BIODIVERSITY CONSERVATION AS A SUSTAINABLE FOREST MANAGEMENT TOOL

Dr. D.S. Hammond
International Institute of Entomology, United Kingdom

1. INTRODUCTION

Tropical forests continue to be used at an ever-increasing rate for the timber, wildlife, and other saleable products they house. Recent estimates suggest that nearly 1.9 x 10^6 km^2 of forest was utilised during the 1980=s, and current rates are running at 1.69 x 10^5 km^2 per annum (FAO, 1991; WRI, 1994). Whilst clearance for slash-and-burn cultivation once accounted for the majority of forest lands utilised each year, growth in the total area under timber production has now become the main form of use as vast tracts of previously inaccessible forest are opened up in the face of dwindling global timber supplies, increasing demand, and an ever-increasing availability of time-saving technologies.

Non-timber plant products are also playing an increasing role in the international economy, as the demand for alternative materials used in high-value goods, such as home furnishings, and the prospects of biochemical discovery accelerate (Table 1).

International, regional, and local trade in wildlife continue to provide income to rural residents, local businesses, and international export/import companies (Table 2). The pressures on a dwindling forest resource are enormous as increasing numbers of stake-holders, with a multitude of often conflicting objectives, seek to subsist or profit from the large biomass locked in the remaining unexploited stands.

2. BIODIVERSITY CONSERVATION AND FOREST UTILISATION: CONTRASTING ISSUES?

Everyone talks about biodiversity. In most cases, biodiversity conservation is discussed as an issue separate from forest production, often in conflict with large-scale extractive industries (McNeely, 1994). Preservationists traditionally believe that biodiversity is a quantity that must be maintained; all species are important and have value. Conservationists, while more pragmatic, often view large-scale, extractive industries as a threat to biodiversity. Most frequently, their view of the relationship between extractive industry and biodiversity is focused on whether or not the intensity of industrial extraction will negatively impact upon populations and communities of indicator, flagship, or commercial species (Johns, 1985; Sayer *et al*., 1995; Laurance and Laurance, 1996). The issue has become polarised as conservationists and industrial users stand firmly for antithetical solutions, and then try to reconcile these divergent views through arbitration. The outcome is rarely agreeable to all parties because the solutions tendered are often poorly integrated (e.g. see Alpert, 1996).

Table 1 Why tropical forest plants are harvested by non-indigenous[1] forest users

[1] Three factor groups are considered important in conserving biodiversity as part of sustainable management, viz. 1) ecological, 2) economic and 3) cultural groups. Social factors are considered here to be composed of economic and cultural components. Traditional indigenous methods of harvesting and valuation are not covered in this paper because the cultural values and motivations for harvesting of many forest species and habitats is complex and not entirely open to accurate interpretation based on standard Western economic theory. As such, they are not the focus of this paper, though this in no way suggests that indigenous views are less important than those of industry, but simply require

Plant Part	Use		Scale of extraction
	General	Specific	
Whole plant	Ornamental	Trade	Industrial/Cottage
Stems	Timber	Sawn lumber Plywood Veneer Poles/Piles Charcoal/Firewood Paper	Industrial/Cottage Industrial Industrial Industrial/Cottage Cottage/Household Industrial
	Food	Palm heart	Industrial/Cottage
	Flexi-craft	Furniture Scaffolding	Cottage Industrial/Cottage
	Extracts	Rubber/Balata Resins Biocides	Industrial/Cottage Cottage Household
Leaves	Biochemical activity	Medical	Cottage/Household
Fruit	Food Oil Flavouring	 Edible Lubricants Drinks/Food	Household/Cottage/Industrial Industrial/Cottage Industrial Industrial/Cottage
Seeds	Food Fats & Oils Provenance/ Genetic improvement	 Edible Fuel	Household/Cottage Cottage/Industrial Cottage Industrial
Roots	Food Flexi-craft (aerial)		Household/Cottage Cottage

We know that biodiversity is important for our own well-being. Important food, medicine, and building materials - harvested or domesticated in the past from wild stocks - are the building blocks of modern civilisation. Yet, we know next to nothing about what constitutes biodiversity, and whether certain parts are more important than others. We know that certain countries contain a disproportionately large part of global biodiversity, but we do not know whether this means that these areas are in all cases more valuable than others because we do not yet understand the relative significance of each individual species to ecological and economic sustainability. It is unlikely that we will ever know the value of all species, though attempts at inventorying all organisms in a limited area (All-Taxa Biological Inventory, or ATBI) have been proposed as a conduit to understanding their value (D. Janzen, pers.comm.). While ATBI=s may provide unprecedented scientific insight, they are not a practical approach to valuing organisms and finding solutions to problems of biodiversity conservation in the face of increasing human appropriation of global resources (Vitousek *et al*., 1986). Time is short and resources are strained. On the other hand, selective inventory methods such as Rapid Biodiversity Assessments (RBA=s) tend to provide useful information for only the most common species, though some taxa (understorey plants, birds) are clearly more amenable than others to such an approach. RBA=s are

alternative analysis.

likely to overvalue those taxa which are most abundant at the time of assessment and which are most intensively studied.

Table 2 Why tropical forest animals are harvested by non-indigenous forest users

Animal group	**Use**		**Scale of extraction**
	General	Specific	
Mammals	Rodents	Meat	Household/Cottage
	Ungulates	Meat	Household/Cottage
		Skins	Cottage/Industrial
		Traditional Medicine	Industrial/Cottage
	Primates	Meat	Household/Cottage
		Trade	Cottage
Birds	Ground-dwelling	Meat	Household/Cottage
		Eggs	Household
	Arboreal	Trade	Cottage/Industrial
		Meat	Household/Cottage
		Feathers	Household/Cottage
Reptiles	Crocodilians	Skins	Household/Cottage
		Trade	Household/Cottage
	Snakes	Skins	Household/Cottage
		Trade	Household/Cottage
	Turtles/Tortoises	Meat	Household
		Eggs	Household
	Lizards	Meat	Household
		Trade	Cottage
Amphibians	Frogs	Trade	Cottage
	Salamanders	Trade	Cottage
Fish	Large	Meat	Household/Cottage/ Industrial
		Trade	Cottage/Industrial
	Small	Trade	Cottage/Industrial
Insects	Butterflies	Trade	Cottage
	Parasitic wasps	Trade (IPM)	Cottage
	Beetle grubs	Food	Household
	Ants	Food	Household/Cottage
	Bees	Honey	Household

