the south and Sumatra to the northeast are relatively shallow. All three islands have been part of larger island land masses at various points even as recently as the late Pleistocene. The age of these larger land masses may be an important variable but is not well-determined for Fergusson and Burnaby Island.

Spatial and temporal patterns of colonization may be key variables especially for areas that have been glaciated or which underwent major ecological changes in the Pleistocene or more recently. Age and colonization in this sense might suggest that why Siberut is so diverse because its environments have been relatively stable for the longest time while having relatively secure sources for colonization. But whether the species associated with this relative stability would be less able to survive in fragmented forest than the colonizers of formerly glaciated areas or dry forest and grassland is debatable.

3. terrain and other physical parameters

More mountainous terrain involves increased variation in terms of landform, climate, micro-climate and soils - and this usually manifests in different types of vegetation and communities. All these factors increase environmental heterogeneity and more barriers which complicate the fragmentation equation. Terrain factors which support narrow bands of habitat types may well increase the vulnerability of an island ecosystem to fragmentation. Thus the complexity of the post-glacial landforms of Burnaby Island make its depauperate ecosystems particularly prone to species loss from fragmentation and so too are the bands of distinct habitat types around the mountains of Fergusson Island. But a further look at various scales suggests that even relatively flat areas such as Siberut have biota associated with landforms such as heavily incised tropical streams and certain species dependent on certain bands of various edaphic and hydrologically related communities (Whitten 1982) may also be vulnerable. This suggests that relative vulnerability as related to landform is a function of the areas and widths of habitat types across larger mosaics.

4. ecosystem structure

Ecosystems that are relatively low in productivity, such as those at higher latitudes and elevations, are particularly vulnerable where rapid regrowth and turnover are necessary to maintain certain habitat features and key portions of distributions. This is the case where the introduced deer are destroying the shrub layer in the slow-growing forests of Burnaby Island. This in turn becomes important in the dynamics of isolation for particular species in disturbed areas.

The different kinds of ecosystems on these islands are fragmented differently and involve divergent responses to disturbance. This is clearly the case between primary rainforest, dry seasonal forest, beach communities and coral reefs. Many of the ecosystems of Fergusson Island are probably not as vulnerable to broad-scale disturbance and isolation factors as are the more interior forest dependent species on Siberut **but** the size of overall habitat units on Fergusson, with its wide environmental gradients, are more vulnerable because they will often be relatively smaller in area.

Particular responses to fragmentation, as manifested in the size, spatial extent and densities of particular populations, are in part a reflection of the pre-disturbance extent of homogeneity and isolation of patches. Coral reefs and dry forests both tend to support species which are more adapted to such patchiness though the same may be argued for primary forest - but at finer scales. So perhaps the determinants involve patch size and scale of the new disturbance with an added dimension of time.

5. pre-human disturbance regimens

There are fine lines between ecosystem processes, cyclical disturbance, and stochastic events. There are some relative scale and time factors that suggest that for every species and habitat unit, there is a narrow amplitude within which local persistence is not jeopardized. Burnaby Island has a relatively high frequency of landslides and mass wasting but the disturbance associated with logging and road building might have easily lead to a higher magnitude of habitat loss and instability which could have trigged the loss of certain species of anadromous fish such as salmon, Oncorhynchus spp.

An analysis of vulnerability to fragmentation might consider the relative extent of severity of the natural disturbnace processes in terms of succession, scale and time. Within this analytical framework, the selective logging on Siberut is a far less alien regimen of disturbance than the efforts to convert primary rainforest to pasture on Fergusson Island.

6. patterns of endemism, rarity and intra-specific variation

Species which are rare, which have low densities or which are limited to a small number of sites are particularly vulnerable to fragmentation. Respective populations can be easily depressed and further isolated. An area with a greater portion of the total number of respective species with these vulnerabile characteristics is, as is the case with the two tropical examples, probably going to be more vulnerable to loss of a larger number of species from fragmentation.

The patchiness of many patterns of endemism suggest that the vulnerability to fragmentation may be more a function of site-specific disturbance factors. This is also the case with areas low in diversity such as Burnaby Island where most of the less common plant and vertebrate species have very site-specific requirements and if these relatively small areas are disturbed, such as through camping associated with kayaking, a significant portion of the higher order of biota could disappear locally. The vulnerability to fragmentation, as related to rarity and endemism, may be more the function of the interaction between particular distributions and densities and intensities of the spatial and temporal distribution of human-induced disturbance factors.

