

Gordon Brent Ingram, Ph.D.  
Landscape Architecture Program, Dept. of Plant Science &  
Dept. of Forests Resources Management  
University of British Columbia

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## **Archipelagoes on Archipelagoes: Relationships between successional mosaics and requirements for networks of protected habitat on islands with rainforest**

### **abstract**

What can spatial and temporal aspects of natural and cultural successional mosaics tell us about requirements for protected habitat for the conservation of biological diversity? What are some of the typologies of both natural and culturally modified, successional mosaics on small islands dominated by humid forest ecosystems? What indices can be employed to describe aspects of time, edge and habitat fragmentation for island settings that are already relatively dynamic and fragmented? This discussion considers a number of islands in the Pacific Rim that have less humanly disturbed landscapes and that are dominated by mature phases of "rainforest". Various natural and human-induced disturbance factors are reviewed and their spatial impacts are described. Each island system is considered as a unique set of membranes for supporting for island-specific evolutionary processes while suppressing other organisms. Networks of protected areas are considered as part of strategies for maintaining unique configurations of biogeographic processes across districts and large landscape units. Approaches to better identifying dynamic landscape processes with prescriptions for adaptive land management are discussed.

### **Introduction:**

#### **The Need for Systematic Conservation Programmes on Islands with Primary Rain Forest**

Both islands and moist forest on islands are under-represented in internationally recognized networks of protected areas (IUCN/UNEP 1986) though such areas could provide relatively secure sites for long-term monitoring and control of disturbance. Unfortunately, this promise has been jeopardized in recent years by global warming and possible sea level rise.

In his review of the status on the biota on South Pacific islands, Dahl (1984) states that "there are probably more endangered species per capita in the South Pacific islands than anywhere else in the world." He attributes this to: the naturally low numbers of certain species and small areas of habitat types; the introduction of predators and weedy and aggressive species which over-exploit or displace island species; and the relative ease with which land use expansion can destroy these small and often unique habitat units. In the most extensive review of conservation needs in the South Pacific, focused on the roughly 50 islands in Oceania, with significant tracts of natural habitat, Dahl (IUCN/UNEP 1986) noted that less than 25 have island-wide habitat protection, and these are very small in size. The remainder have < 1 % of their total areas in protection. Most of the protected

forest habitat on islands are on high islands and there is still little conservation on atolls.

If we are to develop programmes for the conservation of the unique ecosystems of the remaining islands, with relatively undisturbed mosaics with primary forest, a range of land use strategies, involving various combinations of protected cores and well-managed buffers (Battisse 1982, along with corridors (Groome 1990, Hobbs et al. 1990) and barriers must be explored. The formation processes that have created "natural" spatial units and habitats (and respective levels of fragmentation and insularization) may provide some clues as to the plasticity available for expansion of economic activities (Hamnett 1990) and land management that will also allow for the maintenance of local biological diversity.

### **Successional Mosaics on Islands with Primary Rainforest**

Tropical islands with "rain forest" (Richards 1952) and adjacent coral reefs may well comprise the most biologically rich complexes of ecosystems on the planet. As the interest in conservation of "biodiversity" (Wilson 1988, Ehrlich 1988) increases, the remaining islands with rainforest will take on greater significance for research and non-consumptive recreation as well as to the many communities that are struggling to maintain traditional conservation systems (Ingram 1990).

Island systems support and intensify linkages between marine and terrestrial food webs, such as with mangrove and Maser's (et al. 1988) more obscure, temperate example of dead wood on the north Pacific coast. Islands with mosaics with primary rainforest represent a distinct setting for inventorying, monitoring (Burley 1988, Hamnett 1990) and conservation for the following reasons:

1. the insular nature of the shoreline and the terrestrial-marine interface;
2. the vulnerability of island biodiversity to extirpations and extinctions;
3. the vulnerability to fragmentation of small areas of (natural) forest; and
4. the pressures on islands for logging, settlement, tourism and for the maintenance of local cultures.

Mosaics of tropical forest, with a range of ecosystem structures as related to moisture availability, as well as with a diversity of habitat types and successional phases, are the most species-rich terrestrial ecosystems on Earth. This is as much the result of the combined set of gaps and edges, the level of landscape heterogeneity, as the habitats and food webs which are afforded by the relative stability and accumulation of biomass.