How can we integrate biodiversity conservation issues into forest management practices? Biodiversity conservation is typically integrated into forest land-use planning by spatially partitioning and then earmarking areas for utilisation (often the most productive) and for conservation (often the least productive or most inaccessible). It is now reasonably well-established, however, that small patches of intact forest surrounded by much larger areas of intensive exploitation rarely retain their conservation value (Laurance and Bierregaard ,1997), even when these reserves are representative of regional forest habitat diversity, if the interstitial habitat is unsuited to forest species. This is not to say that all species are unable to persist in isolated fragments; some plant, invertebrate, and small vertebrate species can remain for long periods (e.g. Gascon, 1993). Most of the largest-bodied species, however, are unable to maintain viable local populations under such conditions, though some vertebrate herbivores may go through transitory periods of hyperabundance when released from their natural predator community (Terborgh *et al*.,. 1997). In such cases, many species are unable to maintain their local populations because of edge effects, dwindling resource availability, and - perhaps most importantly - the fragmentation of their larger, metapopulation structure. Metapopulations buffer against local population extinction or decline through a source to sink immigration process (e.g. Harrison, 1989). In order to effectively buffer against local losses, the metapopulation structure must show a good degree of connectivity between local populations, and this requires large tracts of favourable habitat in most cases where a species is sensitive to rapid habitat transition (e.g. Levins, 1969).

Partitioning forest lands solely on the basis of mutually exclusive forest land-use practices would lead to more intensive exploitation of areas outside reserves. Earmarking certain areas for conservation may increase the pressure on remaining lands in order to achieve short-term profitability while at the same time suggesting that biodiversity has been conserved and thus the process of extraction can proceed unabated. While the need for forest reserves as regenerating foci for species whose populations decline as a result of harvesting practices is clear (Johns, 1992), this should not supplant sound harvesting practices which maximise the value of the regenerating forest to biodiversity conservation (Johns, 1997). Often, regenerating forest stands will support species which cannot persist in isolated forest reserves (e.g. Kavanagh and Bamkin, 1995).

3. A CONTEMPORARY VIEW OF TROPICAL FOREST BIODIVERSITY

While deep integration of biodiversity conservation and utilisation is necessary, few workable frameworks on which to do so have been posited by tropical forest scientists, who rarely see themselves as decision-makers. Which species should be conserved and how?

Firstly, conservation of biodiversity should be seen solely in the context of the present and future needs of humans at local, regional, national and international levels. The preservation of present-day biodiversity on ethical grounds (e.g. Regan, 1981), while noble, is counter-intuitive when viewed in the context of the magnitude of palaeoextinctions and their putative role as catalysts to several of the greatest diversification periods on our planet, including the one which eventually led to the emergence of modern humans (Jablonski, 1986). Biodiversity has evolved in habitat which is under a constant state of flux and thus should be robust to moderate levels of modification (Whitmore and Sayer, 1992). Though current rates of extinction may appear unprecedented (Wilson, 1988), we should not exclude the possibility that this may be an artefact of our inability to maintain the same level of resolution when analysing past trends (10^2 to 10^4 yrs; e.g. Angel, 1994) as applied to contemporary (10^{-5} yrs and upwards) events; our power to detect details diminishes with antiquity (Hammond et al. in prep.). Ironically, at the same time as we discuss conserving the set of present-day species inhabiting tropical forests, we maintain a vast expenditure on efforts to debilitate or eradicate other species that impinge on our existence. What part of biodiversity exactly are we trying to conserve? Clearly, it is those species that we deem beneficial to human society through the material (e.g. timber) or service (e.g. water, tourism) economies they underpin.

Recent studies of temperate ecosystems under experimental manipulation suggest, in fact, that the number of Latin binomials present are less important than the diversity of functional characteristics exhibited by these species in maintaining the productivity of the system (Tilman *et al*., 1997, but see Hooper and Vitousek, 1997). Clinal character convergence of tropical canopy trees across Guyana suggest more complex, long-term attenuation of species assemblages to both contemporary and historical disturbance events (ter Steege and Hammond, in press.; Hammond *et al*. in prep.).

Thus, while retaining all species may be the ideal way to secure our current resource base, maintaining functional integrity of tropical forests would appear to be a more expeditious approach if we wish to reap material benefit from forests far into the future. While many processes contribute substantially to forest functioning, those which somehow directly affect plant reproduction are most likely to influence, in the short-term, the cycle of regeneration on which nearly all wet tropical forest species are dependent (i.e. disturbance events, *sensu* Whitmore, 1975). Moreover, processes that directly impinge on reproduction and reproductive success often are the source of intense character selection over longer, evolutionary time (e.g. floral morphology). The relationships between plants and animals figures prominently among these processes through pollination, seed dispersal, seed predation, herbivory, and decomposition.

Animals account for nearly three-quarters of all species expected to occur on Earth. Most species are found in the tropics, particularly in neotropical forests, which house the largest number of forest rodent, bird, primate, butterfly, and bat species, among others (e.g. Fleming *et al*., 1987). Many of these species directly promote or impinge on the reproductive success of forest trees, lianas, shrubs, and epiphytes through their selective consumption of pollen, nectar, fruit, seeds, leaves, and stems. At the same time, these resources sustain animal populations, often in an otherwise resource-limited environment. The outcome of these processes is for the most part determined by the factors that influence vertebrate and invertebrate foraging patterns and population dynamics. The way in which a forest stand is utilised by humans will inevitably change the way in which these factors influence foraging patterns and population dynamics of forest animals, and through these, plant reproductive success (e.g. Dirzo and Miranda, 1990).

4. TOWARDS INTEGRATION: THE FOREST MANAGEMENT FRAMEWORK

Available information suggests that management based on natural regeneration holds the greatest prospect for long-term timber production under current market structures, because costs of immediate intervention are difficult to reconcile with the prospect of higher future yields and an uncertain price economy. Other non-timber forest products, by default, rely on natural regeneration to maintain viable populations and buffer harvesting effects. Natural regeneration of plants depends to a certain degree on those processes, such as seed dispersal and predation and herbivory, which influence colonisation and recruitment of juveniles in recently harvested areas. At the same time, natural rejuvenation of animal populations can depend to some extent on resource availability and the ability of population size to buffer against losses brought on by periods of resource scarcity or disease.