Both our understandings of endemism and intra-specific variation are very much the products are our knowledge bases and the social resources allocated to biological inventorying. In virtually every instance, even in low diversity situations, more inventory efforts have yielded information that has suggested the presence of previously less-known species some of which are vulnerable to certain fragmentation-inducing factors. The spatially related vulnerability of non-vascular plants and invertebrates, as well as intra-specific variation within even some of the more common species, may further confirm the axiom that the finer-scaled is the spatial and taxonomic information, the greater is the extent of the cognizance of vulnerability to fragmentation. In addition, the species of the humid tropics and coral reef ecosystems, that are highly limited in their distributions, are particularly at risk even from relatively low-intensity disturbance.

7. requirements of vulnerable organisms and the viability of particular populations

Species become extirpated or go extinct when key habitat features are lost, internal population factors induce declines at the time of loss of habitat and when there is unsustainable predation or competition. Species that have highly site-specific requirements, ecological amplitudes or which already exist close to a margin below which resilience or fitness cannot be assured, whether in tropical or temperate ecosystems, are particularly vulnerable to regional environmental change. Particular environments, by their natural histories and the structures of their ecosystems such as partially recolonized post-glacial islands are already prone to disequilibrium.

In the case of the two tropical islands, the most vulnerable species may in fact be those species requiring relatively stable and finely heterogeneous mosaics of complex ecosystems such as tropical rainforest. The data compiled on Siberut Island (Ingram 1989) suggests this.

8. traditional cultural factors and the potential impacts of particular technologies

All ecosystems on Earth are now culturally influenced which causes the intensification or suppression of processes which were previously natural. This is certainly the case with the temperate island ecosystem which was probably heavily influenced in the current post-glacial period by various waves of human immigration (Fladmark 1975). Oddly enough, Siberut may well have not supported regular human populations until the last several thousand years.

The cultural landscapes of these islands are as much products of the instability of patterns of local settlement and resource exploitation as of more prolonged human-ecosystem interactions. For most species, the cultural landscape template has simply added an additional layer of complexity - especially for organisms that are edge-dependent or opportunistic. By contrast, the prospects of the more stability-dependent species with complex requirements are usually jeopardized.

Cultural factors are usually a negative force for local biological diversity even in the societies which are relatively stable with sustained patterns of exploitation. But the margins of erosion of local biological diversity vary markedly as related to patterns of human occupation, agriculture and land utilization. For example, in comparisons between the two tropical study areas, the Mentawai tend to exploit a wider spectrum of plant and animal species while the impacts of the peoples of Fergusson Island are more focused on lowland areas of swidden agriculture, which because of warfare, were relatively undisturbed until a century ago.

The technologies of both indigenous and globally oriented societies along with more cumulative impacts of fragmentation can be devastating for large portions of local biota. Even an introduced species can be considered as a form of technology and is, as in the case of Burnaby Island, creating a new form of fragmentation as based on the small number of unbrowsed areas on the tops of fallen trees. Along with new kinds of micro-fragmentation, technologies such as guns can virtually destroy populations even where large tracts of viable natural habitat are reserved.

The new technologies to over-exploit marine resources are having a comparable kind of fragmentation-inducing influences in shallow coastal areas. In addition, without adequate assessment and education, the more benign technologies associated with eco-tourism, as we see with the kayakers of Burnaby Island, still hold the potential of being devastating to vulnerable organisms.

Implications to making land use planning frameworks more ecologically oriented

Better frameworks for the modelling of the impacts of fragmentation will aid in the conservation of biological diversity on islands with rainforest and adjacent marine areas in two ways. Ecological guidelines (MacEachern and Towle 1974, Poore 1974, Bakus 1982 / 1983, Salm 1984) for general development planning can be expanded for particular archipelagoes.

More than just for providing general guidelines, such a framework for studying islands lays a powerful framework for environmental impact analysis (Soemarwoto 1989) of valuation, use and conservation of the biological resources of the world's remaining islands with large tracts of primary forest particularly in Indonesia, Malaysia, Papua New Guinea, the Philippines and other parts of the Pacific Rim.