There are a range of forces which have sustained the spectacular evolution of species which has taken place in the world's humid tropical forests. One hypothesis explaining plant species diversity views the forest environment to be particularly heterogenous (Ricklefs 1977) and relates this to greater biomass, high nutrient levels within vegetation, rapid decomposition and equatorial sunlight.

There are some modest parallels between humid tropical forests and temperate rain forests such as on the north Pacific coast of North America. There is a subset of forest species that are "associated" with successional mosaics dominated by large living trees and dead trees that are either standing or fallen, along with structures such as tree cavities for nesting (Carey 1989). But even though these species often utilize "old-growth" (Franklin 1981) habitat attributes, "dependence" correlations have been poorly confirmed, and the diversity of overall vertebrates and vascular plants

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in these cool, slow cycling ecosystems is still relatively low. The similarities between temperate and tropical humid forest ecosystems on islands are more related to:

- high levels of standing biomass;
- the complexity of forest structures, gaps and edges;
- the relatively small and therefore fragmentation-prone habitat units; and
- the significance of shore areas to virtually all terrestrial and shallow marine food webs.

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### **Island Successional Mosaics and Biodiversity**

The evolutionary factors which combine to make some island populations and communities unique involve:

- isolation and the subsequent low prehistoric rates of colonisation (Carlquist 1974);
- acute reduction of gene flow as a stimulus for local speciation;
- the lack of some selection factors involving predation and competition; and
- unique patterns of adaptive radiation resulting from unique island niches.

All four factors are most pronounced on oceanic islands and decline in significance as spatial and temporal isolation diminishes.

There are different types of island ecosystems as related to age and isolation. The simple dichotomy of oceanic and continental islands, originally outlined by Wallace, has been expanded. There are at least three general types of island system types in the Pacific Rim and these categories can be broken down by formation processes, age and climate.

**continental** - These islands share plates with continental land masses. There has been intermittent disconnection and reconnection through land bridges. Periods of isolation have intensified fragmentation processes, subsequently lowered species richness, in comparison to adjacent mainland areas, and sometimes have fostered endemism. Bali, linked to south east Asia, and the Queen Charlotte Islands (Foster 1984), linked to North America, are examples of such mildly pronounced island ecosystems.

**transitional / micro-continent** - These islands are associated with mountain building and isolated land masses formerly part of continents. Long-isolated remnants of continental biotas have given rise to divergent evolutionary lines. The relative size of these areas, and long periods of isolation, have allowed for the survival of numerous relict and endemic species as well as highly distinct ecosystems as in the case of New Zealand and New Caledonia.

**oceanic** - Because of extreme isolation, there are barriers to entire groups of organisms, such as amphibians. Because of the limited pool of terrestrial species, ecosystem structures are usually simpler than in continental ecosystems. Relatively open niches can lead to rapid speciation (Berry 1983) as suggested by Darwin's observations on the Galapagos Islands, which laid the basis for the modern theory of evolution. The Hawaiian Islands are one of the most pronounced oceanic archipelagoes though there are additional isolation factors that cause less spatially distant groups, such as the Banda Islands of eastern Indonesia, to also be in this category of archipelagoes.

Island endemics often occur away from shore areas. The post-Pleistocene fluctuations in sea level may not have been sufficient time for recolonization back into previously inundated areas especially for highly specialized species associated with stable types of forest habitat. Biota of mountainous islands are vulnerable through climatic change which often cause populations to be particularly marginal, unstable and therefore under particularly active selection pressures.

The concept of disharmonious biota has been employed in consideration of terrestrial zones of island ecosystems. This derives from the earliest formulations of the equilibrium theory of island biogeography (MacArthur and Wilson 1967, Connor and McCoy 1979). Rates of colonization and extinction might eventually balance as a function of the total area of land-mass and isolation (Diamond 1971, Faeth and Connor 1979). Where colonization is particularly slow, there are lags in attaining an intrinsic saturation point. On islands, this can be complicated by the continued speciation of the organisms which have already become successfully established - and factors which cause cataclysmic losses of species.