Thus, an important part of managing natural regeneration is managing the interactions between plants and animals. Management on this basis assumes, however, that intervention is kept to a minimum (Johns, 1997) and many forests are now so depleted that natural regeneration of target species is no longer possible; management of natural regeneration has become synonymous with forest restoration. In such degraded states, the degree to which inhabiting plants and animals rely on one another has deviated significantly from the tightly-bound community that characterises most unexploited forests stands. The degree of intervention, and thus the cost, of catalysing the re-establishment of relationships between plants and animals in these areas is likely to be high. However, sound ecological knowledge can provide a basis on which to identify plant-animal relationships which may have a disproportionate influence on the rate and trajectory of regeneration. Optimising rates and trajectories will increase cost-effectiveness of a forest amelioration programme by minimising intervention. The identification of plant-animal relationships which might catalyse the restoration of a community will depend to some extent on the predominance and evolutionary success of certain taxonomic groups and the degree to which they critically depend on the ecology of other species.

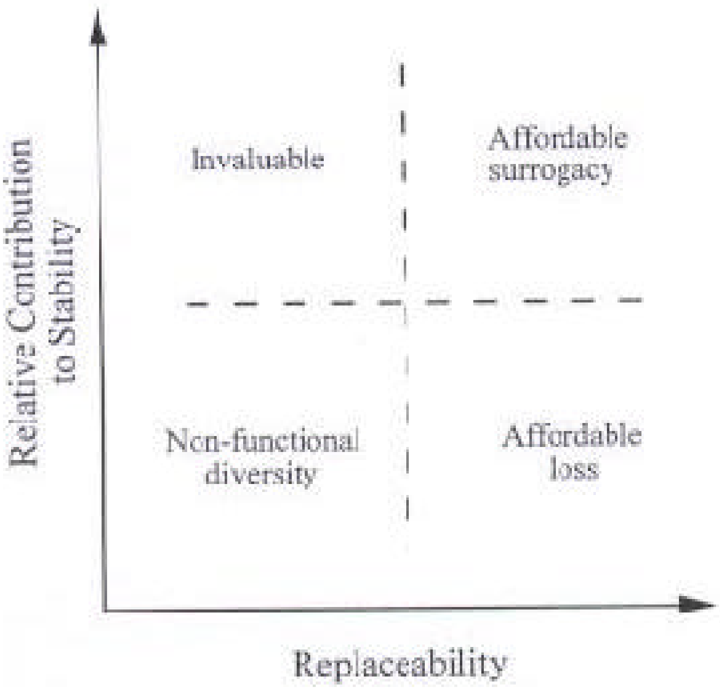

Figure 1 The relationship between a species contribution to community stability, its replaceability, and the emphasis placed on its retention as part of forest management

The predominance of certain taxa would suggest that they are more likely to play an important role in the contemporary forest regeneration process. In contrast, species which are a relict of past forest environments or cultural deprivation, the >living dead=, should be characterised by their declining abundance and poor regeneration (Janzen, 1985). The functional significance of a given taxonomic group, however, hinges not only on the success of their lineage, but on the nature of the contemporary role they play, viz. 1) how important is the role to community stability and 2) the degree to which other taxa, or abiotic processes, can fulfil their role - their replaceability. If their contribution to community stability is marginal, then their loss is more affordable. If few substitutes prove to exist and their contribution to community stability is great, then these taxa are of paramount importance, and their retention must be made a priority (Figure 1). The application of functional significance to sustainable forest management is manifest in the way that taxa pollinate, disperse, consume, and decompose plants of commercial value.

Pollination. Most woody tropical species are obligate outcrossers, either bearing self-incompatible bisexual flowers or separate male and female plants (dioecy) which require some form of pollen transfer between individual flowers for fertilisation (Bawa, 1974). Animal-assisted pollination, mainly by bees, butterflies, moths, beetles, birds, and bats, is characteristic of most tropical forests plants (Bawa *et al*., 1985), though wind-pollination does occur. However, the prevalence - and thus the importance - of different pollen transport mechanisms varies considerably by region because the relative abundance of different host plants weights the impact of the various pollination strategies. For example, many of the main dipterocarp trees in the drier regions of South-East Asian forests are wind-pollinated, and the pollination of many confamilial species of wetter forests has been attributed to thrips (Thysanoptera) and other small, fast-breeding insects (Cicadellidae, Miridae) (Appanah and Chan, 1981; Appanah, 1987), though the small size of these fragile animals makes a combination of floral feeding and wind the more likely pollination route (Roubik, 1993). In some dipterocarp forests, facultative apomixis is common, making pollination in general unnecessary for reproduction (Ashton, 1969), though a prolonged reliance on apomictic reproduction will most likely lead to reduced genetic variation within a population. Fig wasps are important pollinators in Papua New Guinea, given the abundance and species richness of *Ficus* in these forests. Small beetles and flies dominate the pollinator community in lowland rainforests of North Queensland, Australia (Irvine and Armstrong, 1989). In contrast, long-tongue bats (Glossophaginae), large bees (Apidae, Euglosinni, etc.), flies, and moths appear to be particularly important pollinators of trees in eastern Amazonia and Central America (e.g. Bawa *et al*., 1985; Renner and Feil, 1993) and smaller, stingless bees (Meliponinae) are important agents throughout the tropics.

Seed Dispersal. The seeds of tropical woody angiosperms are for the most part dispersed by vertebrates, ants, wind, water, gravity, or explosive dehiscence. The majority of timber tree species have seeds which are dispersed by vertebrates or wind. Again, however, the functional significance of animals as dispersal agents varies by region. South-East Asian forest dipterocarps have seeds which are dispersed over relatively short-distances by wind-driven processes, such as complex gyration (Burgess, 1970). Dipterocarps can account for 35-50% of basal area, 10-15% of tree species richness, and 20-25% of all individuals (>10 cm dbh) in a stand (Smits, 1994; Schulte and Schöne, 1996). This suggests that animals as dispersal agents do not play a pivotal role in shaping community structure in these forests, though the seeds of other well-represented families, such as the Sapotaceae, Lauraceae, Euphorbiaceae, and Myrtaceae have fruit characteristics typical of vertebrate dispersal. In contrast, over 70% of timber trees are vertebrate dispersed in Guianan forests (Hammond *et al*., 1996), with rodents playing a particularly important role in some locations (ter Steege and Hammond, in prep.). In mixed forest stands, these species can account for more than 90% of the basal area, tree species richness, and number of individuals. Rodents consume and disperse the seeds of a large number of tree and liana species in eastern Amazonia. Caviomorph rodents, such as the agouti (*Dasyprocta* spp.) and paca (*Agouti paca*) are specialised seed consumers found commonly throughout neotropics but do not occur in the Old World tropics. Rodents in general appear to have a more limited role in the dispersal of seeds in tropical forests of West Africa and South-East Asia.