Within such a framework for the analysis of vulnerability to fragmentation, various hypotheses can be tested and projections can be made and revised with on-going monitoring. Such assessments can be undertaken at various points in land use planning and management and the decisions that are made should reflected the (limited) level of information that is currently available on local ecosystems, species compositions and population dynamics.

In conservation areas that are particularly rich, biologically, and important as distinct units of wildland such as these three islands, a deferral approach to planning both extractive and non-consumptive activities is necessary. Less understood and potentially fragmentation-inducing activities would only be allowable after measures to minimize their impacts on vulnerable species could be minimized. Only with cautious research which is and district and site-specific can the cumulative impacts of an array of potentially manageable fragmentation processes be understood and these crude models can provide the basis for both protected area design and management and the corresponding regulation of adjacent land use activities.

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references

Balser, D., A. Bielak, G. De Boer, T. Tobias, G. Adindu and R. S. Dorney. 1981. Nature reserve designation in a cultural landscape incorporating island biogeography theory. Landscape Planning 8: 329 - 347.

Beehler, B. 1985. Conservation of New Guinea rainforest birds. ICBP Technical Publication No. 4.

Berry, R. J. 1983. Diversity and differentiation: The importance of island biology for general theory. Oikos 41: 523 - 529.

Brady, W. W. and T. A. Hanley. 1984. The role of disturbance in old-growth forests: Some theoretical implications for southeastern Alaska. In Fish and Wildlife Relationships in Old-growth Forests. Proceedings of a symposium held in Juneau, Alaska, 12 - 15 April, 1982. W. R. Meehan, T. R. Merrell and T. A. Hanley (editors). 213 - 218. Morehead City, North Carolina, American Institute of Fishery Biologists.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66 (3): 682 - 687.

Bakus, G. J. 1982 / 1983. The selection and management of coral reef preserves. Ocean

Management 8: 305 - 316.

Carlquist, S. 1974. Island Biology. New York, Columbia University Press.

Case, T. J. and M. L. Cody. 1987. Testing theories of island biogeography. American Scientist 75 (4): 402 - 411.

Cole, B. J. 1981. Colonizing abilities, island size, and the number of species on archipelagoes. American Naturalist 117 (5): 629 - 638.

Connor, E. F. and E. D. McCoy. 1979. The statistics and biology of the species - area relationship. The American Naturalist 113 (6): 791 - 833.

Dahl, A. L. 1985a. The potential for management of island ecosystems. In Environment and Resources in the Pacific. A. L. Dahl and J. Carew-Reid (editors). 13 - 17. Geneva, UNEP.

Dahl, A. L. 1985b. The challenge of conserving and managing coral reef ecosystems. Environment and Resources in the Pacific. A. L. Dahl and J. Carew-Reid (editors). 85 - 87. Geneva, UNEP.

Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12 (2): 47 - 55.

Diamond, J. M. 1971. Comparison of faunal equilbrium turnover rates on a tropical island and a temperate island. Proceedings of the National Academy of Sciences (USA): 68 (11):2742 - 2745.

Diamond, J. M. 1972. Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific Islands. Proceedings of the National Academy of Sciences (USA): 69 (11): 3199 - 3203.

Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7 (2): 129 - 146.

Dickert, T. G. and A. E. Tuttle. 1985. Cumulative impact assessment in environmental planning: A coastal wetland watershed example. Environmental Impact Assessment Review 5: 37 - 64.

Ehrlich, P. R. 1988. The loss of diversity: Causes of consequences. In Biodiversity. E. O. Wilson (editor).21 - 27. Washington, D. C., National Academy Press.

Ewel, J. l983. Succession. In Tropical Rain Forest Ecosystems: Structure and function.
F. B. Golley (editor): 217 - 224. New York, Elsevier Scientific.

Faeth, S. H. and G. F. Connor. 1979. Supersaturated and relaxing island faunas: A critique of the species-age relationship. Journal of Biogeography 6: 311 - 316.

Fladmark, K. R. 1975. A Paleoecological Model for Northwest Coast Prehistory. Archaeological Surveys of Canada paper 43. Ottawa, National Museum of Canada.