The ecological boundaries of islands are not limited to shores and shallow marine areas. Rather than simply a barrier, a shoreline is a zone of overlap between terrestrial and marine food webs and involves a distinct and added set of habitat types. The shape of these habitat units are usually long and narrow and therefore prone to breakup in times of environmental change.

Within these island forest settings, there is often a tremendous diversity of vegetation types - both of humid and more drier types. Drier, seasonal forests (Janzen 1988) are often more vulnerable to forest conversion and fragmentation because of the attractiveness of associated sites to clearing for agriculture and slower rates of forest regrowth.

### **Human Impacts on Successional Mosaics**

"Tropical islands are microcosms of the variety of coastal ecosystems on continents - with more limited resources. These limitations render the resources more vulnerable to outside perturbations, including development. Human activities on islands and beaches usually adversely affect natural communities." (Maragos et al. 1983)

There is currently a tremendous economic incentive to log most lowland rainforest. Because of relatively high human population densities in many coastal areas, lowland forests near the sea and along waterways have largely been cleared or severely altered. Remaining forests in areas close to water access, such as on the smaller islands, are attractive for commercial timber harvesting because

less road construction is necessary. Nearly all of the primary forests on accessible islands, which are outside of nature reserves (Shafer 1990), will be liquidated through logging concessions or agricultural clearing in the coming decade. This is already the case across large areas such as much of the Philippines.

The capital necessary to establish logging activities in such remote areas usually requires that extractive operations be intensive. This severe pressure for high rates of profit has tended to support obstacles to the conservation of primary forest habitat as well as to establishment of management areas with high values for aboriginal land use and wilderness recreation.

Portions of moist forest biota have some dependence on mature successional stages and relatively undisturbed sites though these relationships are clearer for tropical areas (Johns 1983, Ingram 1989). Modern alterations of island forests 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 of modern change are often much greater. The tracts of primary forest that remain are often degraded on an indefinite basis due to expansion of edges and decreasing size of habitat units.

The availability of technologies such as chainsaws, the almost complete intrusion of the global economy with reduction of peripheral areas to resource extraction, and increased human populations have all exacerbated more natural extirpation and extinction processes. Solutions have not always been clear. On small islands, the Twentieth Century dichotomies of preservationism and multiple-use conservationism are often problematic (Dahl 1985) as there are shortages of land for a range of consumptive and non-consumptive needs.

It should be possible to predict the vulnerability to fragmentation (Temple and Wilcox 1985, Wilcox and Murphy 1985, Harris 1985, Lovejoy et al. 1984) of particular islands and archipelagoes in terms of:

- sizes of islands (MacArthur and Wilson 1967, Diamond 1972, Cole 1981);
- ecosystem and community types and "spatial pattern" (Turner 1989);
- landform types (Swanson et al. 1988);
- frequencies and sizes of natural patches and gaps as related to regimens of disturbance (Brady and Hanley 1984);
- typologies of vulnerability for communities and species as related to current or past response to change (Hunter et al. 1988); and
- "spatial landscape models" of the responses of particular populations and sub-areas of communities (Baker 1989) to change agents such as forest clearing.

Conservation / development typologies could be based on island size, shape (Diamond 1975), topography, age, pattern of isolation, and chronology of change of ecosystem structure over geologic time.

The size, shape and formation patterns of patches and gaps (Brokaw 1985, Denslow 1980) within successional mosaics (Forman 1982, Ewel 1983) is particularly central in determining sensitivity to fragmentation of a particular archipelago. Similarly, there are variable regimens of disturbance and ecotones (Raney et al. 1981, Schonewald-Cox and Bayless 1986, Hansen et al. 1988, Wiens et al. 1988) which enter in to the equation of "intrinsic vulnerability" of loss of species from fragmentation. Cultural factors that exacerbate sensitivity to fragmentation and spur extirpations (Balser et al. 1981) can then be analyzed in terms of:

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- the extent of traditional modification of ecosystems;
- prospects for the use of technologies and respective intensities and sites across landscape units and regions (Giacomini and Romani 1978, Janzen 1983);
- prospective species introductions (Carlquist 1974, Vitousek 1988); and
- long-term demands for tourism and recreation.