Herbivory and Seed Predation. Many animals feed on the leaves, stems, bark, and roots of plants. If the object of the herbivore's feeding is a small juvenile, the loss of biomass may kill it, reduce its tolerance of stress, such as drought, or impair its ability to compete with siblings and the offspring of other sympatric species (Whitmore and Brown, 1996). As an adult, a plant=s longevity may be reduced by severe attack, often as a consequence of the pathogen infection that follows such events. Sub-lethal attack on adults may lessen their reproductive capacity, reducing seed crop size and/or the size of their offspring.

Again, certain groups of dedicated herbivores tend to be more speciose and/or abundant in one region than another. For example, sap-feeding treehoppers (Membracoidea, Membracidae) are particularly diverse in Neotropical forests (Wood, 1993) and are renowned for spreading disease along with other phloem-feeders (Nault and Ammar, 1989). Leaf-cutting ants (the Attini) are restricted to the neotropics, consuming an estimated 600 kg (dry wt) of vegetation per hectare per year, or 0.5% of total non-woody primary production, on Barro Colorado Island, Panama, alone (Leigh and Windsor, 1982).

Vertebrate herbivores can consume up to 10 times as much non-woody plant parts as invertebrates (Leigh and Windsor, 1982). Forest-dwelling browsers tend to be much larger in South-East Asian and

African forests than in the neotropics. The largest browser in the neotropics, the tapir (*Tapirus* spp.), has only one twentieth the body weight of the largest Old World forest browser, the elephant, and is not restricted to South and Central America.

Decomposers. Decomposer organisms interact with plants by catalysing the breakdown of dead material and, ultimately, increasing the rate at which this material is incorporated into new biomass. The actions of macrodecomposers, such as termites, collembola, and certain groups of beetles, is of particular significance to forest trees, because their relatively large body size allows them to process quickly large amounts of solid, lignified materials over a relatively large area. Foremost among macrodecomposers are the termites. While found throughout the tropics, many taxa are best represented in the paleaotropics, and several others, such as the fungus-feeding termites (Macrotermitidae), are restricted to South-East Asia and Africa.

5. VALUATION OF FOREST RESOURCES, RESOURCE USE, AND PROFITABILITY

The way in which tropical forest resources are integrated into modern human economies is typically swift and narrowly focused; there is a singular purpose which defines harvesting practices by a forest user. Thus, it is not surprising that the value of most forest resources are also singularly defined; a market has been found and the achievable revenue calculated. In reality, the tangible value of most forest plants and animals is composed of a combination of different real and potential commodities and services (Tables 1 and 2). Often these values conflict, such that the capture of one component value invariably leads to a devaluation of another component. The best solution to this conflict is to optimise for current and future values for both commodities and services (Figure 2a and b). Though short-run profitability from any single market is not maximised in this instance, the overall profitability from repeated marketisation would outstrip that achieved under a singular valuation model as long as the total profit margin achieved from this process does not fall below that achieved by a single valuation approach (e.g. timber harvesting alone). Inefficiencies in capital investment and discounting can lead to pessimistic profit forecasts under repeated marketisation, just as is the case with single valuation, though discounting future income based on re-investment of present income from forest resources into higher- yielding alternatives may systematically underrate the profitability of managed natural regeneration (Leslie, 1987) and are not connected to growth rates of forest resources through any established economic relationship (Fearnside, 1989). Despite these caveats, well-coordinated harvesting of the same resources for different markets may enhance the profitability of forest operations that are guided by sustainable management plans. To date, few harvesting operations are profitable and sustainably managed at the same time. Pre-planning market strategies so that harvesting intensities take into account current and expected commodity and service values is likely to be more profitable in the medium to long-run because adjustments in profitability are not necessary after profit stabilisation (Figure 2c and d).

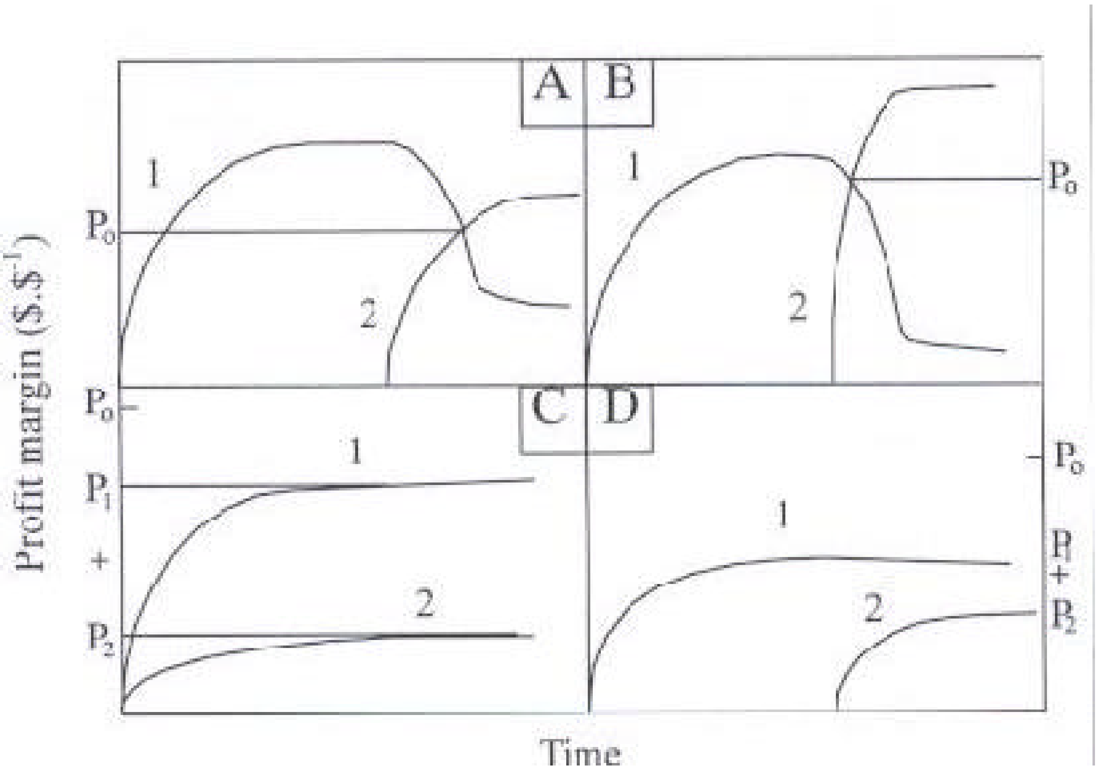

Figure 2 Dual marketisation of tropical forest products based on primary (1) and secondary (2) production goals. A) Optimisation of profit margin (P_O) given future secondary market with stable $P_2 < P_1$. B) Optimisation when stable $P_2 > P_1$. Optimal profit margins are the sum of P_2 and P_1 when dual marketisation is pre-planned under simultaneous (C) and staggered (D) entrance scenarios.

It is clear that the relationships between certain plants and animals are essential in maintaining the functional integrity of forest ecosystems and play an important role in the reproduction and recruitment of commercially valuable biota. The loss of these species through poor design and implementation of management practices will invariably lead to a devaluation of the residual forest stand because many species are locally extirpated without accounting for their contribution to the future market value of other commercial species. The relationships between wildlife use, silvicultural intervention, and timber harvesting provide good examples of how management practices that do not fully integrate biodiversity conservation value at the present may lead to substantial income loss in the future.

Table 3 The value of wildlife when considering more than one valuation axis

	Present value	Future value
	Meat	Revalued meat
Commodity	Live trade	Revalued live trade
	Skins/feathers	Sport hunting
	Edological process	Increased/sustained timber volumes
Service	Ecosystem process	Increased abundance of useful NTFP trees
	Tourism	More efficient regeneration after over-harvesting

Wildlife use and timber harvesting. For example, species such as seed and seedling-eating mammals which regulate competitive effects between individuals through seed dispersal, predation, and seedling herbivory often selectively promote regeneration of commercial species. Viewed in this way, they are a component of that species future market value since they contribute to the regeneration success and thus influence future supply. However, many forest animals also have a considerable value as food or as highly sought-after specimens in the wildlife trade.

Hunting and the intensive collection of live animals can have a devastating impact on the local animal communities because these practices typically select out those healthy, adult individuals that contribute most to reproduction, much like the selective harvesting of the most fecund, best-formed trees can promote dysgenic effects (Jonkers, 1987). Often when harvesting is intense, the population crashes after it becomes too small to sustain growth, and local extinction ensues (Redford, 1992). While rapid depletion of wildlife to extinction can be, in theory, the economically optimal strategy if a discount rate is applied to harvesting of fluctuating populations (Lande *et al*., 1994), the income earned from local extirpation of forest game species is unlikely to provide lucrative re-investment opportunities, which are more strongly influenced by other sectors of the national and global economy.

The role of wildlife in timber tree regeneration is rarely addressed when attempting to value biodiversity. Often the value is based only on the direct income achieved from harvesting, rather than the support services that wildlife may provide by sustaining growth of desirable timber species under a low-input management system based on natural regeneration (e.g. Redford, 1993). As supplies of the commercial species diminish worldwide, the unit price achieved for remaining stocks will increase, assuming that demand is relatively inelastic or at least not declining because of product substitution. If the future return on this supply is greater once harvested than the current gain made by harvesting wildlife that supports timber tree regeneration, then it is most economic, in the long run, to conserve these support species. While increasing silvicultural intervention might reduce the need for services provided by wildlife, it is unlikely that the income generated through wildlife harvesting would outstrip the cost of silvicultural intervention. However, since the role of wildlife in timber tree regeneration varies from region to region and taxon to taxon, the value of seed predators, dispersers, and pollinators as support species will also vary.

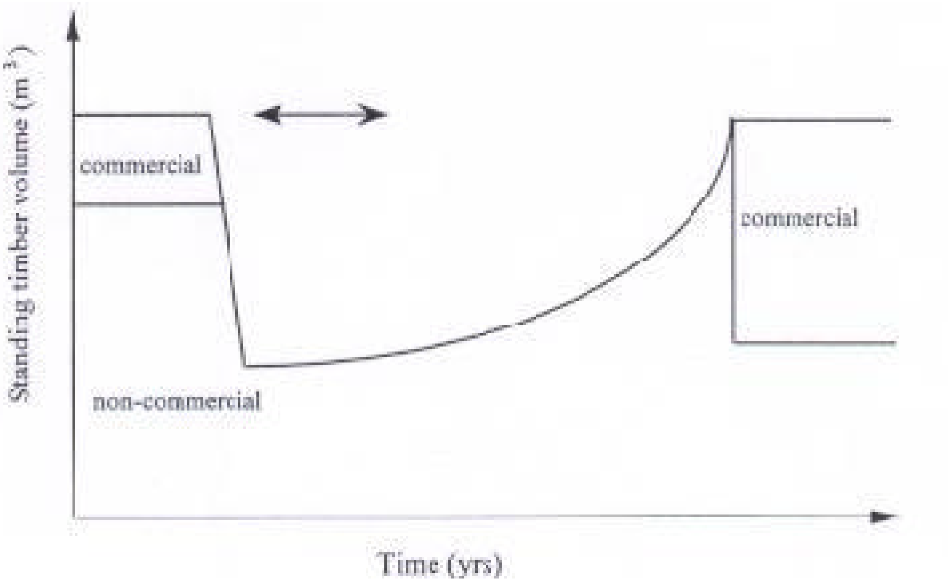

Figure 3 A heuristic representation of the increase in commercial stock as a proportion of total forest volume resulting from extensive silvicultural treatment. The horizontal arrow indicates the forest productivity limit. Adapted from de Graaf (1986).

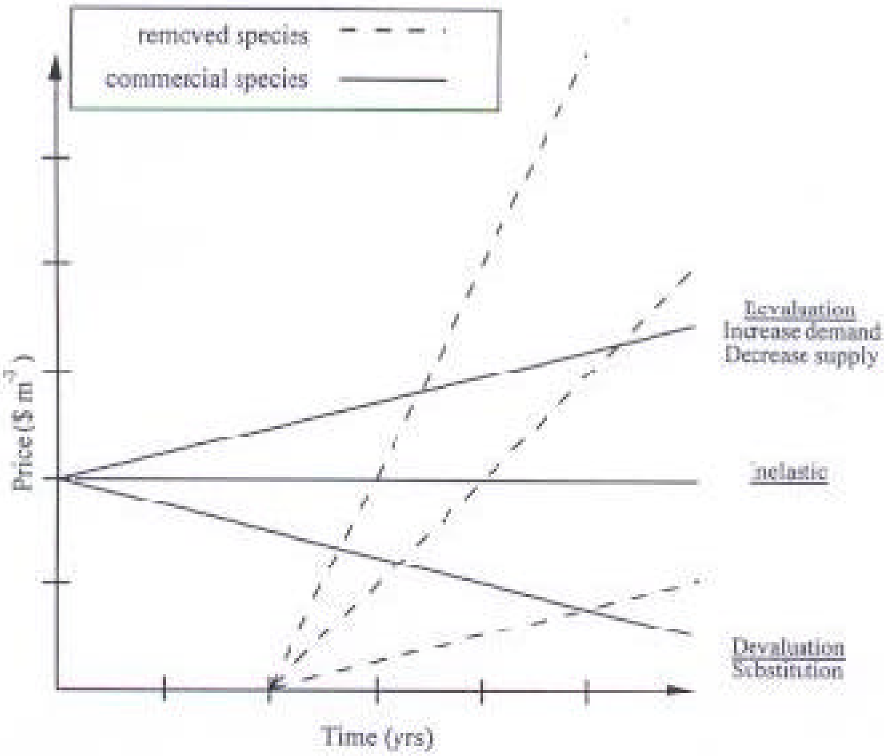

Figure 4 Trade-off between price structures for established (at t = 0) commercial species and future commercial species when the rate of price change varies linearly for both groups under one case scenario. Multiple revaluation of species previously considered non-commercials would in reality lead to more complex trade-off scenarios.

Silvicultural treatments and lesser-known timber species. Most refinements, such as enrichment planting or liberation, are unlikely to be cost-effective (e.g. Chai and Urbade, 1977; Rankin, 1979; Jonkers, 1987) and conversion to plantation is not sustainable from a nutrient standpoint in most instances (e.g. Jari Project, Brazil, Johns, 1996). However, most traditional tropical timber management systems call for some form of post-harvest silvicultural intervention (e.g. Dawkins, 1958; Taylor, 1962; Wyatt-Smith, 1963) and the growth of commercial species can more than double after liberation in some trials, leading many to prescribe such treatments as part of modern sustainable forest management systems (e.g. de Graaf, 1986; Jonkers and Schmidt, 1984).

Increasing the incremental growth of commercial species can increase the future value of the stand as the volume of marketable wood in the stand represents a larger proportion of the biomass than prior to the first harvest (Figure 3). Alternatively, species which do not have a commercial value at time of harvesting, may be saleable in the future. Under most silvicultural prescriptions involving liberation treatments, such as poison and girdling, trees are categorised by their present saleability alone. Often markets are later found for those lesser-known species which had been removed (Freezaillah, 1984; Buschbacher, 1990). If the new market achieves a higher rate of price increase, or the volume of timber from species killed exceeds the additional income received from the enhanced growth of the traditional timber species which were preferentially conserved under the silvicultural prescription, then it is best to leave the forest untreated (Figure 4).

6. WHERE TO GO?

If investment in research and development is going to be of any significant value, forest management models and the guidelines they generate must be implemented. The degree to which results of applied and pure research are used by governmental regulatory bodies, private industry, and local inhabitants is wholly a matter of acceptance. Participation by all stakeholders in the formulation of management models - such as experienced public service staff or trainees, local guides and respected members of local communities, industrial forest workers and managers, governmental policy-makers, and foreign donor representatives, if required - maximises the likelihood that management models will be implemented.

In nearly all instances, a compromise between biodiversity conservation and development must be made (McNeely, 1994; Peres, 1994). The nature of this trade-off, however, is crucial. When forest management models or guidelines are drawn up with the heedless assumption that trade-offs will take place, but without explicitly characterising and quantifying these compromises, they languish as the applicability surrounding oversimplified assumptions (constants) declines with each step in the implementation process. Ultimately, those responsible for implementation will begin to view guidelines as peripheral, rather than pivotal, to the process of conservation and development.

Thus, a model is only as good as its assumptions. If assumptions are too broad and too numerous, the guidelines will be ineffective. If assumptions are poorly characterised, then they may lead to detailed, but erroneous, guidelines. If assumptions are too few, guidelines may prove too detailed and unimplementable (Figure 5). While models that embrace the conservation/development trade-off are rare, several programmes of field research have addressed the issue in a tangible way (Integrated Conservation and Development Projects/ICDP=s; Wells and Brandon, 1993), but are focused, at this stage, on a narrowly delimited set of objectives (Alpert, 1996).

If biodiversity conservation is to be integrated as a tool in forest management, we need to construct flexible management models that are implementable in most scenarios, profitable to most forest-users, and acceptable to most stakeholders within specified limits (geographical, temporal, and social). A plural problem-solving approach to a plural solution cannot be overemphasised, but divergence in stakeholder views should not be initially arbitrated, which is traditionally done, but used as a means of calibrating the degree of flexibility required in the model. Once established, the proto-framework can then be revised on the basis of the information required to refine assumptions and define component variables.

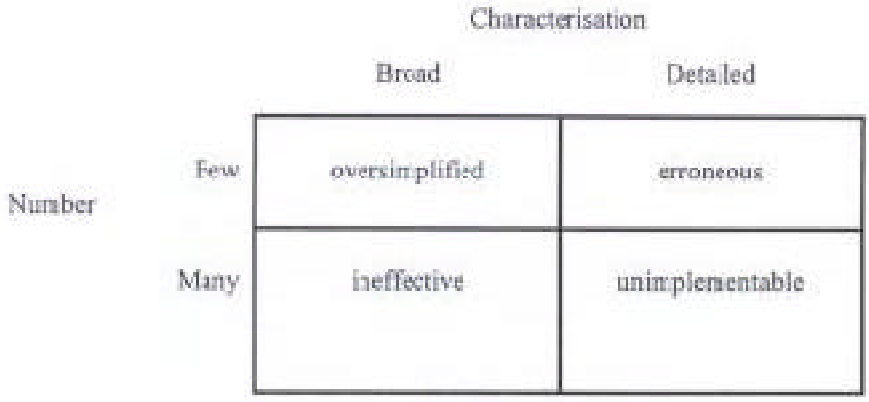

Figure 5 The potential adverse affects of model assumptions on guidelines generated from a forest management model as a function of the number of assumptions and the degree to which they are characterised.

While the need to integrate biodiversity conservation into forest management models is the focus of this paper, the regulatory effects of other abiotic processes, such as water and nutrient cycling, are of obvious - and well-established - significance and largely underpin most current dynamic models of forest ecosystems. Integrating these modules, with like modules addressing biotic processes and socio-economic aspects, into a more comprehensive model should be the mainstay of future forest management research. While developing a computerised management model with a user-friendly interface is technically possible, characterising the component variables, assumptions, and trade-offs is a much larger task, requiring a system of coordinated, small-scale field research programmes. No doubt field researchers need to retain independence in dissemination of their findings, but these findings need to be fed concomitantly to a core team given the task of translating the views, experience, and findings of many participants into acceptable management models. A good deal of information that could be used in characterising model variables and assumptions is already available. Field research in tropical forests is laborious, time-consuming, and, in many cases, expensive. The most parsimonious route would attempt to identify which variables and assumptions are 1) most sensitive to variation in other variables or assumptions, and 2) least supported by hard data. Given the long history of tropical forest data collection in many regions and the explosion of research carried out in the last two decades, it is increasingly possible for a researcher to inadvertently >re-invent= prior knowledge, which is not very cost-effective.

The shape of future biodiversity is largely bound by the decisions which human society, mainly citizens of tropical forest countries, make today. There are several genre of options available. If the entire species assemblage in existence should be maintained, then ATBI=s and RBA=s, combined with a strong preservation ethic and a substantive system of large forest reserves, should be adopted. Alternatively - though perhaps the least desirable but most well-founded - society can exhaustively harvest what is presently available from tropical forests and hope that reinvestment will yield a higher return than less intensive approaches to harvesting over the long-term. No doubt intensively exploited forest remnants would achieve some degree of revaluation, but the opportunities for optimising revenue over longer periods are likely to be lost in the face of growing human pressure on forest resources. The opportunities for prolonged forest recovery, like that which occurred after the cessation of activities of early Amerindian civilisation (e.g. Piperno, 1994), appear unlikely when viewed in the context of modern globalisation. However, if the task set out is to maintain the functional integrity and sustainable economic well-being of tropical forests and forest users, respectively, then an integrated problem-solving approach needs to be considered, mainly through the development of comprehensive, user-friendly forest management models and continued collection of hard data in the field.

7. ACKNOWLEDGEMENTS

The author would like to thank the office and field staff of the Tropenbos-Guyana programme for their continued assistance. Financial support from the Department for International Development (DFID), U.K., the Darwin Initiative, U.K., and the Tropenbos Foundation, the Netherlands, is gratefully acknowledged.

8. REFERENCES

Alpert, P. (1996). Integrated conservation and development projects. *Bioscience* 46: 845-855.

Angel, M.V. (1994). ‘Spatial distribution of marine organisms: patterns and processes’, in P.J. Edwards, R.M. May and N.R. Webb, *Large-Scale Ecology and Conservation Biology*. Blackwell Scientific, Oxford, UK.

Appanah, S. (1987). ‘Insect pollination and the diversity of dipterocarps’, in A.J.G.H. Kostermans (ed.), *Proceedings of the Third Roundtable Conference on Dipterocarps*. UNESCO, Jakarta, Indonesia.

Appanah, S. and Chan, H.T. (1981). Thrips: the pollinators of some dipterocarps. *Malaysian Forester* 44: 234-252.

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

Bawa, K.S. (1974). Breeding systems of tree species of a lowland tropical community. *Evolution* 28: 85-92.

Bawa, K.S., Bullock, S.H., Perry, D.R., Coville, R.E. and Grayum, M.H. (1985). Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* 72: 346-356.

Buschbacher, R.J. (1990). Natural forest management in the humid tropics: ecological, social, and economic considerations. *Ambio* 19: 253-258.

Burgess, P.F. (1970). An approach toward a silvicultural system for the hill forests of the Malay Peninsula. *Malayan Forester* 33: 126-134.

Chai, D.N.P. and Udarbe, M.P. (1977). The effectiveness of current silvicultural practices in Sabah. *Malaysian Forester* 40: 27-35.

Dawkins, H.C. (1958). The management of natural tropical high forest with special reference to Uganda. IFI Paper 34. IFI, Oxford.

Dirzo,R. and Miranda, A. (1990). Contemporary neotropical defaunation and forest structure. Function and diversity- a sequel to John Terborgh. *Conservation Biology* 4: 444-447.

Fearnside, P.M. (1989). Forest management in Amazonia: the need for new criteria in evaluating development options. *Forest Ecology & Management* 27: 61-79.

Fleming, T.H., Breitwisch, R. and Whitesides, G.H. (1987). Patterns of tropical frugivore diversity. *Annual Review of Ecology & Systematics* 18:91-109.

Food & Agriculture Organisation. (1991). *Second Interim Report on the State of Tropical Forests: Forest Resources Assessment 1990 Project*. FAO, Rome, Italy.

Freezaillah, C.Y. (1984). Lesser-known tropical wood species: how bright is their future? *Unasylva* 145: 2-16.

Gascon, C. (1993). Breeding-habitat use by five Amazonian frogs at forest edge. *Biodiversity and Conservation* 2: 438-444.

Graaf, N.R. de. (1986). *A Silvicultural System for Natural Regeneration of Tropical Rain Forest in Suriname*. Wageningen Agricultural University, the Netherlands.

Hammond, D.S., Gourlet-Fleury, S., Hout, P. van der, Steege, H. ter and Brown, V.K. (1996). A compilation of known Guianan timber trees and the significance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. *Forest Ecology & Management* 83: 99-106.

Hammond, D.S., Zagt, R.J., Gourlet-Fleury, S. and Rankin-de-Merona, J. (*in prep.*). 'Guianan forest dynamics: action and reaction in contemporary, historical and evolutionary time', in H.ter Steege and D.S. Hammond (eds.), *Tropical Rain Forests of the Guianas*. Kluwer Academic Press, Dordrecht, the Netherlands.

Harrison, S. (1989). Long-distance dispersal and colonization in the bay checkerspot butterfly. *Ecology* 70: 1236-1243.

Hooper, D.U. and Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science* 277: 1302-1305.

Irvine, A.K. and Armstrong, J.E. (1989). >Beetle pollination and comparisons in some tropical forests of Australia and America=, in K.S. Bawa and M.Hadley (eds.), *Reproductive Ecology of Tropical Forest Plants*. MAB Series, Unesco, Parthenon Publishing, Paris, France.

Jablonski, D. (1986). 'Causes and consequences of mass extinctions: a comparative approach', in D.K. Elliot (ed.), *Dynamics of Extinction*. Wiley Press, London, UK.

Janzen, D.H. (1985). *Spondias mombin* is culturally deprived in megafauna-free forest. *Journal of Tropical Ecology* 1: 131-155.

Johns, A.G. (1985). Selective logging and wildlife conservation in tropical rain-forest: problems and recommendations. *Biological Conservation* 31: 355-375.

Johns, A.G. (1992). 'Species conservation in managed tropical forests', in T.C.Whitmore and J.A. Sayer (eds.), *Tropical Deforestation and Species Extinction*. Chapman & Hall, London, UK.

Johns, A.G. (1997). *Timber Production and Biodiversity Conservation in Tropical Rain Forests*. Cambridge University Press, Cambridge, UK.

Jonkers, W.B.J. (1987). *Vegetation Structure, Logging Damage, and Silviculture in a Tropical Rain Forest in Suriname*. Wageningen Agricultural University, the Netherlands.

Jonkers, W.B.J. and Schmidt, P. (1984). Ecology and timber production in tropical rainforest in Suriname. *Interciencia* 9: 290-297.

Kavanagh, R.P. and Bamkin, K.L. (1995). Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biological Conservation* 71: 41-53.

Lande, R., Steinar, E. and Saether, B-E. (1994). Optimal harvesting, economic discounting and extinction risk in fluctuating populations. *Nature* 372: 88-90.

Laurence, W.F. and Bierregaard Jr., R.O. (1997). *Tropical Forest Remnants*. University of Chicago Press, London, UK.

Laurance, W.F. and Laurance, S.G.W. (1996). Responses of five arboreal marsupials to recent selective logging in tropical Australia. *Biotropica* 28: 310-322.

Leigh Jr., E.G. and Windsor, D.M. (1982). ‘Forest production and the regulation of primary consumers on Barro Colorado Island’, in E.G. Leigh Jr., A.S. Rand and D.M.Windsor, (eds.) *The Ecology of a Tropical Forest*. Smithsonian Institution Press, Washington DC, USA.

Leslie, A.J. (1987). A second look at the economics of natural management systems in tropical mixed forests. *Unasylva* 155: 46-58.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237-240.

McNeely, J.A. (1994). Lessons from the past:forest and biodiversity. *Biodiversity and Conservation* 3: 3-20.

Nault, L.R. and Ammar, E.D. (1989). Leafhopper and planthopper transmission of plant viruses. *Annual Review of Entomology* 34: 503-529.

Peres, C.A. (1994). Exploring solutions for the tropical biodiversity crisis. *Trends in Ecology & Evolution* 9: 164-165.

Piperno, D.R. (1994). Phytolith and charcoal evidence for prehistoric slash-and-burn agriculture in the Darien rain forest of Panama. *Holocene* 4: 321-325.

Rankin, J.M. (1979). Manejo florestal ecológico. *Acta Amazonica* 9: 115-122.

Redford, K.H. (1992). The empty forest. *Bioscience* 42:412-422.

Redford, K.H. (1993). ‘Hunting in Neotropical forests: a subsidy from nature’, in C.M. Hladik, A. Hladik, O.F. Linares, H. Pagezy, A. Semple and M. Hadley (eds.), *Tropical Forests, People and Food*. Parthenon Publishing/Unesco, Paris, France.

Regan, T. (1981). The nature and possibility of an environmental ethic. *Environmental Ethics* 3: 19-34.

Renner, S.S. and Feil, J.P. (1993). Pollinators of tropical dioecious angiosperms. *American Journal of Botany* 80: 1100-1107.

Roubik, D.W. (1993). Direct costs of forest reproduction, bee-cycling and the efficiency of pollination modes. *Journal of Biosciences* 18: 537-552.

Sayer, J.A., Zuidema, P.A. and Rijks, M.H. (1995). Managing for biodiversity in humid tropical forests. *Commonwealth Forestry Review* 74: 282-287.

Schulte, A. and Schöne, D. (eds). (1996). *Dipterocarp Forest Ecosystems. Towards Sustainable Management*. World Scientific, London, UK.

Smits, W.T.M. (1984). *Dipterocarpaceae: Mycorrhizae and Regeneration*. Tropenbos Series 9, the Tropenbos Foundation, Wageningen, the Netherlands.

Taylor, C.J. (1962). *Tropical Forestry*. Oxford University Press, Oxford, UK.

Terborgh, J., Lopez, L., Tello, J., Yu, D. and Bruni, A.R. (1997). ‘Transitory states in relaxing ecosystems of land bridge islands’ in W.F. Laurence and R.O. Bierregaard Jr. (eds.), *Tropical Forest Remnants*. University of Chicago Press, London, UK.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302.

Vitousek, P.M., Ehrlich, P.R., Ehrlich, A.H. and Watson, P.M. (1986). Human appropriation of the products of photosynthesis. *BioScience* 36: 368-373.

Wells, M.P. and Brandon, K.E. (1993). The principles and practice of buffer zones and local participation in biodiversity conservation. *Ambio* 22:157-162.

Whitmore, T.C. (1975). *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford, UK.

Whitmore, T.C. and Sayer, J.A. (eds). (1992). *Tropical Deforestation and Species Extinction*. IUCN, Chapman & Hall, London, UK.

Whitmore, T.C. and Brown, N.D. (1996). Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Phil.Trans. R. Soc. Lond. B*, 351: 1195-1203.
Wilson, E.O. (1988). 'The current state of biological diversity', in E.O. Wilson (ed.), *Biodiversity*. National Academy Press, Washington DC, USA.
Wood, T.K. (1993). Diversity in the New World Membracidae. *Annual Review of Entomology* 38: 409-435.
World Resources Institute. (1994). *World Resources 1994-5*. Oxford University Press, New York, USA.
Wyatt-Smith, J. (1963). *Manual of Malayan Silviculture for Inland Forests*. Malayan Forest Record No. 23. Forestry Dept., Kuala Lumpur, Malaysia.

BIODIVERSITY CONSERVATION AS A SUSTAINABLE FOREST MANAGEMENT TOOL

Challenges and Problems; Information Needs
- Small patches of intact forest surrounded by much larger areas of intensive exploitation rarely retain their conservation value, if the interstitial habitat is unsuited to forest species.
- There is no established framework for setting priorities in spcies conservation.
- Importance of plant-animal relations for maintenance of functional integrity of rain forests is little recognised.
- Biodiversity conservation is not truly integrated in forest manegement models.

Points for Future Research
- Research on trade-offs and assumptions underlying forest management models.

Conclusions
- The preservation of present-day biodiversity on ethical grounds, while noble, is counter-intuitive.
- Diversity of functional characteristics appears to be more important than diversity per se, which suggests that management should be aimed at maintenance of functional integrity of forests.
- Forest management should simultaneously optimise current and future values for commodities and services.
- Wildlife represents a future value in terms of regenerated timber species rather than a direct value in terms of meat.
- Dissemination and integration of research results should be jointly done by field researchers and a team with the specific task to translate information into management models.