Forman, R. T. T. 1982. Interaction among landscape elements: A core of landscape ecology. In Perspectives in Landscape Ecology. S. P. Tjallingii and A. A. de Veer (editors). 29 - 34. Wageningen, Netherlands, Pudoc.

Franklin, J. F. 1981. Ecological Characteristics of Old - Growth Forest. Portland, Oregon, United States Department of Agriculture Forest Service.

Foster, J. B. 1984. The Canadian Galapagos. In Islands At The Edge: Preserving the Queen Charlotte Islands Wilderness. Islands Protection Society (editors). 35 - 47.
Vancouver, Douglas & McIntyre.

Giacomini, V. and V. Romani. 1978. National parks as open systems: An Italian overview. Landscape Planning 5: 89 - 108.

Gilpin, M. E. 1987. Spatial structure and population vulnerability. In Viable Populations for Conservation. M. E. Soule' (editor). 125 - 139. New York, Cambridge University Press.

Golley, F. B. 1983. Ecodevelopment. In Tropical Rain Forest Ecosystems: Structure and function. F. B. Golley (editor). 335 - 344. New York, Elsevier Scientific.

Gorman, M. 1979. Island Ecology. London, Chapman and Hall.

Gunatilleke, I. A. U. N. and C. V. S. Gunatilleke. 1984. Distributions of endemics in the tree flora of a lowland hill forest of Sri Lanka. Biological Conservation 28: 275 - 285.

Hansen, A. J., F. di Castri and R. J. Naiman. 1988. Ecotones: What and why? Biology International 17: 9 - 46. In A New Look at Ecotones: Emerging international projects on landscape boundaries. F. di Castri, A. J. Hansen and M. M. Holland (eds.). Paris, International Union of Biological Sciences.

Harris, L. D. 1985. The Fragmented Forest. Chicago, Illinois, University of Chicago Press.
Hodgson, G. 1988. The effects of sedimentation on Indo-Pacific reef corals. Ph.D. dissertation, on file, Zoology Department, University of Hawaii, Honolulu, Hawai'i.

Hodgson, G. and J. A. Dixon. 1988. Logging Versus Fisheries and Tourism in Palawan. Occasional paper of the East-West Environment and Policy Institute No. 7. Honolulu, Hawai'i, East-West Center.

Ingram, G. B. 1987. Conservation of wild plants in crop genepools and their intraspecific variation: current needs and opportunities in the moist forests of SouthEast Asia. In Conservation and Management of Endangered Plants and Animals. Proceedings of the Symposium on the Conservation and Management of Endangered Plants and Animals, June 18 - 29, 1986. C. Santiapillai and K. R. Ashby. (editors). Bogor, Indonesia, BIOTROP.

Ingram, G. B. 1989. Planning district networks of protected habitat for conservation of biological diversity: A manual with applications for marine islands with primary rainforest. Ph. D. dissertation in Environmental Planning. On file, University of California at Berkeley.

Ingram, G. B. in press. Integration of concerns for biological, visual and recreational resources into the planning of extractive development and protected areas: A tale of three islands. Landscape and Urban Planning.

Janzen, D. H. 1983. No park is an island: Increase in interference from outside as park size decreases. Oikos 41: 402 - 410.

Johannes, R. E. 1982. Traditional conservation methods and protected marine areas in Oceania. Ambio 11 (5): 258 - 267.

Johannes, R. E. 1986. Shallow tropical marine environments. In Conservation Biology: The science of scarcity and diversity. M. E. Soule' (editor). 371 - 382. Sunderland, Massachusetts, Sinauer Associates.

Johns, A. D. 1983. Tropical forest animals and logging - can they co-exist?. Oryx XVII: 114 - 118.

Kuhn, T. S. 1970. The Structure of Scientific Revolutions. Chicago, Illinois. University of Chicago Press.

Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, K. E. Brown, L. H. Emmons and M. E. Van der Voort. 1984. Ecosystem decay of Amazon forest remnants. In Extinctions. M. H. Nitecki (editor). 295 - 325. London, University of Chicago Press.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton, New Jersey, Princeton University Press.