A long-term threat, to the continuing evolution and the prospects for successful management of island biotas, is that of the disruption of patterns of colonization across entire archipelagoes. There is a similarity, here, with networks of protected habitat. As natural habitats and respective populations on mainlands and adjacent islands decline, the functional distance / time factor increases for potential recolonization. Maintenance of connectivity (Shafer 1990), no matter how tenuous are the colonization pathways, should therefore be a major criteria in planning protected areas within archipelagoes.

Insularization (Shafer 1990) is compounded by inevitable catastrophes and stochastic losses, including problems in environmental regulation and the implementation of conservation planning, which destabilize already unstable systems. Human beings are making virtually all islands more "oceanic" and oceanic islands are relatively depauperate and derive much of their global significance, in terms of biodiversity, from the organisms that have persisted and evolved over long periods of relative stability - a stability that has not been afforded with human beings even where there are well-protected reserves.

The structure of many island ecosystems tend to be especially vulnerable to displacement by invasions of alien species (Vitousek 1988). Island forms are often pre-disposed to extinction.

Island vegetation is susceptible through loss of species, from mechanical interference (cutting and bulldozing), introduced grazing animals and introduced plants (Moore 1983). On oceanic islands, such as Hawai'i, native plants are particularly prone to displacement by invasive aliens when there are also land use-induced disturbance factors (Mueller-Dombois et al. 1981).

Archipelagoes with pressures for exploitation of extensive tracts of rainforest deserve some of the greatest attention for habitat conservation in the coming decade due to:

- the high species diversity spanning a range of forest and shallow marine communities;
- the high levels of endemism and disjunct species associated with island ecosystems;

- low or negligible rates of recolonization; and
- the rapid destruction of island ecosystems as they existed before European intrusion (Crosby 1986).

### **Typologies of Vulnerability to Fragmentation**

Most of the world's islands that were dominated by mosaics of primary rainforest have been radically altered in the Nineteenth and Twentieth Centuries. There are virtually no truly oceanic islands where the majority of the lowland forests were not largely altered or converted within a century of European intrusion. Similarly, nearly all of the lowland forests of the world's transitional islands, with the notable exception of Seram and Halmahera of eastern Indonesia, have been altered.

There is more primary rainforest and relatively pristine shallow marine areas on continental islands because adjacent mainland areas have been more attractive for extractive activities. The prospects of conservation are more promising and most of the remaining large islands with primary rainforest are in this category. The islands off-shore of New Guinea, the Solomon Islands to the east and the Moluccas to the west have the largest remaining pristine areas of island / forest / shallow marine configurations.

Four sets of human impacts comprise the most severe threats to the biological diversity to the remaining islands dominated by primary rainforest:

1. conversion and alteration of primary rainforest;
2. fragmentation of natural habitat particularly in forested areas;
3. the impacts of terrestrial land use on marine areas; and
4. generalized degradation of the marine environment.

All four categories of impacts work synergistically and can produce cumulative impacts (Dickert and Tuttle 1985) which can be rapid, devastating and largely irreversible.

### **Frameworks for Conservation Planning and Management of Fragmentation of Islands with Rainforest**

Islands that are relatively pristine with complex forest mosaics may well become the central metaphor in humanity's conception of "nature" and natural habitat in coming decades: archipelagoes on archipelagoes that are almost saturated with biological richness and linked by highly permeable membranes (marine areas) and yet which are perpetually vulnerable to isolation. The prospects of additional activities in these areas, no matter how careful, not producing negative impacts on some elements of local biodiversity are slim. But even if pressures for logging and mining are removed, as in the case of the establishment of national parks, programmes of inventorying and monitoring

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must be quickly initiated (Ingram 1989).

If an expanded international programme of island conservation goes ahead, it will need to be in the next decade and be within the imperfect contexts of national and provincial frameworks of planning and land management. Given the traditional communities that currently occupy many areas and pressures for settlement or tourism on most of these islands, it is highly unlikely that many wilderness preserves will be possible. Even on remote islands such as Siberut, Mentawai Islands, Indonesia, that still are largely covered by more mature phases of forest, the impacts of logging and tourism suggest that large, multiple-use management units with small, only partially pristine cores are inevitable (Ingram 1989, Mitchell and Tilson 1986)

Priority sites for habitat conservation on islands with large tracts of primary forest can be evaluated through matrices with one axis which includes the following parameters:

#### ecosystems

- shore zones
- shallow marine ecosystems requiring clean water
- terrestrial-marine pathways such as estuaries and mangroves
- relatively stable terrestrial mosaics with relatively small gaps such as ever-wet forest
- marginal habitats with more extreme seasonal and diurnal fluctuations

#### successional mosaics

- edges between habitat types and life zones
- habitat isolates that are comparatively smaller to similar types in adjacent mainland areas
- long and narrow habitat units such as long shorelines and in foothill areas

#### species

- "representative" of ecosystems and complexes of species
- vulnerable to fragmentation
- vulnerable to aspects of land use practices
- traditionally exploited
- harvested for export
- holding potentials as genetic resources (Ingram 1989).

Another axis in the matrix could include prospective change factors as related to logging, mining, agriculture, tourism and more cumulative impacts. Such matrices would be linked to site-specific inventory data to allow for impact assessment, mitigation formulation, and incremental conservation planning on an on-going basis - if there is the political will to make conservation, both ecological and cultural, the over-riding priority for development.

There are major gaps in the theory and methodology of conservation of biological diversity on islands, surrounding marine areas and in rain forest. All protected areas and management

regimens that have or are currently being proposed may be inadequate for the conservation of local biological diversity as international standards coalesce over the coming decade. The linking of initial and revised criteria for conservation and reserve design with data on on-going responses of protected populations is crucial to effective maintenance of the more sensitive elements of local biological diversity.

Monitoring frameworks could be standardized within matrices of ecological and land use typologies to test hypotheses for island conservation biology. In order to inform land use planning (Beller et al. 1990 page 401) on how to minimize threats to local biological diversity and to identify the latitude available for development, research programmes can include:

- verification of species-area curves between and within archipelagoes through more complete inventorying
- identification and mapping of successional mosaics, with respective gaps and isolates, over time
- verification of cause-effect linkages between natural and cultural disturbance factors and mosaic dynamics
- verification of the representativeness of species for complexes of species - particularly for terrestrial-marine areas and relatively unique ecosystems
- verification of the vulnerability of species to fragmentation and human-induced change and descriptions of the structure of the cause-effect linkages
- tracking of cumulative impacts on particular species and across complexes of terrestrial and marine ecosystems
- tracking the impacts of human activities in areas of more closed systems and
- tracking the roles of traditional conservation practices in such relatively closed systems.

## **Conclusions**

We live on a planet that has become painfully finite in its life-support system and its ability to evolve with the havoc that human beings can reap on ecosystems. These islands confirm the limitations of all ecosystems when over-whelmed but perhaps island boundaries, no matter how permeable and problematic, can also provide some clues on how to maintain and rebuild regional ecosystems. These islands require an international response not only for their uniqueness but also for the opportunities that they provide for linkages across great distances - no matter how tenuous these might be at the present time.

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## References

- Baker, W. L. 1989. A review of models of landscape change. Landscape Ecology 2(2):111-133.
- Balsler, 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.
- Batisse, M. 1982. The biosphere reserve: a tool for environmental conservation and management. Environmental Conservation 9(2):101-111.
- Beller, W., P. d'Ayala and P. Hein. 1990. Regional recommendations. In *Sustainable Development and Environmental Management of Small Islands*. W. Beller, P. d'Ayala and P. Hein (editors). Paris, Unesco.
- 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.
- Burley, F. W. 1988. Monitoring biological diversity for setting priorities in conservation. In Biodiversity. E. O. Wilson (editor). 227-230. Washington, D. C., National Academy Press.
- Carey, A. B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. Natural Areas Journal 9(3):151-162.
- Carlquist, S. 1974. Island Biology. New York, Columbia University Press.

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successional mosaics and requirements for networks of protected habitat on islands with rainforest  
Biodiversity and Sustainable Development, Symposium, XVII Pacific Science Congress, Honolulu, May 1991

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. 1984. Biogeographical aspects of isolation in the Pacific. Ambio 13(5-6):302-305.

Dahl, A. L. 1985. 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.

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

Diamond, J. M. 1971. Comparison of faunal equilibrium 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. 1983. 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.

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.

Gordon Brent Ingram,  
Archipelagoes on Archipelagoes: Relationships between  
successional mosaics and requirements for networks of protected habitat on islands with rainforest  
Biodiversity and Sustainable Development, Symposium, XVII Pacific Science Congress, Honolulu, May 1991

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.

Groome, D. 1990. Green corridors - a discussion of a planning concept. *Landscape and Urban Planning* 19 (4): 393 - 387.

Hobbs, R. J., B. M. J. Hussey, D. A. Saunders. 1990. Nature conservation - the role of corridors. *Ekologia CSSR* 9 (3): 340 - 342.

Hamnett, M. P. 1990. Pacific islands resource development and environmental management. In Sustainable Development and Environmental Management of Small Islands. W. Beller, P. d'Ayala and P. Hein. 227-257. Paris, Unesco / Parthenon.

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.

Hunter, M. L., G. L. Jacobson and T. Webb. 1988. Paleoecology and the course-filer approach to maintaining biological diversity. Conservation Biology 2(4):375-385.

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. Ann Arbor, Michigan, University Microfilms International.

Ingram, G. B. 1990. The need for knowledge from indigenous communities in planning networks of protected habitat for the conservation of biological diversity: Three island settings. in Ethnobiology: Implications and applications. Proceedings of the First International Congress of Ethnobiology (Belem, 1988). Volume 2. M. J. Plotkin (ed.). 87-105.

IUCN / UNEP. 1986. Review of the Protected Areas System in Oceania. Gland, Switzerland. IUCN.

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

Janzen, D. H. 1988. Tropical dry forests: The most endangered major tropical ecosystem. In

Gordon Brent Ingram,  
Archipelagoes on Archipelagoes: Relationships between  
successional mosaics and requirements for networks of protected habitat on islands with rainforest  
Biodiversity and Sustainable Development, Symposium, XVII Pacific Science Congress, Honolulu, May 1991

Biodiversity. E. O. Wilson (ed.). 130-137. Washington, D.C. National Academy Press.

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

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.

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

Maragos, J. E., A. Soegiarto, E. D. Gomez and M. A. Dow. 1983. Development planning for tropical coastal ecosystems. In Natural Systems for Development: What planners need to know. R. A. Carpenter (editor). 229-298. New York, MacMillan.

Maser, C., R. F. Tarrant, J. M. Trappe, J. F. Franklin. 1988. From the Forest to the Sea: A story of fallen trees. Portland, Oregon, United States Department of Agriculture Forest Service (General Technical Report PNW-GTR-229).

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.

Menard, H. W. 1986 Islands. New York, Scientific American Books.

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.

Moore, D. M. 1983. Origins of temperate island floras. In Plants and Islands. D. Bramwell (ed). 69-86. London, Academic Press.

Mueller - Dombois, D., K. W. Bridges, and H. L. Carson (editors). 1981. Island Ecosystems: Biological organization in selected Hawaiian communities. USA International Biological Programme Synthesis Series 15. Stroudsburg, Pennsylvania, Hutchinson - Ross Publishing.

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

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.

Gordon Brent Ingram,  
Archipelagoes on Archipelagoes: Relationships between  
successional mosaics and requirements for networks of protected habitat on islands with rainforest  
Biodiversity and Sustainable Development, Symposium, XVII Pacific Science Congress, Honolulu, May 1991

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

Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: A hypothesis. American Naturalist III (987):376-381.

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

Shafer, C. L. 1990. Nature Reserves: Island theory and conservation practice. Washington, D.C., Smithsonian Institution Press.

Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience. 38(2):92-98.

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.

Turner, M. G. 1989. Landscape ecology: The effect of pattern on process. Annual Review of Ecology and Systematics 20:171-97.

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.

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

Wilson, E. O. 1988. The current state of biological diversity. In Biodiversity. E. O. Wilson (ed.). 3-18. Washington, D.C. National Academy Press.