Meentemeyer, V. and E. O. Box. 1987. Scale effects in landscape studies. In Landscape Heterogeneity and Disturbance. M. G. Turner (editor). 15 - 34. New York, Springer-Verlag.
Merriam, G. 1988. Landscape ecology: The ecology of heterogenous systems. In Landscape Ecology and Management. M. R. Moss (editor). 43 - 50. Montreal, Quebec, Polyscience Publications.

Mitchell, A. H. 1982. Siberut Nature Conservation Area: Management Plan 1983 - 1988. Bogor, Indonesia, WWF/IUCN Report.

Mitchell, A. H. and R. L. Tilson. 1986. Restoring the balance: Traditional hunting and primate conservation in the Mentawai Islands, Indonesia. In Primate Ecology and Conservation. Volume 2. J. G. Else and P. C. Lee (editors). 249 - 260. London, Cambridge University Press.

Noss, R. F. and L. D. Harris. 1986. Nodes, networks, and MUMs: Preserving diversity at all scales. Environmental Management 10 (3): 299 - 309.

Pickett, S. T. A. and N. J. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13: 27 - 37.

Poore, D. E. M. 1976. Ecological Guidelines for Development in the Humid Tropics.
Morges, Switzerland, IUCN

McEachern, J. and E. Towle. 1974. Ecological Guidelines for Island Development.
Morges, Switzerland, IUCN.

Rambo, A. T. 1982. Orang asli adaptive strategies: Implications for Malaysian natural resource development planning. In Too Rapid Rural Development: Perceptions and Perspectives from Southeast Asia. MacAndrews and C. L. Sien (editors). Athens, Ohio, Ohio University Press.

Raney, J.W., M.C. Bruner and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. In Forest Island Dynamics in Man - Dominated Landscapes. R. L. Burgess and D. M. Sharpe (editors): 67 - 95, New York, Springer-Verlag.
Ray, G. C. 1988. Ecological diversity in coastal zones and oceans. In Biodiversity. E. O. Wilson (editor). 36 - 50. Washington, D. C., National Academy Press.

Richards, P. W. 1952. The Tropical Rain Forest. Cambridge, England, University Press.

Sachs, I. 1984. Developing in harmony with nature: Consumption patterns, time and space uses, resource profiles, and technological choices. In Ecodevelopment: Concepts, projects, strategies. Oxford, England, Pergamon.

Salm, R. V. 1984. Ecological boundaries for coral-reef reserves: Principles and guidelines. Environmental Conservation 11(2): 209 - 215.

Schonewald-Cox, C. M. and J. W. Bayless. 1986. The boundary model: A geographical analysis of design and conservation of nature reserves. Biological Conservation 38: 305 -322.

Soemarwoto, O., 1989. Analisi Dampak Lingkungan. Yogyakarta, Indonesia, Gadjah Mada University Press.

Temple, S. A. and B. A Wilcox. 1985. The effects of habitat fragmentation. In Modelling Habitat Relationships of Terrestrial Vertebrates. J. Verner, M. C. Morrison, C. J. Ralph and R. H. Barrett (editor). 1 - 6. Madison, Wisconsin, University of Wisconsin Press.

Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. In Biodiversity. E. O. Wilson (editor). 181 - 189. Washington, D. C., National Academy Press.

Whitten, A. J. 1982. A numerical analysis of tropical rain forest, using floristic and structural data, and its application to an analysis of Gibbon ranging behaviour. Journal of Ecology 70: 249 - 271.

Wilcove, D. S., C. H. McLellan and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. In Conservation Biology: The science of scarcity and diversity. M. E. Soule' (editor). 237 - 256. Sunderland, Massachusetts, Sinauer Associates.

Wiens, J. A., C. S. Crawford, J. R. Gosz. 1985. Boundary dynamics: A conceptual framework for studying landscape ecosystems. Oikos 45: 421 - 427.

Wilcox, B. A. 1978. Supersaturated island faunas: A species-age relationships for land-bridge islands. Science 199 (4332): 996 - 998.

Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy: The effects of fragmentation on extinction. American Naturalist 125: 879 - 887.

WWF - Indonesia. 1980. Saving Siberut: A conservation master plan. Bogor, Indonesia, WWF - Indonesia.

list of figures: