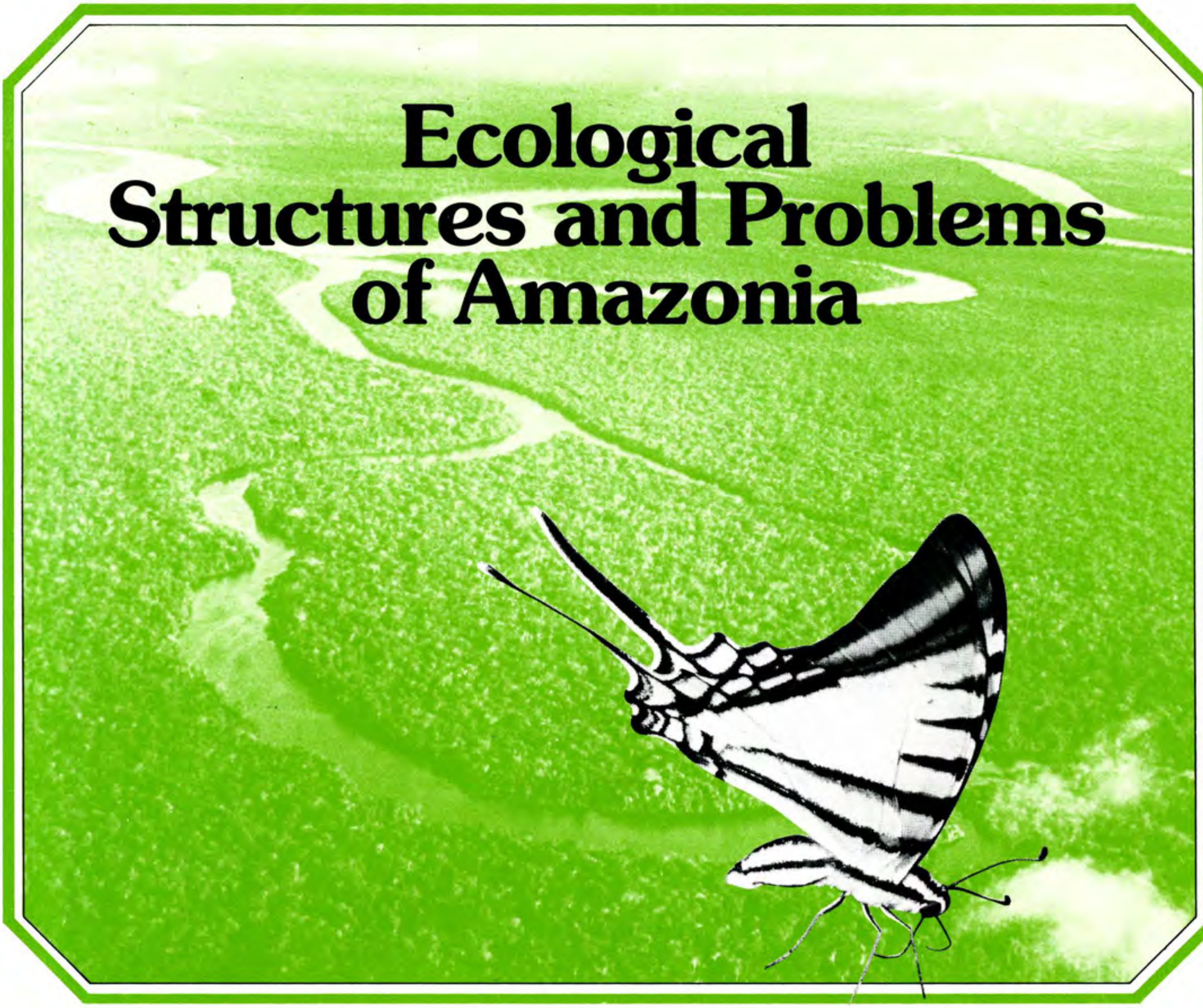
Ecological Structures and Problems of Amazonia



Proceedings of a Symposium organised by the Department of Biological Sciences of the Federal University of São Carlos, and the IUCN Commission on Ecology at São Carlos, Brazil, the 18th of March 1982

Commission on Ecology Papers Number 5

International Union for Conservation of Nature and Natural Resources

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1. Amazonia: A Challenge for the Future. Introductory Remarks

Conservation tends to be reactive. It is activated when there is an acute threat to natural resources which should be used but not abused. In these circumstances and particularly when there is some short-term gain, conservation is at a disadvantage. Conservationists must try to foresee threats and to act before it is necessary to react. This is one of the central issues of the World Conservation Strategy. It is a challenge which must be met with in respect of the tropical rainforest in its last big stronghold, in Amazonia.

Too much tropical rainforest has been lost already in the Old World tropics. Some tiny refugia of the tropical forests of Indonesia, Malaysia or Africa may survive in an island-like situation with the increasing demand for land in these overpopulated regions of the earth. It is questionable if continuous areas of tropical rainforest will remain. The policy of IUCN has been to react and try to save what might be set aside from the pressures on timber and land resources. This is an important task, of course, and the best people and organizations must cooperate to do everything possible. IUCN gave highest priority to the conservation of tropical rainforest. It continues to emphasise the need for more action and to seek increasing political power and pressure from the industrialized nations to prevent the nearly total destruction of this immeasurable resource of mankind. Looking at the pace of forest destruction there is only a faint glimpse of hope. Australia, a rich nation with a wealth of natural resources, has destroyed most of its tropical forest and is only now appreciating the need to preserve the remnants. How then should poor nations cope with the problem?

Perhaps the answer lies in the other half of the world. The New World tropics still harbour the most extensive tropical forest of the world, the Amazonian forest. Despite the increasing pressure in the marginal areas and along the major rivers, most of the 'Hylea' of Alexander von Humboldt exists in an untouched or only slightly modified natural state.

Amazonia offers an opportunity, which has gone for all other major ecosystems of the world except the polar ice caps, to initiate planned action before it is necessary to react. This is the challenge for the emerging economical and political power of Brazil, which owns the greatest part of Amazonia. The rational use of this vast region must also be met in other countries, Peru, Venezuela, Colombia, Ecuador and Bolivia.

The results of the Commission on Ecology Symposium "Ecological Structures and Problems of Amazonia" are brought together in this volume. The Symposium was an attempt to present a concise picture of what is known about the ecology of this region as well as special problems and features which have to be taken into consideration for immediate action and planning. This ambitious aim is an attempt by the IUCN/COE to sort out the relevant information from the huge amount of data available yet difficult to handle from a political or administrative point of view.

Information or data are not completely lacking, what is needed now is their proper application. Most of our experience on the sustained use of wet tropical regions originates from research in the Old World tropics. There the ecological conditions are quite different in many respects. Appropriate strategies for land use there may result in an abuse when applied to Amazonia. The failure of many large-scale development projects in Amazonia is a matter of history. The rubber story is well-known but not unique. Single species plantations worked quite well in South-East Asia but were disastrous in Amazonia.

In short, whilst some knowledge is available it is still too scanty, and much more research is necessary and indispensable if we are to understand the patterns and the functions of the Amazonian world of water and forest. Currently, we need to make a thorough inventory of the vast number of species and life forms and an analysis of functions and ecological processes, and to bring these together in a general synthesis.

Many scientists are trying to achieve this. Most are centered in the big research institute for Amazonia at Manaus, Brazil, the INPA (Instituto Nacional de Pesquisas da Amazonia). This institution, multidisciplinatory in its work and with an international staff, has the leading role in the general research of Amazonia. It has well trained scientists and proper field stations and as a result first rate scientific material is emerging from INPA studies. The research is published mainly in

◀ Rio Cuieiras, tributary of the Rio Negro, Central Amazonia (Photo credit: Dr E. J. Fittkau).

Acta Amazônica and in *Amazoniana* or *Biotropica*. A great deal of the research work is applied ecology. Second in size but comparable in importance is research in Venezuela in northern Amazonia; again well linked with international science.

In the light of this scientific effort the need for the COE Symposium may be questioned. The South American countries which participate in research in Amazonia of necessity predominantly center their scientific effort on aspects of the use and exploitation of the resources found in the region. This is understandable but it has to be recognised that Amazonia is more than the economic resource of a few nations. It is of international interest being the area with the greatest diversity of species and a genetic reservoir the global value of which cannot be measured. In cooperation with national representatives of conservation, like SEMA, IUCN must launch, on the basis of the World Conservation Strategy, regional strategies before it is too late. The Symposium, therefore, should provide some guidelines for the wise use of the natural resources of Amazonia recognising their global significance.

The proposals are not perfect in any sense. But they may be useful in places or helpful in the formulation of appropriate measurements and evaluations. The matter is too complicated intrinsically for simple and broad generalizations. But in a number of cases the dimensions of Amazonia will allow well planned large-scale experiments to solve the questions in time.

The structure of the symposium follows a broad ecosystem approach. The first three papers by Leopoldo Klinge and Jung deal with the hydrology, the forest and the rivers. These major elements of the Amazonian landscape, which is in fact an intrinsic network of waters and forests, are so predominant in importance, that most ecological processes are influenced by these components. An understanding of the interactions of forest and water is indispensable.

From the human point of view the special situations in which higher vertebrates made their living may provide some interesting insights. It is the scope of the papers of Reichholf and Fittkau to give an ecological explanation for the low density of bigger-sized, warm-blooded vertebrates in the Amazonian forest and why it never has been more than a transitional refugia for human beings.

The destruction of the forest and its replacement by open country had been the strategy of the early settlers up to recent times. Costa gives a comprehensive account of the various impacts of people on the forests of Brazil. The history of forest use and destruction is of interest. It is presented by him for the big marginal areas in Brazil, the area from which the most massive threat on the true Amazonian forests is exerted nowadays.

Lovejoy and Davidson give some practicable but still investigatory proposals for a rational use of the Amazonian forest as a renewable resource and formulate testable hypotheses. There is still space and time to act, but neither the Amazonian countries nor international organizations must wait any longer to start these actions to save the future of Amazonia, its animal and plant life—and last but not least its people.

A good beginning has been made by Brazil with the establishment of a network of 'Preserved Areas'. This network comprises national parks, biological reserves and ecological stations. The present situation is summarised at the end of this volume. In addition other areas are protected in Peru and Venezuela.

Nevertheless, the network is inadequate, for there are large gaps between protected areas outside of which total or nearly total destruction of all the forests may occur. Planned use of the forest resources without their destruction must be achieved. This involves sustained use on the base of the life spans of the trees, not the short-term gain of low productive grasslands. We have to explore now, how this sustained use can be achieved.

E. J. FITTKAU and J. H. REICHHOLF

2. The Hydrology of the Amazon Region

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Introduction

The Amazon Basin is a geographic region extending through almost all of the central-west of South America. It is the largest drainage basin of the world, with an area of about 5.8×10^6 km^2, or approximately 40% of the Continent. Of this total, 4.8×10^6 km^2 are located in Brazil amounting to about 52% of the country.

The borders of this basin are: in the south the 'Planalto Brasileiro', in the north the 'Planalto das Guianas' and in the west by the Cordilheira dos Andes. These have altitudes of approx. 700 m, 1000 m and 5000 m, respectively.

The principal river of this drainage basin is the Amazon River, with an annual outflow of 5.5×10^{12} m^3 (Oltman *et al.*, 1964). This volume corresponds to a mean discharge of 175 000 m^3/s and constitutes about 15% of the total fresh water in the world. The river flows across a vast plain with an altitude difference of only about 120 m in a length of 3400 km. The water discharge increases slowly from a minimum in late October or early November to a maximum in late May or early July.

The number of tributaries of the Amazon River is estimated to be 1100. About 20 000 km of the waterways are navigable for small and mean size ships.

The rivers of the Amazon Region have been classified as rivers of 'black water', 'white water', and 'clear water'. The rivers of 'black water' have a pH of 3.7 to 5.4 and are dark brown (marron-café), due to humic substance from organic material decomposition. 'Negro' is an example of this kind of river (Fig. 2.1). The rivers of 'white water' are yellow-brown in color, due to the transportation of considerable clay quantity in suspension. The rivers Amazon, Madeira, and others which originate in Cordilheira dos Andes are typical of this kind of river (Fig. 2.2). The 'clear water' rivers, represented by Xingu, Tapajós, Tocantins and others occur mainly in Central Brazil. They have received the name 'clear water' because their waters are limpid and transparent for some meters depth. They transport little sediment in suspension.

Amazon Ecosystem

Most of the Amazon Basin is occupied by the Amazonian rainforest, which is the greatest forest ecosystem of the world. In Brazil this forest covers an area of 3.6×10^6 km^2, corresponding to 42% of the Brazilian surface.

The Amazon forest ecosystem, although apparently homogeneous in appearance, is composed of various vegetation types (Table 1).

TABLE 1

Vegetation types and estimated areas in Brazil

Vegetation types	Area (km^2)
'Terra firma' forest (never flooded)	3 375 000
High Forest, with great biomass	3 050 000
Ligneous liane forest, in Tocantins and Xingu Region	100 000
Low forest, with little biomass	10 000
Dry forest, in transition areas	15 000
Others types of terra firme forest	200 000
'Varzea' and 'Igapo' forest	70 000
'Varzea' (temporarily flooded)	55 000
'Igapo' (always flooded)	15 000
Savannah on 'terra firma' (never flooded)	150 000
Amapa Region	17 000
Cachimbo-Cururu Region	15 000
Madeira Region	5000
Roraima Region	41 000
Trombetas-Para Region	45 000
Marajo Region	17 000
Other Regions	10 000

Other vegetation types represented by
savannah 'varzea' (ever flooded)
'campina', vegetation of mountains, in north borders of Amazon vegetation Basin of the littoral region.

In relation to the Amazon flora, currently more than 23 000 species have been classified and many more remain to be classified.

As to the fauna, the Amazon ecosystem is very rich, having an approximate composition, as follows:

- 35 families of mammals already catalogued.
- 1170 species of birds already classified with a total number estimated at about 1800.

Fig. 2.1. Example of 'black water'—Rio Negro (Photo credit: Dr E. J. Fittkau).

Fig. 2.2. Example of 'white water' with 'air' roots—Rio Napo, Ecuador (Photo credit: Dr H. Jungius).

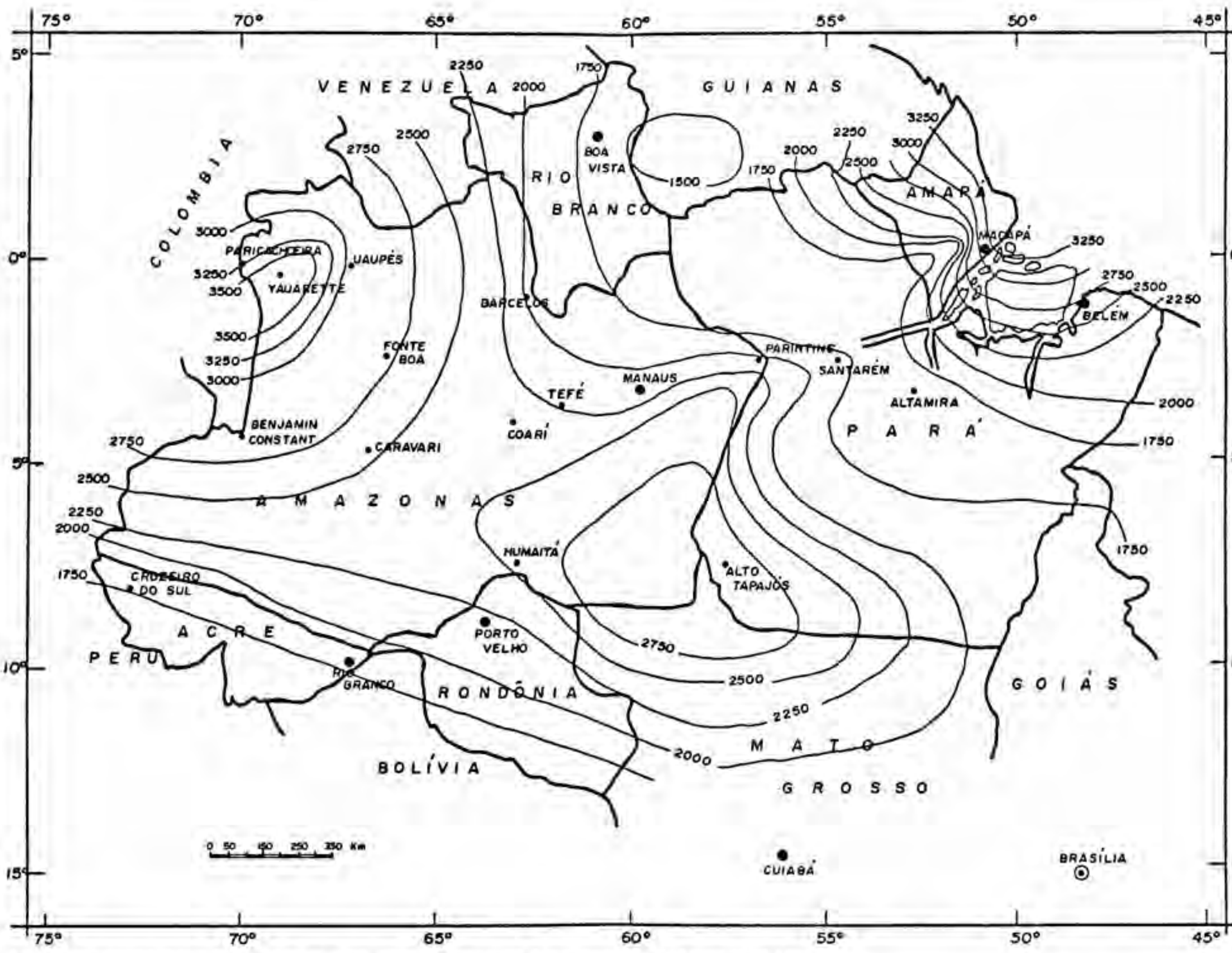

Fig. 2.3. Annual rainfall (mm) in the Brazilian portion of Amazonia, after Nimer (1977).

– 60 species of reptiles.
– 60 families of fish, with a total number of species estimated at about 2000. In comparison, the Mississippi river has only 250 species of fish and the Congo river about 1000 species.

With the opening of roads, followed by irrational deforestation it is clear that some animal and plant species will be made extinct.

Rainfall Distribution in the Brazilian Portion of Amazonia

The Amazon Region is characterized by a high rainfall over its greatest part. This wetness with high temperatures provides the necessary conditions for intensive photosynthesis and the development of dense forest. With respect to temperature, the region displays spatial and temporal homogeneity, with a small but relatively insignificant seasonal variation.

The region is less homogeneous with respect to precipitation (Fig. 2.3). Along the Atlantic Ocean Coast and in the occidental section of the region, rainfall exceeds 3000 mm/year, whereas in the Central Amazon Region it is not so high. Average monthly rainfall values for some sites in the Amazon Basin are given for various observation periods in Table 2. In some regions of the basin, there is a relatively dry period, usually from June to September or October.

The Hydrological Cycle of the Amazon Basin

Recently interest has increased in the hydrological cycle of the Amazon Basin and its forest because of the possibility that the water balance may be changed by intensive deforestation.

According to Villa Nova *et al.* (1976), the Amazon Basin receives by precipitation a mean volume of water of 14.4×10^2 m^3/year, and of this total, 5.5×10^{12} m^3/year are discharged in the Atlantic Ocean by the Amazon River. From this balance evapotranspiration is estimated to be 8.9×10^{12} m^3/year, corresponding to an average of 4 mm/day. Villa Nova *et al.* (1976) report that the actual evapotranspiration is approx. equivalent to the potential.

The Amazon forest plays an important role in maintaining the hydrological equilibrium of the region. According to Marques *et al.* (1977), the inflow of moisture from the Atlantic Ocean accounts for only 52% of the precipitation that falls in the region between Belém and Manaus, while the remaining 48% of rain is derived from water vapor evapotranspired within the basin by the forest. The basin is seen as acting as a source of its own moisture but also as bringing about rain through dynamic processes. In a period of the year, Marques *et al.* (1979), report an inversion of the flux vapor direction to the North–South direction, and suggest this moisture recharges the Platina Basin through precipitation. This observation is very important since the hydrological system of the Platina Basin seems to depend in part on the Amazon Basin.

Salati *et al.* (1979) and Dall'Olio (1976) observed that within the basin an important recirculation of water vapor occurs. The small inland gradient of the isotope composition of the precipitation confirms the importance of the re-evaporated moisture in the water balance of the area. Marques *et al.* (1979) found that the mean time of recirculation of water vapor is about 5.5 days.

The residence time of the runoff water at some hydrographic basins in the Amazon Region was studied by Gonçalves (1979) using isotopic composition. This author estimated that the mean residence time of water varies from 1.1 to 2.3 months.

Based on experimental data, Salati and Ribeiro (1979) believe that deforestation, among other things, will reduce the water residence time in the basin. They also conclude that a reduction of the precipitation of 10 to 20% will be enough to cause strong modification on the present ecosystem. The forest is also seen as playing an important role in returning directly part of the precipitation that falls in the region, since rain intercepted by the canopy is returned by evaporation to the atmosphere.

Jordan and Heuveldop (1981) carried out research in an Amazonian rainforest near San Carlos de Rio Negro, Venezuela, and they concluded that for an average yearly precipitation of 3.664 mm, throughfall was 87% of precipitation, stem flow 8%, transpiration 47% and interception by the canopy forest only 5%. The stem flow average of 8% of precipitation is a higher value than previously reported and the interception loss of 5% is less than other results for similar forests.

A study has recently been done by Franken *et al.* (in press) in the 'Bacia Modelo', in a representative plot of the Amazon forest of 'Terra firma' type, located 80 km from Manaus. The results showed that for a precipitation of 1.706 mm, the interception loss was 22%, precipitation reaching the floor forest as throughfall was 77.7% and stem flow was only about 0.3%.

The 'Bacia Modelo', in which some research by INPA is carried out, has an area of 23.5 km^2. The hydrological balance of this experimental basin has been calculated for the period from 02/02/80 to 10/02/81, by Leopoldo *et al.* (in press) (Table 3).

According to the previous reports, the forest is very important in the maintenance of the hydro-

TABLE 2

Average monthly rainfall in mm for sites in the Amazon Basin

Site	Observation Period	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Altamira	1961-1973	223	241	344	269	204	95	81	22	22	33	46	130	1.710
Alto Tapajos	1931-1960	408	375	434	185	128	26	11	33	138	235	315	329	2.717
Barcelos	1931-1960	172	145	174	256	276	234	169	118	105	118	111	125	1.999
Benjamin Constant	1951-1960	340	280	350	280	210	140	120	140	200	220	250	280	2.810
Carauari	1961-1977	330	173	227	336	245	152	89	157	186	230	310	269	2.704
Coari	1931-1960	315	274	280	283	226	134	88	75	99	158	188	222	2.347
Fonte Boa	1931-1960	298	237	278	336	314	238	175	149	150	194	186	247	2.802
Humaitá	1962-1973	261	277	219	250	163	54	21	60	107	184	255	283	2.234
Yauretê	1931-1960	259	246	295	363	389	356	350	278	266	237	227	237	3.503
Macapá	1968-1973	256	325	394	291	349	208	173	99	56	15	66	147	2.379
Manaus	1931-1960	276	277	301	287	193	98	61	41	62	112	165	228	2.101
Parintins	1961-1973	250	279	324	356	346	200	112	88	41	77	142	161	2.376
Porto Velho	1961-1973	265	307	283	254	134	39	27	42	111	186	222	288	2.158
Rio Branco	1969-1973	202	252	227	175	99	31	28	48	88	154	226	236	1.766
Santarém	1931-1960	179	275	358	362	293	174	112	50	39	46	85	123	2.096
Tefé	1970-1973	220	213	289	299	229	166	221	102	117	128	177	160	2.321
Uaupés	1931-1960	274	250	285	267	317	250	246	195	148	173	202	305	2.912

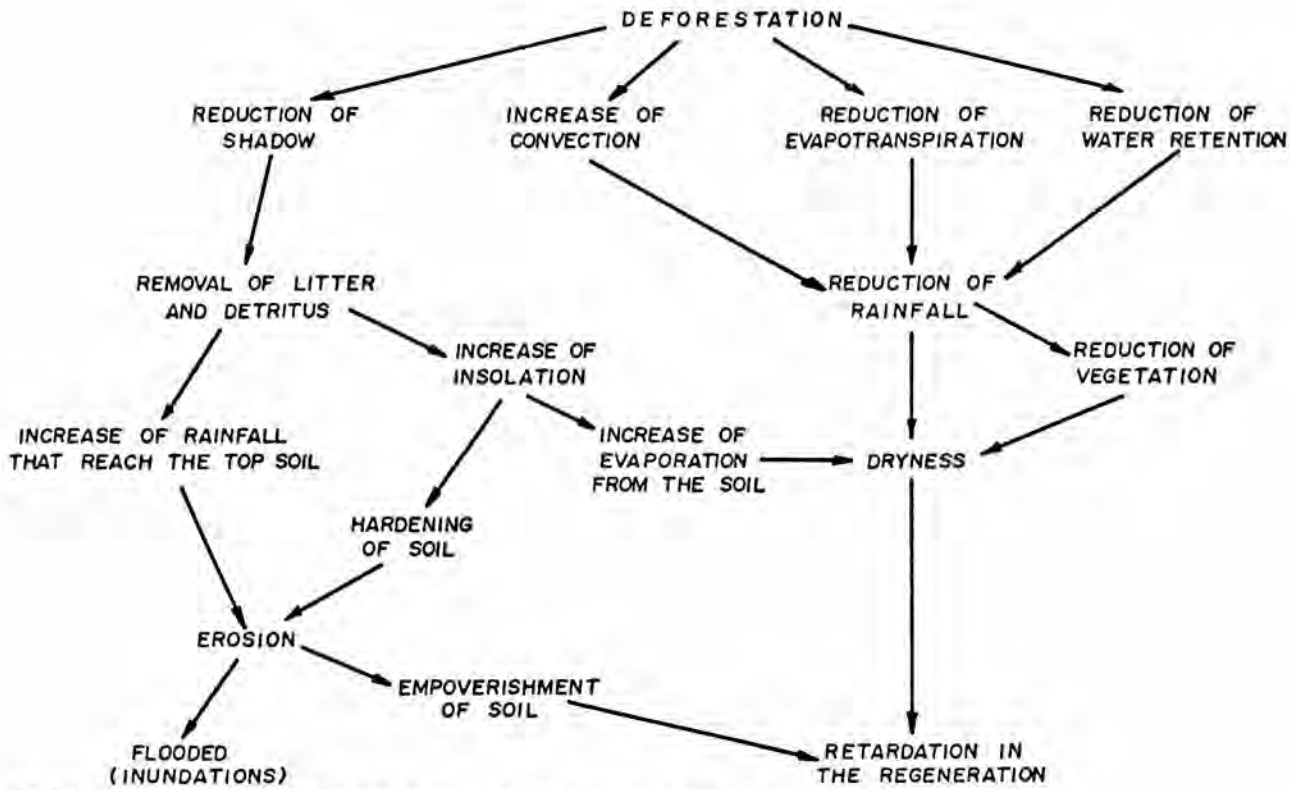

Fig. 2.4. Ecological disturbances that may be caused by deforestation, after Goodland and Irwin (1975).

TABLE 3

Hydrological balance of 'Bacia Modelo'

	mm	%
Precipitation	2088.9	100
Interception	533.9	25.6
Runoff	540.7	25.9
Transpiration	1014.3	48.5
Evapotranspiration*	1548.2	74.1

*Evapotranspiration assumed to be interception plus transpiration.

logical equilibrium of the region and discharges into the atmosphere considerable quantities of water vapor by evapotranspiration.

Goodland and Irwin (1975) observed that an intense destruction of the forest might cause serious and irreversible ecological disturbance with strong modification of the interaction of the water and the environment (Fig. 2.4).

This region has not been intensively studied and is in its initial phase of exploitation by man. Adequate and rational exploitation depends on basic studies to avoid serious and irreversible disequilibrium arising from different causes. Clearly there is a need to gather the greatest amount of information about the Amazonian forest ecosystem. This could establish a model for the use of land and natural resources according to the local ecological reality.

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3. Forest Structures in Amazonia

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Introduction

The international literature dealing with tropical rainforest in both the paleo- and neotropics is tremendously voluminous. The literature on neotropical rainforest alone comprises hundreds of titles of publications varying in both length and quality. It was compiled partially by Klinge (1983a).

Equalling volume with content, the many titles suggest that the Amazon rainforest is almost exhaustively studied. Well edited books containing marvellous colour photographs (Sterling, 1974; Fisher, 1979; Baumann-Patzelt, 1980) seem to confirm this view. A closer look into the literature reveals however that this view is misleading. Most of what is known about the Amazon rainforest falls into the area of architectural structure including floristics, while serious studies of the functioning of neotropical rainforest ecosystems are extremely scarce.

The limitations of the present knowledge about the functioning of these ecosystems are well documented (Unesco, 1978). Considering South America we have described the situation in a paper (Brünig and Klinge, 1975) and for the state-of-knowledge report on tropical forest ecosystems (Unesco, 1978). Characteristic for the situation are also calls for ecosystem research in neotropical rainforest (Jordan and Medina, 1977; Prance, 1977a; Sioli, 1977; Unesco, 1978; Nat. Res. Counc., 1980; among others). The urgent need for such studies is also evident from the fact that these studies have top priority in Unesco's 'Man and the Biosphere' Programme (Batisse, 1980; di Castri *et al.*, 1981; Unesco, 1981a).

Nevertheless, considerable progress has been achieved in the general understanding of neotropical rainforests. This becomes evident when comparing the relevant chapters in the classic textbook on tropical rainforest (Richards, 1951) to those in 'The forests of South America' (Hueck, 1966) and the 'State of Knowledge Report' (Unesco, 1978), respectively, and to Goodland and Irwin's (1975) book.

Why do we need to study rainforest ecosystems and functioning?

Exclusively the comprehensive, holistic approach to the study of ecosystems as parts of the biosphere may provide the information on their organization and functioning (Unesco, 1970), one of the functions of particular interest to man being productivity.

Where the information is available man-made ecosystems may be designed which imitate nature and are adapted to the specific site conditions and correspond to man's needs. If it is known how a natural ecosystem is organized and functions in the long term, its reaction to disturbance or man's interference may be predicted (Fränzle, 1978). Thus, a sound basis for planning development and conservation programmes (Alvim, 1977) is provided and ecological guidelines for development may be set up (IUCN, 1975).

Man has begun to interfere in the tropical rainforest biome by large-scale deforestation to meet various human needs (Richards, 1977). This is happening to an extent that the biome as such is endangered (Myers, 1980). The tropical rainforest biome should be studied using the ecosystem approach. This is particularly true for the largest tropical rainforest formation, *i.e.*, the tropical rainforest in South America or A. v. Humboldt's hylea (Goodland, 1980).

Ecosystem Research

Ecosystem research in tropical rainforest in general began during the execution of the International Biological Programme. Examples are Pasoh forest/Malaysia (*Malay. Nat. J.*, 1978) and Tai forest/Ivory Coast (*La Terre et la Vie*, 1975; Dosso *et al.*, 1981). Both projects are being continued as Man and the Biosphere projects. Projects in South America were also started under the auspices of MAB. Examples are ECEREX project/French Guyane (Aubert, 1977; Bull. Liaison, 1979), Kabo project/Surinam (CELOS, 1981) and San Carlos de Rio Negro project/

Venezuela (Brünig *et al.*, 1977; Medina *et al.*, 1977; Herrera *et al.*, 1978a, 1981, in press). Some projects were initiated independently from both international programmes, like El Verde project/ Puerto Rico (Odum and Pigeon, 1970), Manaus forest project/Brazil (Fittkau and Klinge, 1973), Panama project (Golley *et al.*, 1975; Golley and Richardson, 1977) and a comparative study of tropical mountain forests including Carribean islands (Edwards and Grubb, 1977; Grubb and Tanner, 1976; Tanner, 1977, 1980).

The following few examples have been selected from different areas in order to emphasize the importance of ecosystem-related research in the Amazon Region to provide ecological understanding.

The first example is taken from research into the global carbon cycle (Bolin *et al.*, 1979; Stein, 1981; Unesco, 1981b; Degens, 1982). It is expected that cutting the rainforest and the subsequent burning of the forest biomass or its decay will release considerable amounts of CO_2 into the atmosphere and so cause drastic changes of the earth climate. However, the actual standing store of forest biomass is known for only a few Amazon lowland localities (Cannell, 1982). The biomass amounts vary, particularly regarding the underground fraction (Klinge and Herrera, in press). The role of carbon fixation by rapidly growing secondary plant communities established on former forest soil, in relation to the CO_2 issue, has been studied even less (Uhl *et al.*, 1982). In addition, there is no reliable estimate of carbon export via the rivers to the sea (Degens, 1982). In short, the Amazonian data to be used in the computation of the global and regional carbon cycles are scarce.

The second example is related to the potential agricultural productivity of the Amazon Region and the humid tropics in general. It was originally believed that this region could provide shelter and food for a much more numerous human population. The natural productivity was much overestimated. Only a few years ago, Weischet (1977) demonstrated that the humid tropics as a whole are ecologically restricted (Golley and Jordan, 1980). Recently, the development of productivity systems was begun by imitating the natural forest ecosystem in putting together a variety of utilizable plant and animal species (agroforestry systems, Heuveldop 1980a). An example from Ecuadorian Amazonia is the one Bishop (1978, 1980) has developed using the reliable experience of local Amerindians.

The third example demonstrates the impact of the forest on the climate of Amazonia. Salati *et al.* (1978) have shown that about 50% of the rain falling over Amazonia is derived from the evapotranspiration of its vegetation, predominantly tropical rainforest. Jordan and Heuveldop (1981) have confirmed this value from a local study in southern Venezuela. Large-scale deforestation in Amazonia will automatically lead to an alteration of the rainfall regime, to a change of the discharge rate of the rivers and, finally, to a change of water output into the ocean (Fränzle, 1976; Sioli, 1980a, b).

The last example is the Jari project (Palmer, 1977; Fearnside and Rankin, 1979; Greaves, 1979; Goodland, 1980; McIntyre, 1980) (Fig. 3.1). In common with previous schemes (Zona bragantina colonization scheme, Ford rubber plantation, Russell, 1942; Sioli, 1969) it failed. The failure is attributed to bureaucratic, administrative and political constraints, but not to ecological ones (Irion, 1981; Kinkead 1981, *Financial Times* 1982, January 8; *Time* 1982, January 25, p. 49). The failure of the expensive large-scale planting of exotic tree species for pulp production and rice may be considered as a proof of nature's potence. 'In the end, not even a billionaire had enough resources alone to tame the jungle by himself' (*Time,* 1982). Ecosystem research carried out prior to cutting the forest and planting crops would have helped in guiding the planning of the exercise and resulted in the saving of the forest and much money.

Diversity of Amazon Forests

The present knowledge of Amazon forests is based on a wide network of research localities of mostly limited extent and on a few large-scale inventories performed in Brazil, Guyana and Venezuela mostly by FAO (Soares, 1970; Somberg *et al.*, 1973; Brünig and Klinge, 1975; Palmer, 1977). In addition, there are the inventories of natural resources of the Amazon territories of Brazil and Colombia, by the RADAM and PRORADAM projects.

Although being far from perfectly understood, some general conclusions can be made about the ecology of the Amazon (Klinge, 1982b). This is particularly true for the freshwater. Terrestrial ecology of Amazonia is less developed but the Amazon forests are known to differ according to climate, topography, hydrology and soil. The ecological differences are reflected by the phytogeography of the forest species (Ducke and Black, 1953; Hueck, 1956, 1966; Rizzini, 1963; Prance 1977b, 1978).

According to the hydrological conditions in the lowlands, two major groups of forest types are

(a)

(b)

Fig. 3.1. 'Forest' ranch (1 200 000 ha) of Daniel Ludwig in Jara, Amapa, Brazil. (a) Railroad complex on very poor soils, (b) deforestation is done by hand. (Photo credit: WWF/Gerardo Budwoski.)

distinguished: inundation forests and terra firma forests (Pires, 1973, 1974; Prance, 1978, 1979; Hueck and Seibert, 1972; Sternberg, 1975; Palmer, 1977; Klinge *et al.*, 1981). The subdivision into floodable and non-floodable land, respectively, is much too general to provide a reliable basis for developmental planning on a regional scale (Moran, 1981), since each major forest type comprises a series of individual types on specific sites and ecological conditions.

Freshwater inundation forests

The local inhabitants distinguish between várzea forests and igapó forests (Aubréville, 1961; Sioli, 1964, 1965; Junk, 1975; Sternberg, 1975). The popular terminology lacked a scientific basis until Irmler (1977, 1978a) and Prance (1979, 1980) defined várzea forests as flooded by rivers carrying turbid and relatively nutrient-rich water, whilst igapó forests are flooded by clear and nutrient-poor water which may be humic-stained (blackwater, Klinge, 1967). In the meantime, limnologists and water chemists have defined the water quality chemically (Furch 1976, in prep.; Furch and Klinge, 1978; Furch and Junk, 1980; Furch *et al.*, 1982; Sioli, 1964, 1965, 1968; Gibbs, 1967, 1970, 1972; Stallard, 1980).

As judged from the small number of botanical studies carried out in inundation forests (Pires and Koury, 1959; Rodrigues, 1961; Takeuchi, 1962; Keel and Prance, 1979; Revilla, 1981; Klinge *et al.*, 1983), flora and vegetation of inundation forests are imperfectly known. Less known are the respective ecosystems. Generally, inundation areas in Amazonia and elsewhere in the tropics have been much neglected (Junk, 1981), although they are a very attractive subject for aquatic biologists and ecologists as well as for their terrestrial counterparts.

Among the initial attempts to analyse inundation forest ecosystems are the estimation of litterfalls (Adis, in press a; Adis *et al.*, 1979) and the studies of litter decomposition (Irmler and Furch, 1979, 1980). Relying on these results and his field experience, Irmler (1979) designed a model of the ecosystems várzea and igapó forests and issued a nitrogen balance of the igapó forest (Irmler, 1982). Locally, the invertebrate fauna has been studied intensively (Irmler, 1975, 1976, 1978b, c, 1981; Beck, 1976; Junk, 1976; Adis 1977, in press b).

In further subdividing the inundation forests, the mean expectation of both the duration and height of flooding may be helpful. Nutrient poverty of both the igapó forest soil and the water flooding this type of forest suggests the existence of nutrient stress (Williams *et al.*, 1972) which is reflected in the size, anatomical structure and chemical composition of the leaves (Klinge *et al.*, in press). The leaves are essentially sclerophyllous (Medina, 1981, in press).

The imperfect knowledge of the ecology of inundation forests is evidenced by the fact that it is not known how evergreen igapó leaves survive the period they are immersed in the river water (Gessner, 1958, 1968). Pneumatophores being absent, Worbes (1983) is studying the growth periodicity of boles.

Terra firma forests

The term Amazon rainforest, when popularly used, refers generally to the terra firma forest (Fittkau, 1973; Beck, 1974). Its scientific denomination is 'dense humid evergreen forest of plains' (Rollet, 1974). It occurs on well drained sites above the high water line of the rivers and also locally on wet or swampy sites in depressions or along water courses within the terra firma. While on dry sites stemless palms are abundant in the undergrowth, tall palms are conspicuous on wet sites (Takeuchi, 1960).

Terra firma forests are extremely species-rich evergreen broadleaved forests (Prance *et al.*, 1976; Kubitzki, 1977; Lamprecht, 1977; Anderson and Benson, 1980). The area they cover is much more extensive than the inundation forest area. They are probably not uniform in terms of structure and floristic composition whilst on the basis of nutrient status they represent different types of ecosystems.

Differences in the nutrient status of the terra firma forests are suggested by the heterogeneity of the soils (Sombroek, 1966; Wambeke, 1978) and soil-forming rocks. Soft rocks (sands, sandy clays) are more widespread in the lowlands than hard rocks (Fittkau, 1974; Putzer, in prep.). The chemical heterogeneity of the terra firma is also reflected by the differences in freshwater chemistry previously referred to.

The nutrient status of the terra firma forest ecosystems merits particular attention. Jordan and Herrera (1981) have clearly shown that tropical rainforest occurs along a nutrient gradient with oligotrophic representatives at one end. This is also true for Amazon terra firma forests considered as fragile ecosystems (Farnworth and Golley, 1974). They seem to occupy mostly the oligotrophic end of the gradient. The regional geochemical differences in the Amazon Basin were used by Fittkau (1971a, b) to subdivide it into 4 geochemical provinces. Except for one, they are considered geochemically and chemically very poor. This confirms the concept developed by Weischet (1977) that the humid tropics in general present disadvantageous conditions regarding nutrients.

The increase of annual precipitation towards the northwest (Walter *et al.*, 1975; Salati *et al.*, 1978, Fig. 2) which is coupled to the transition from a more seasonal to a permanent humid climate, makes probable a differentiation of the forest cover from more seasonal forests in the southeast to aseasonal ones in the northwest.

Based on the amount of biomass and its composition, biomass-rich tall terra firma forests, palm- or climber-rich forests as well as low biomass edaphic forests occur (Pires, 1974, 1976, 1978; Pires and Prance, 1977; Klinge and Herrera, in press). Rizzini (1963) lists the edaphic forests as sclerophyll forests (Amazon Caatinga and campina on quartz-sandy soil, Anderson 1981). Associated with the latter forests are low woodlands which partly resemble Amazon savanna (Pires and Rodrigues, 1964; Lisboa, 1975; Klinge and Herrera, 1977; Cooper, 1979; Klinge and Medina, 1979; Sobrado and Medina, 1980; Garcia *et al.*, 1980; Huber, 1982; Bongers *et al.*, in press).

Central Amazon forest at Manaus

The forest in the vicinity of Manaus, Brazil, can be regarded as the first studied terra firma forest (Fig. 3.2). The flora, biomass, structure and nutrient status have been investigated (Lechthaler, 1956; Takeuchi, 1961; Rodrigues, 1967; Klinge, 1973a; Klinge and Rodrigues, 1974; Klinge *et al.*, 1975; Brünig and Klinge, 1976; Prance *et al.*, 1976; Klinge, 1977; Alençar *et al.*, 1979).

When harvesting the aboveground biomass in an area of 2000 m^2 the total phytomass of about 500 t ha^{-1} (dry matter) was found to be derived from 502 tree species varying in height between 1 and 40 m (Klinge, 1973b). Among these were 62 legumes, 43 sapotaceous species, 40 species of the Lauraceae, 38 species of the Chrysobalanaceae, 32 species of the Rubiaceae, and 27 burseraceous species. The richness in legumes is typical for the terra firma forest (Takeuchi, 1960). However, no species of this or any other family is dominant in terms of basal area or phytomass. A biomass dominance is exclusively observed in Amazon Caatingas and related forest types (Richards, 1957; Klinge, 1978a, b; Klinge and Herrera, in press).

Total biomass amounts of between 300 and 500 t ha^{-1} are reported also for other terra firma forests (South Venezuela: Jordan and Uhl, 1978; Klinge and Herrera, in press; Surinam: Ohler, 1980; French Guyane: Lescure *et al.*, in press). While the root amount is usually equivalent to less than 20% of the aboveground dry weight (Cannell, 1982), the percentage is strikingly greater in the Amazon Caatinga and woodland on poor sands (Klinge and Herrera, 1978, in press; Bongers *et al.*, in press). The animal biomass of the Manaus forest was estimated as 200 kg ha^{-1} (fresh weight) by Fittkau and Klinge (1973).

The Manaus forest has some layering and emergents are absent (Rodrigues, 1963; Brünig and Klinge, 1976). The undergrowth is much richer in species than the upper layers and there is no continuous herb layer. The 4-year average annual leaffall, which is classified as evergreen seasonal forest, is 6 t ha^{-1} (Franken *et al.*, 1979). Maximum leaffall occurs in the dry season Klinge and Rodrigues, 1968a). The mineral nutrient content of the litterfall is comparatively low, except for nitrogen (Klinge and Rodrigues, 1968b). The living biomass was also relatively low in mineral nutrients (Klinge, 1976a; Golley *et al.*, 1980). The bulk of sodium, potassium, magnesium and calcium of the forest–soil system was immobilized in the plant biomass. The root biomass contained much greater mineral nutrient amounts than the rooted soil (Klinge, 1976b).

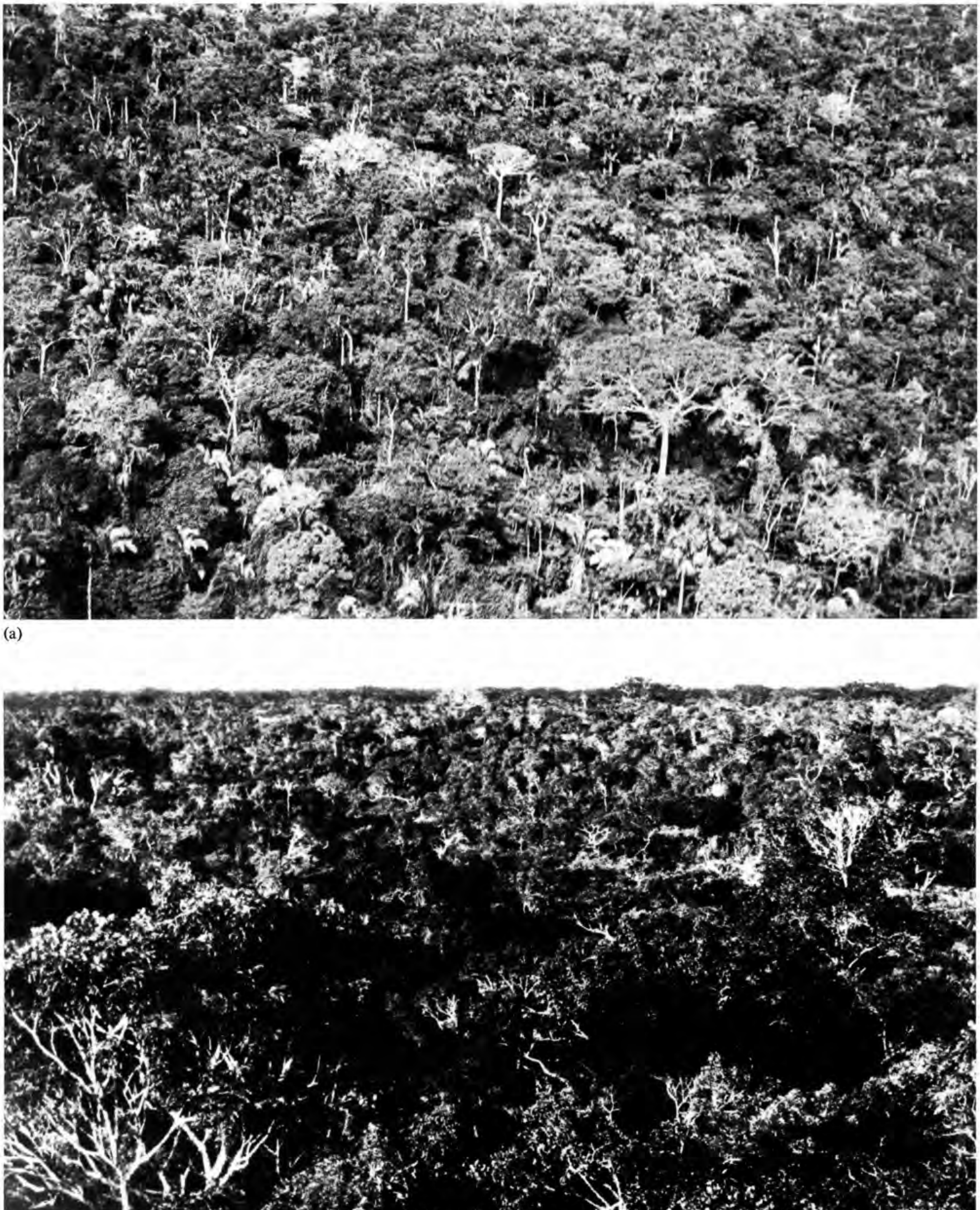
Attempting to explain the high forest biomass accumulated on a nutrient-poor soil, Klinge and Fittkau (1972) put forward the hypothesis that the ecosystem functions as a filter of nutrients imported via rainfall (Ungemach, 1971; Anon., 1972). One observation which lead to the hypothesis is that the roots are mostly superficial (Klinge, 1973b). The efficiency of the filter system in scavenging nutrients from the rain and to use them conservatively within the ecosystem, was indicated by the low nutrient content of the creeks draining the forest site. A relatively high productivity of 18 t ha^{-1} yr^{-1} (leaf fall times 3) was derived from the leaffall (Murphy, 1975).

Terra firma forests of Southern Venezuela

The nutrient poverty of most Amazon waters was originally interpreted by the water chemists in terms of a low nutrient status of the soil cover in the catchment. The expected low soil nutrient status was held responsible for the low productivity of shifting cultivation plots which usually were abandoned after 2 to 3 years. The results of the Manaus study did not conflict with these views.

In order to confirm the nutrient filter hypothesis for terra firma forest on nutrient-poor soil, an ecosystem study including input and output analyses was needed. Such a study was carried out in the upper Rio Negro Basin, near San Carlos de Rio Negro/Venezuela (Medina *et al.*, 1977). Results have been published in some 100 papers partially listed in Brünig *et al.* (1977, 1979). More comprehensive reports were published by Herrera *et al.* (1978a, 1981, in press).

The published data refer to a terra firma forest on well-drained oxisol and a Tall Amazon Caatinga on periodically waterlogged spodosol. Together with a terra firma forest on ultisol and woodland on quartz sand, the forest and soil types account for the soil–vegetation pattern of the study area.



(a)

(b)

Fig. 3.2. Terra firma forest (a) Central Amazonia, (b) Manaus, Brazil (Photo credit: Dr E. J. Fittkau).

Fifty-two percent of the annual rainfall (equal to about 3600 mm) is evapotranspired and an amount of water equivalent to 1770 mm rainfall passes through the ecosystem (Jordan and Heuveldop, 1981; Heuveldop, 1980b). During the passage, rainwater nutrients are transferred to the surface of the forest trees, i.e., to the foliage, bark and epiphytic organisms living on the surfaces.

When the water finally reaches the forest floor, it is strongly impoverished (Jordan *et al.*, 1980; Jordan, in press). Thus, the San Carlos forests are also systems filtering the rainwater nutrients.

In addition to the scavenging of nutrients from the rainwater, several ecosystem properties were observed directly or deduced from the results of measurements of water and nutrient fluxes which are interpreted as nutrient retention mechanisms. Also called nutrient conserving mechanisms they contribute to the protection of nutrients against leaching losses. Among them is particularly conspicuous a very superficial and dense root mat. In the oxisol forest it is developed on top of the mineral soil, accounting for below 20% of the aboveground dry biomass. In the spodosol forest the root mat is developed in the top mineral soil which is very rich in organic matter. It accounts for 18 to 59% of the aboveground dry forest biomass. The percentage is even higher in the woodland. The root mat consists of fine to very fine roots, mostly feeder roots, associated with mycorrhizal mycelium. While Herrera *et al.* (1978b) have demonstrated for phosphorus in the oxisol root mat that this element is taken up by the mycelium attached to leaves of the litter layer and channelled directly into the roots, Cuevas and Medina (1982) have shown in the same forest that this pathway also exists for other nutrients. Thus, the 'direct nutrient-cycling hypothesis' (Went and Stark, 1968a, b) between dead leaves and roots has been confirmed.

Other nutrient conserving mechanisms are associated with the foliage. The evergreen, sclerophyllous leaves may contain increased amounts of polyphenols. Their nutrient levels are low, particularly so in nitrogen and phosphorus. Leaves are relatively small which is reflected by the Leaf Area Index of 5 in oxisol and spodosol forest. The hard leaves are unattractive for herbivores, so that generally little frass is produced.

While the oxisol forest does not tend to single-species dominance, this tendency is marked in the spodosol forest indicating the non-optimum conditions of the sandy sites (Richards, 1957). Compared to other Amazon and tropical forests, the aboveground productivity of the San Carlos forests is low. Root productivity however is high, particularly in the spodosol forest.

Nutrient loss of the ecosystem to the streamflow is almost in equilibrium with nutrient input in the rainfall. Thus, the forest ecosystems as such make a conservative use of the nutrients provided by the rainfall.

Conclusions

The Amazon Region is the domaine of tropical rainforest. The urgent need for ecosystem research in natural forests has been identified as a tool for the study of the biosphere and its components. Such research will provide a more adequate insight into the structure and functioning of the ecosystems and the knowledge gained can be used in planning ecologically sound development and in its execution (Schubert, 1977). Emphasis was given to the terra firma forest, specifically to terra firma forests in southern Venezuela where ecosystem research has been carried out.

Soil scientists, ecologists, agronomists and foresters are aware that large tracts of the Amazon Region are poor in nutrients and possess soils of low natural fertility. Soils of better quality also exist. While the research carried out in southern Venezuela contributes much to the understanding of forest structure and functioning in nutrient-poor sites (Golley, 1981) and may, in addition, be extrapolated to similar sites elsewhere in the region, there is an absolute lack of knowledge concerning forest ecosystems on soils of better nutrient status. The latter should receive high priority for investigation.

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4. Aquatic Habitats in Amazonia

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Introduction

The Amazon river and its tributaries are the greatest river system on earth. High yearly precipitation rates, between 2000 mm and 3000 mm in most parts of the catchment area, result in a mean discharge of the Amazon of 175 000 m^3 per s (without Rio Tocantins). This discharge is more or less one sixth of the total discharge of all rivers on earth to the oceans (Oltman *et al.*, 1964; Sternberg and Parde, 1965; Oltman, 1967). Considering a catchment area of about 7 000 000 km^2, the number and variety of waterbodies is very large. It is of interest to group these into a small number of categories, based on important characteristics, to facilitate the work of ecologists.

Tentative classifications have already been made, using various criteria such as hydrochemical, production-biological and biological parameters. However, most refer to some specific waterbodies only, or are based on criteria which do not show the great variety of aquatic habitats found in Amazonia. These attempts will be discussed later and an additional approach will be proposed based principally on hydrological and morphological criteria, having a decisive influence on the limnology and using easily identifiable units. These units are not necessarily in the same ecological order of precedence; some are easily-defined as habitats whereas others have to be considered as a complex of habitats or even as ecosystems.

Based on this classification, our state of knowledge about frequency, distribution and ecology of the different units established will be discussed and reference made to some of the extensive literature. Furthermore, human impact and their vulnerability to it will be evaluated. This tentative classification does not claim to be complete or even generally accepted but because of the limited state of knowledge about aquatic habitats in Amazonia, it should serve as a basis for discussion.

Existing Attempts of Classification

Physico-chemical Classification

The first attempt to classify Amazonian waterbodies was based on differences in water colour. Names like Rio Preto, Rio Branco, Rio Verde indicate that this type of differentiation has been used by the people for centuries. Sioli (1950, 1965) established three different 'water types', based on water colour and physico-chemical parameters: 'White water' is rich in inorganic suspensoids, is turbid and has a pH value of about 7. The concentration of dissolved minerals is relatively high. 'Black water' is rich in dissolved humic substances, has a dark brownish colour and is transparent. The pH value is extremely low, about 4. The concentration of dissolved minerals is very low. 'Clear water' is greenish and transparent, the pH value ranging between very acid and neutral. Concentration of dissolved minerals may range from very low to relatively high.

The transition between these water types is fluent. Recent studies (Furch, 1976; Furch and Klinge, 1978; Junk and Furch, 1980; Furch *et al.*, 1982) show that white water is a carbonate water with a high percentage of alkali-earth metals, whereas black water is a non-carbonate water with high percentage of alkali metals. Clear water generally is non-carbonate water, but may be carbonate water, as well, for example in carboniferous areas. The classification of Amazonian waters by hydrochemical parameters is not yet satisfactory. Detailed studies, already underway, will increase our knowledge considerably in the next years, and will possibly allow more detailed correlation between the geology of the catchment area and the hydrochemical conditions in the water. Such a classification has to be considered as a very important contribution to the definition of aquatic habitats and ecological niches in Amazonia.

Biological Classification

Attempts at biological classification are only beginning and are partly based on physico-chemical classifications. From the point of view of production biology, Amazonian waters can be classified as highly productive, medium productive and low productive; since they are autochthonous primary production is the basis for this division. It corresponds to the hydrochemical classification of Sioli (1950). White water is of high productivity, clear water of medium to low productivity and black water of low productivity (Sioli, 1968; Schmidt, 1973b, 1976, 1982). Fittkau's ecological division of the Amazon basin (1974) is based on this classification.

However, there exist great differences in primary productivity, even under hydrochemically equal conditions, because other factors influence production rates. Light, for example, may be the limiting factor in strongly shadowed forest creeks, whereas it is not in savannah creeks. Heavy turbidity and water colour have a strong influence on phytoplankton production. How far primary production rates correspond to secondary production is not yet sufficiently known. Food webs may be based on allochthonous material. This has been shown for the fauna of extremely nutrient-poor forest creeks of Central Amazonia. The fish fauna is astonishingly well represented, terrestrial insects and plant material forming much of its diet (Knöppel, 1970; Soares, 1979).

For the big rivers this classification in very general terms works. Additional investigations are necessary and complete fisheries statistics of the principal parts of the Amazon will improve our knowledge.

Characterisation of waterbodies by key organisms is not yet possible. However, Sioli (1953) indicates that hydrochemical parameters like low pH values and/or low concentrations of dissolved minerals, principally lack of alkali-earth metals in black water and in some clear waters, have impacts on the distribution of molluscs. Geisler *et al.* (1971) and Roberts (1972) indicate possible eco-physiological impacts of the hydrochemical conditions on the fish fauna, and Junk (1970) does this for some aquatic macrophytic communities.

Reiss (1976b, 1977) discusses a characterization of central Amazonian lakes in respect to the macrobenthos fauna, whereas Rai and Hill (1980) use microbiological and physio-chemical characteristics. Actual studies in the floodplains indicate that a classification of habitats may be possible based on the fish fauna. Species composition is strongly influenced by several factors, for instance food availibility, shelter and current. A very important factor seems to be oxygen concentration which depends on lake morphology and production-biological conditions (Junk *et al.*, 1983). However, the problems are very complex and not yet fully understood.

Characterization of Amazonian Waterbodies by Morphological and Hydrobiological Characteristics

Rivers

Rivers are one of the most impressive manifestations of aquatic ecosystems in Amazonia (Fig. 4.1). All rivers are influenced by strong waterlevel fluctuations. Maximum flooding is reached in the southern affluents earlier than in the northern ones, the period with highest waterlevel in the south being February to April, and in the north June to August. In the Amazon, flooding reaches its maximum normally at the end of June. Waterlevel fluctuations decrease in the Amazon from the Andes to the mouth, being between 16–20 m at Iquitos, 8–15 m at Manaus, and on the lower courses about 4–6 m. Regular measurements of waterlevel exist only for the Amazon itself and its most important affluents (Salati, 1975).

Studies of the river morphology have been carried out by Sternberg (1960), Sioli (1967) and Irion (1976). They show that the river valleys were strongly influenced by the fluctuations of the sealevel during the ice-ages.

Data about hydrochemistry exist principally about the Amazon and the Rio Negro (Gibbs, 1967; Anon., 1972; Schmidt, 1972a; Leenheer and Santos, 1980; Stallard, 1980). For most of the large affluents, little information is available (Gibbs, 1967, 1972; Stallard, 1980). Rivers are open ecosystems with a discharging character. Huge amounts of material are transported by them to the sea; the quantity of carbon transported by the Amazon is calculated as 100 million tons per year (Richey *et al.*, 1980; Richey, 1982). These quantities have to be considered as they are important for the balance of elements of the whole planet (Schlesinger and Melack,1981). Biological and ecological information exists about some of the rivers, principally about fish fauna, because of the great importance of inland fisheries (Junk and Honda, 1976; Petrere, Jr., 1978a, b; Goulding, 1979; Bayley, 1981; Worthmann, 1982). However, additional studies are very important because of the increasing fishing effort resulting from rapidly growing population.

Over the next years, some of the big affluents of the Amazon will suffer from strong human impact. Modifications in the catchment areas may

Fig. 4.1. Manu River inside National Park, Peru 1974, as seen from plane (Photo credit: Dr H. Jungius).

change the amount of discharge, sediments, suspensoids and dissolved substances. Lack of baseline data will make it very difficult to detect such modifications. For example, Nordin and Meade (1981) criticize data on a change in the discharge of the Amazon by Gentry and Lopez Parodi (1980) because of the inadequacy of the data.

The construction of huge hydroelectric power plants will have a direct impact on several of the big affluents of the Amazon. Tucurui, a man-made lake on the Rio Tocantins, will cover an area of 2300 km^2. Many other reservoirs are in construction or are being planned. Additional impacts may result from industrial pollution, for example by great amounts of red mud or other industrial wastes put into the rivers, and by pesticides from agriculture. These impacts will not only affect the respective affluents but connected habitats as well, such as the floodplains, the main river and even coastal areas, as will be shown later.

Several projects about sediment load and transport of dissolved substances of the Amazon and its main tributaries are underway and will help to increase our knowledge.

Creeks

The Amazon Basin has the greatest density of creeks on earth (Fig. 4.2). The total area occupied by the creeks may be much bigger than the area occupied by the big rivers themselves. Unfortunately, there is a tendency to consider all the creeks as a whole.

It is a very big simplification to consider all creeks as one ecologically uniform habitat. Differences in hydrochemistry have already been indicated. Other differences can be shown in respect to solar irradiation. Creeks in the Campo Cerrado are little shadowed by a gallery forest and are strongly colonised by aquatic macrophytes, whereas forest creeks in Central Amazonia are lacking most of these species, probably because of lack of light. Ecological differences are supposed to exist between perennial and temporary creeks. The fish fauna of creeks with rapids is quite different from the fauna of slowly running creeks in the lowlands. Other differences are to be expected in respect to the creeks in the Andes which also belong to the Amazon Basin.

Studies of rivers and creeks in temperate regions have shown a zonation which allows a division into areas of springs, upper, medium and lower course (Illies, 1961; Illies and Botosaneanu, 1963). These areas can be characterized limnologically as well as by the ichthyofauna. This may be different in Amazonian lowland creeks, because temperature does not change as it does in temperate regions. But there may exist other important ecological factors, for example oxygen content, if we differentiate between bank areas,

Fig. 4.2. Example of a creek (Photo credit: Dr E. J. Fittkau).

ground water inputs, accumulation of leaves or mud, etc. Considering these aspects, creeks are very complex systems of different habitats (Fittkau, 1973, 1976; Soares, 1979). This is indicated by a huge species diversity. Knoppel (1970) determined in a reach of 300 m of a little forest creek of 1–2 m width about 40 different fish species. Compared with this, an inventory of the fish fauna in a reach of 100 km of Rio Tocantins, a very big affluent of the Amazon, has shown until now little more than 150 species (M. G. M. Soares, pers. comm.). Even supposing that this number will increase up to 200 species, the species diversity in the small creeks is astonishing.

The fish fauna of creeks is relatively well-documented. However, considering the fact that until now 1500 freshwater fish species are known to science, and about 2000 species are supposed to exist in Amazonia, our knowledge is limited. Other animal groups, like aquatic insects, are very little known.

An increasing amount of information exists about hydrochemistry (Schmidt, 1972b; Furch, 1976; Junk and Furch, 1980). Recent studies may lead to a hydrochemical classification of creeks in relation to the geology of the respective catchment areas. The importance of such a classification has already been stressed.

Considering their small size, creeks have to be considered as very vulnerable to human impact. Deforestation and pollution will change the hydrology (Salati, 1978) and hydrochemistry, and consequently the plant and animal communities to a much greater extent than, for example, the actual collection of ornamental fish. Therefore, intensive studies on specific creek systems are very important. Such studies started some years ago. Furthermore, comparative studies are necessary to determine how far creeks are ecologically uniform, and if they have individual aspects. Without this information nobody knows which creeks to protect, where to protect and how to protect them.

Waterfalls

Waterfalls are very special habitats. The colonizing fauna and flora have to be adapted to high current speed, rocky substrate, living in part in an air–water interspace. Waterfalls are known as typical localities for Podostemonaceae, a highly specialised family of aquatic macrophytes. Beside this, waterfalls may be a barrier for the fauna, inhibiting upstream migrations and gene-flow. In Amazonia, waterfalls exist mostly in the area of the archaic shields of the Guianas and Central Brazil and the Andes. Little is known about their importance as a fauna barrier. Because of their beauty, they should be protected as national monuments.

Deep Closed Lakes

Deep closed lakes are accumulating systems. They show special limnological conditions like physical, chemical and biological stratifications. Because of their age and lack of communication with other aquatic systems, they favour the development of endemic organisms. Deep lakes with more or less closed lake basins are rarely found in Amazonia. This is probably due to the geology of the region. The Amazon Basin is the greatest tertiary sedimentation area on earth. Depressions, which could have led to the building of lake basins, were filled up with sediments during the tertiary. Later on tectonic movements did not affect the basin, except in the Andean region. During the ice-ages, the decrease of the sealevel by about 100 m resulted in deep river valleys. With a rising sealevel, the valleys in Central Amazonia were flooded and actually represent lakes in the non-floodable 'terra firma' area. They are called 'lagos de terra firme' or 'ria lakes'. These lakes are black and clear water lakes. White water rivers have already filled up their valley with sediments. However, ria lakes have only in part the character of real lakes, and have to be considered as a part of a river with the more or less well developed characteristics of a lake. Probably the only real deep closed lake basins in the Brasilian part of Amazonia occur in the mountains of the upper Rio Negro, called 'Morro de 6 lagos'. Air photographs show six little closed lake basins. The geology of this area differs considerably from the general pattern. There is no information about the lakes, because access is very difficult. In the Andes, some deep closed lakes may also occur.

Shallow Lakes

In the literature the term 'shallow lakes' includes all shallow waterbodies as well as man-made lakes. I prefer to differentiate between closed and open shallow lakes, because they show clear ecological differences, which will be discussed in the respective chapters.

Closed shallow lakes

Closed shallow lakes are very common in the savannah area of Roraima. They are in part perennial, in part temporary and attract attention by their regularly round shape. Reiss (1973) explains their origin and shape by wind erosion. Most of these lakes are supplied by rainwater and consequently the water is very poor in dissolved minerals and very transparent. The fish fauna is very poor in species because of the severe droughts, which affect the area from time to time. Generally, the lakes have to be considered as oligotrophic. However, they may become eutrophic, showing a beautiful number and variety of water birds. Swampy areas, colonized by Cyperaceae may occur. Our knowledge about these habitats is completely insufficient. Human impact seems to be limited to eutrophication effects by cattle raising.

Open shallow lakes (floodplain lakes)

Floodplain lakes are shallow lakes which are connected with the rivers at least during some period of the year. They receive a part of their water from the river, when the flood comes, and devolve it when the water goes down. Combined with the water exchange is the exchange of nutrients, energy and biological material. This has a very strong impact on the lakes, on the river and on the whole floodplain. According to Hutchinson (1957) floodplain lakes include oxbow lakes, lateral levee lakes, lakes in abandoned channels, lakes in depressions formed by uneven aggregation of sediments during flood, and others. These lakes can be considered as intermediate between closed lakes as accumulating systems and rivers as discharging systems. Most of these lakes are subjected to high waterlevel fluctuations and great periodic modifications in area.

The limnology of floodplain lakes and their colonising organisms around Manaus is relatively well-known (Marlier, 1965, 1967, 1968; Förster, 1969, 1974; Junke, 1970, 1973; Koste, 1972; Schmidt, 1973a, b; Reiss, 1976a; Uherkovich, 1976; Uherkovich and Schmidt, 1974; Brandorff, 1977; Fisher, 1978; Ribeiro, 1978; Rai, 1979; Rai and Hill, 1980; Santos, 1980; Martins, 1980; Hardy, 1980; Carvalho, 1981; and many others). Additional information will be elaborated by several existing projects about limnology, ichthyology and fisheries. A detailed study about the limnology of some floodplain lakes on the lower Rio Tapajos was made by Braun (1952). The importance of floodplain lakes and the impact of human activities will be discussed in the following chapter.

Floodplains

The differentiation between floodplain lakes and floodplain may be surprising since during high water the whole area is inundated. However, on the organisation level of habitats, such a differentiation seems justified. Whereas floodplain lakes are habitats of an aquatic character, the floodplain has during certain periods aspects of a terrestrial habitat. Doubtlessly, there is no sharp definition for both, because of the waterlevel fluctuations. However, the biological consequences are evident. The typical floodplain forest of the middle Amazon occurs, for instance, mostly in the higher parts of the floodplain, because it needs a certain period of drought. Many species cannot grow in areas which are permanently flooded. However, there is a special type of forest which obviously tolerates permanent flooding (Prance, 1980). In how far the differentiation between floodplain lakes and connected rivers can be made, will depend on definitions and the viewpoint of the scientist. Welcomme (1979) considers, in respect to fisheries, rivers, lakes and connected floodplains as one unit. This may be true for many fish species which migrate between river and floodplain. However, considering terrestrial game animals, we may consider the floodplain as in part pertaining to the non-floodable terrestrial system. Junk (1980) describes floodplains as transitional systems between aquatic and terrestrial ones. The great number of morphological, physiological and/or ethological adaptations of floodplain organisms on the change between both phases as well as the complex nutrient cycles in the floodplains seem to justify it. In spite of their enormous area, covering in the Amazon Basin alone more than 100 000 km^2, floodplains are very little studied.

Obviously, the change between terrestrial and aquatic phase creates a problem for scientists (Bayley, 1980; Junk, 1980). It signifies a change between limnology and terrestrial ecology, including a fundamental change in methodology.

Relatively good knowledge exists about hydrophytes (Junk, 1970; Howard-Williams and Junk, 1976, 1977; Junk, 1982a) and fishes (Lowe-McConnell, 1975; Smith, 1979; Goulding, 1980). Several ecological studies exist about the invertebrates living during the terrestrial and aquatic phases (Beck, 1969; Irmler, 1975, 1976, 1981; Adis, 1979; Irmler and Furch, 1980; Irmler and Junk, 1982). However, there are great taxonomic problems, 80% of new species in one family are frequent.

Investigations on the ecology of floodplains started some years ago and will increase our knowledge. There is an urgent need for further information, because floodplains have been declared in the whole of Brazil as areas of intensive colonization efforts for utilization by agriculture and husbandry. These projects are financed by the 'provárzea' programme of the government.

In the Amazon Basin utilization of the floodplains of white water rivers (várzeas) can be justified because they belong to the best soils in the whole area (Camargo, 1958; Sternberg, 1960; Sioli, 1969; Petrick, 1978; Junk, 1979, 1982b). Floodplains of black water rivers have very little potential for agriculture and husbandry. Their utilization would create great damage to the ecosystem without long-term economical benefits. Floodplains of clear water rivers may have intermediate status. An overlap of interests may occur with fisheries, which is practised in the same area. A more detailed analysis of this very complex situation is given by Welcomme (1979) and Junk (1982b).

Ecologists have a real chance to influence the development planning in the várzea, when they are able to propose economically feasible alternatives. This is due to the fact that the population density in the floodplains is still very low and there exists very little infrastructure. Once big projects are started, including for example the construction of big and expensive flood control measures, a modification of the development scene is nearly impossible. Other impacts floodplains may suffer derive from the connected rivers. A hydroelectric power plant, for instance, will affect the waterlevel fluctuations and sediment load of the water and change the ecological conditions in the connected floodplains, as has been shown on the River Nile after construction of the Aswan Reservoir.

River pollution will also affect the floodplains and may have long-term effects on fauna and flora. Residues of papermills, for instance, containing mercury, will be deposited in the floodplains during high water and may contaminate the terrestrial fauna and flora, as well as the aquatic ones, for many years.

Swamps

Swamps are areas where the groundwater table reaches the surface most of the year, or where the soil is little flooded. Such areas occur in Central Amazonia mostly along the creeks and small rivers. They are built by the precipitation which comes down from the slopes of the valleys. The waterlevel of the creeks and small rivers is strongly influenced by local rainfall, which may create short-term floods of the adjacent swamp areas. The local name of such areas is 'buritisal', according to a characteristic palm growing there, the buriti (*Mauritia flexuosa*). In Central Amazonia much more than 100 000 km^2 are covered by such areas. Very little is known about their ecology. Hydrological data are being collected.

Permanent Periodic Waterbodies

The high amount of precipitation results in a great number of permanent and periodic small waterbodies, like pools, phytotelmes, etc. Although small and of little attraction for scientists, their importance as aquatic habitats should not be underestimated. They are colonised by many insects with short life cycles and are used by frogs for spawning and living. The fact that some of the insects transmit diseases like malaria, or are troublesome like mosquitoes, underlines the need of studies from a practical point of view. Whilst little is known about them, experimental studies are actually in progress.

Subterranean Waters

Subterranean waters are represented in Amazonia only by groundwater and interstitial water. Subterranean creeks or lakes do not exist because of the geology of the area. Information about subterranean waters in Amazonia is very limited. However, studies on the age, movements, position, etc., of groundwater are very important, because large scale deforestation has a strong influence on the groundwater table and may indirectly affect the whole system. Considering the fact that modifications may show up only after a period of time, and natural fluctuations may occur because of the seasonality of precipitation, base line data are of great interest.

Brackish Coastal Waters

Brackish coastal waters occur in large areas in the mouth areas of the Amazon River. Unfortunately, information about these habitats is insufficient to permit a detailed consideration here. However, from other brackish water regions in the world, the biological and ecological importance of such habitats and their relationship with inland waters as well as with the sea are well documented. Detailed studies in Amazonia are very important, because the great human impact on its big affluents may in the next decades change the hydrological and hydrochemical regime of the Amazon itself to a degree that it influences the coastal waters. Therefore, there is an urgent need for base line data.

Artificial Waterbodies

It may seem strange to include artificial waterbodies in a discussion about aquatic habitats of Amazonia. However, in future such artificial habitats will occur in increasing numbers all over the basin. An understanding of the modification of artificial waterbodies will help us to understand the natural ones if we use artificial waterbodies as large scale experiments. Some ecologists believe that such investigations will be misused for political and economic purposes. In my opinion, we should not lose the possibility to get a maximum of information, because only with sufficient knowledge can alternatives be considered and negative side effects minimised.

Man-made Lakes

In the next decades, several big hydroelectric power plants will be built in Amazonia, like for instance, Tucurui on the Rio Tocantins (2300 km^2), Balbina on the Rio Uatumã (2100 km^2), Samuel on the Rio Jamari (645 km^2), Porteiras on the Rio Trombetas (1400 km^2), Babaquara and Cararão on the Rio Xingu (6100 km^2 and 1200 km^2, respectively), and so on. There is no doubt that those gigantic constructions in combination with connected industrial projects will affect not only the rivers directly involved, but also the ecology of great neighbouring areas. A discussion about the necessity and the benefits of these projects is not possible, because it would include economic, political and other aspects.

In respect to the impact of these big man-made lakes on the rivers, it is likely to be detectable not only in the area directly affected, but as well in the areas upstream and downstream. Dams will be constructed on several very large affluents of the Amazon and the impacts on the discharge and sediment load of the main river and even on the coastal areas cannot be excluded. However, about the dimensions of such impacts nothing can be said specifically. Today, only two small man-made lakes exist in Amazonia: Paredão, north of Belem, and Curuá-Una, south of Santarem. They cover about 100 km^2 and produce 40 mW each. About Paredão there is no information available, whereas Curuá-Una has been studied for 4 years (Junk *et al.*, 1981; Darwich, 1982; Junk, 1982c). These studies show that several negative side effects can be expected, which have been observed in other tropical man-made lakes in Africa and Asia. These effects include, for instance, changes in the fish fauna, mass development of aquatic macrophytes and deterioration of water quality, principally high oxygen deficit. For two years, about 20 manatees (*Trichechus inunguis*) have been introduced into the lake as a tentative biological control of the macrophytes. Even supposing there is only some effect on the macrophyte vegetation, this change probably offers a new habitat for a species in danger of extinction. Unfortunately, studies in Curuá-Una have only been started after the construction of the dam. Therefore, a direct comparison with the former conditions is not possible. This problem has been avoided in Tucurui where intensive studies began before damming up the river. These studies are concerned both with the aquatic habitats as well as the terrestrial ones.

Fish Ponds

At present, fish ponds exist in Amazonia only in a very limited number, because fish culture is not yet economically feasible due to the lack of know-how. This situation will change in the next decade (Saint-Paul and Werder, 1977; Junk, 1979; Saint-Paul, 1982; Werder and Annibal, in press). Fisheries can no longer offer enough fish at low prices to a rapidly growing population. Therefore, fish culture will be of increasing importance for protein production. Besides affecting lakes, swamps and creeks by the construction of the ponds, fish culture may create two big problems for the native fauna: (1) The distribution of fish and fry may distribute diseases and parasites, and (2) The introduction of exotic species may affect the native fauna, when such species escape and become adapted to the new habitats. Over many years, tilapias have been grown in Amazonia and have escaped into natural waters. Obviously, they did not become adapted to the new habitats. However, this problem has to be observed carefully. The best means of avoiding the introduction of exotic species for fish culture is in my opinion, the development of sufficient knowledge about the culture of high price native species. More studies of this are needed.

Rice Fields

The cultivation of rice in Amazonian wetlands is still in the beginning. The largest plantations were started some years ago in the Jari project. However, information about the ecological consequences of large scale rice plantations is not available. Studies in South East Asia have shown that rise plantations represent very complex habitats (Heckman, 1979). They may have negative side effects because of the need to apply pesticides and the propagation of water-borne diseases, like schistosomiasis. On the other hand, combined rice and fish cultivation is one of the most lucrative agricultural activities in South-East Asian wetlands. In the state of Amazonia, experiments with rice cultivation in the várzea have been started recently. Comparative ecological studies should accompany them to get the necessary information.

Pools and Wastewater

Human activities create small waterbodies everywhere. In Amazonia, they can be observed in great numbers, for example along the roadsides of the big highways like the Transamazônica and the South–North connection. They indicate the places where material was collected for road construction and which later on were filled with rainwater or groundwater. Around villages highly polluted pools and even wastewater pools occur. These are very important artificial habitats which serve for the distribution of plants and animals, including parasites and diseases. During the rainy season, the ditches along the highway between Porto Velho and Manaus, for instance, facilitate the distribution of aquatic organisms for many kilometers without interruption. The control of malaria and mosquitoes will depend in part on our knowledge about the ecology of such habitats, but detailed information is lacking.

Protection of Aquatic Habitats

It seems generally accepted that the protection of the terrestrial environment automatically includes an adequate protection of aquatic habitats. In fact this is not the case. The discussion about the creation of National Parks or other types of protected areas in Amazonia is based principally on the theory of refugia. In accordance with actual knowledge, areas which are considered as refugia of several groups of species are of high priority of protection (Wetterberg *et al.*, 1976; Wetterberg and Pádua, 1978; Wetterberg *et al.*, 1981).

However, it has to be stressed that the theory of refugia is based only on the distribution pattern of some terrestrial plants and animals. There are no studies about their applicability to aquatic organisms and systems. Very probably the big river systems of Amazonia have been affected only to a limited degree by climatic changes which are supposed to be the reason for the formation of refugia. Even supposing a change in total discharge and the pattern of waterlevel fluctuations, the existence of the river systems as such was not affected. Therefore, climatic changes may have had relatively little influence on the aquatic fauna and flora. There are several problems in protecting river systems or parts of them. River banks and floodplains are relatively densely colonized and utilized by agriculture, husbandry and timber extraction. The rivers themselves are used by navigation, fisheries and, in future, in some cases by hydroelectric power plants. Therefore, they have to be considered as areas of multiple interests, which overlap with conservation interests. Human impacts on the river, such as pollution or changes in discharge and sediment load outside the protected areas, may affect distant protected areas.

Furthermore, rivers and creeks have to be considered as 'open systems' which transport organisms by drift or allow active migrations over long distances. Many commercially exploited fish species have large feeding and spawning migrations, which are not yet fully understood. *Semaprochilodus* spp. and *Brycon* spp. for instance, migrate from the protected areas of Analvilhanas, an archipelago in the lower Rio Negro, to the Amazon for spawning. Soon after leaving the protected area, they are caught in great quantities. Nobody knows yet if the specimens which migrate back to the Anavilhanas belong to the same stock or are coming at least in part from other affluents of the Amazon. Since such migrations may exceed hundreds of kilometers, there are no National Parks big enough to protect totally these members of the fish fauna. Therefore an attempt should be made to protect well-determined aquatic habitats, including watersheds, in different sections of the big rivers, for instance in specific lake systems in the floodplains or islands in the river channel. These measurements would protect the characteristic landscape, the flora and the more stationary species of animals, whilst migrating species would have at least temporary protection. Several relatively small areas may be more effective than a single very big one. A specific legislation may regulate fisheries. Additionally, highly vulnerable aquatic species, for example the manatee (*Trichechus inunguis*), the big turtle (*Podocnemis expansa*) the giant otter (*Pteronura brasiliensis*) must be protected by special laws (Junk, 1975; Ayres and Best, 1979).

Other aquatic habitats are easier to protect, because they are of smaller size. In part they are already included in the existing National Parks and other protected areas. However, additional studies of the aquatic fauna and flora are needed and will in future indicate further specific waterbodies for protection. In this respect it has to be stressed, that an adequate protection of aquatic habitats must include the protection of the respective watersheds, to guarantee the maintenance of its specific character.

Summary

Different existing concepts for the classification of Amazonian waterbodies are discussed. An additional approach is suggested to characterize aquatic habitats, based on hydrological and morphological parameters. The state of knowledge about the frequency, distribution and ecology of aquatic habitats is discussed. Human impacts on aquatic. habitats in Amazonia and their vulnerability to them are evaluated.

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5. Patterns of Higher Vertebrates Distribution in Tropical South America

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Introduction: Amazonia, the World Climax of Species Diversity

Amazonia probably contains by far the greatest number of species of organisms (Fittkau *et al.*, 1968/69; Lovejoy, 1965; and others) per unit of area or on the whole as a subcontinental region. This broad generalization holds true for many or most groups of living organisms, especially trees, insects, spiders, frogs, or passeriform birds. The number of bird species generally increases exponentially towards the Equator (Fig. 5.1), at least on continental areas. This was proven for the Americas by Macarthur (1972). The highest values are attained in the lowland rainforests of Amazonia (Meggers *et al.*, 1973), South-east Asia, and Africa (Amadon, 1973).

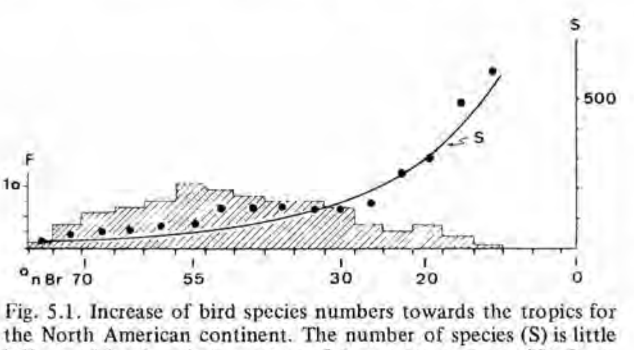

Fig. 5.1. Increase of bird species numbers towards the tropics for the North American continent. The number of species (S) is little influenced by the relative extent of the continental area (F). From Reichholf (1975) after data from Macarthur and Wilson (1967).

Species-area-relationships, which might account for much of the extraordinary high species richness of Amazonia with its most extensive area of continuous or nearly continuous rainforest have been investigated for other tropical and temperate areas. The number of bird species markedly increases from the continental mass of North America towards the narrow isthmus of Middle America despite the sharp decrease in land surface (Fig. 1). Factors other than size alone must be important.

Reasons for High Diversity

Several causes of high species diversity have been put forward to explain the tropical richness, e.g., high age of the rainforest ecosystems, climatic favour, stability, complex systems of Pleistocene refugia, permanent but moderate disturbances, higher rates of mutation/speciation in the tropics, high predation pressure etc. (Macarthur, 1972; Macarthur, and Wilson, 1967; Fittkau, 1973; Meggers *et al.*, 1973; Pielou, 1978; Simpson and Haffer, 1978; with extensive coverage of the relevant literature). The variety of forces which may determine species richness shall not be considered further, since this account is restricted to the identification and interpretation of certain patterns of the distribution of higher vertebrates in the South American tropics.

Another factor likely to be of basic importance for the superimposed patterns of distribution and abundance of certain animals is the pattern of nutrient availability. The studies of Fittkau (1973, 1974) clearly show a high deficiency of some essential nutrients in Central Amazonia and a generally lower level with respect to other parts of the world. Especially calcium, phosphorous, inorganic nitrogen, potassium and a number of trace elements are in short supply or nearly lacking whereas silicon, iron and aluminium dominate and form a super-abundant supply. These elements are of minor importance for higher vertebrates, freshwater snails or mussels. It is interesting to consider this nutrient situation with the exceptions from the general trend of increasing diversity towards the tropics. This consideration might provide a clue for another approach to the problem of diversity. The paucity of snails and mussels is not surprising because of the well-known deficiency of calcium in the rainforest streams. Nevertheless the occurrence of molluscs is well below expectations (Fittkau, 1981), if one takes into account the generally suitable factors of the environment (humidity, warmth, mostly closed vegetation).

For both birds and mammals, some important and highly interesting exceptions to the 'rule' can be detected easily:

– very few species of bigger sized mammals and an extremely low density per unit of area

– few non-arboreal mammals

– scarcity of aquatic or semiaquatic mammals (e.g., moderately to small sized in comparison to Africa)

– a generally low species richness of mammals

– fewer endemic mammals in Central Amazonia than in the marginal areas or in the extratropical parts of the continent

– a comparatively low state of primate evolution with not a single species comparable to the apes

– very few species of aquatic birds (besides the fish-feeding types)

– low species richness in non-passeriform birds in the Central Amazonian areas

– high degree of parapatry and lower values of symparic species than would be predicted by the general level of species numbers.

Whilst the previous list is tentative and not complete, it shows that the rainforests of Amazonia do not automatically provide a high level of species richness for all groups of animals. Since some of the faunal groups contain adaptive types of most importance to Man (e.g., ungulates—the human livestock being the ecological equivalent), their failure in the inner tropics could have some practical consequences for future exploitation and use. To illustrate this principle, the special case of the aquatic bird fauna of South America is examined.

Aquatic Birds

The river Amazon with its tributaries covers the most extensive river system in the world. Forests and water intermingle in a highly complex way. Judging from the vastness of the Amazon Basin, a wealth of waterfowl would be expected. This is not the case except for some exceptional sites at the marginal areas (see Chapter 6). Duck species richness and abundance sharply decrease towards the Amazon Basin, despite the fact that the narrow tip of Southern South America harbors an astonishing array of species. Figures 5.2 and 5.3, based on my field work in South America a decade ago, show this type of distribution. It is important to note that most of the basic adaptational types of ducks occur in Amazonia. So the argument that the tropical conditions of climate might prevent successful breeding of these birds, cannot receive too much weight.

Another possible explanation is the availability of specific food items, i.e., the macrozoobenthos. A number of studies in Amazonian waters show that biomass of the macrozoobenthos is comparably low (Fittkau *et al.*, 1975; Reiss, 1973, 1976,

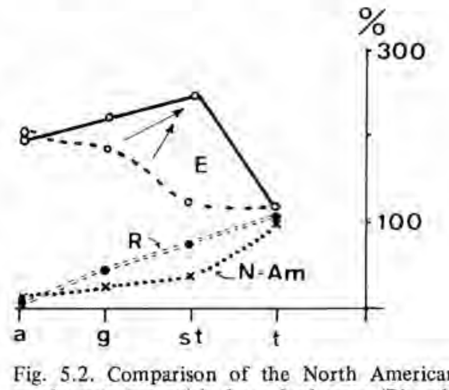

Fig. 5.2. Comparison of the North American trend (N-Am) of species numbers with those for herons (R) and ducks (E) in South America from the antarctic region (a) across the temperate (g) to the subtropical (st) and tropical (t) region. While the total number of duck species attains a maximal value in the subtropical region (solid line) the number of breeding species is declining constantly towards the tropics (dotted line for E). Numbers in percentages of the species numbers in the tropical zone. Drawn from Reichholf (1975).

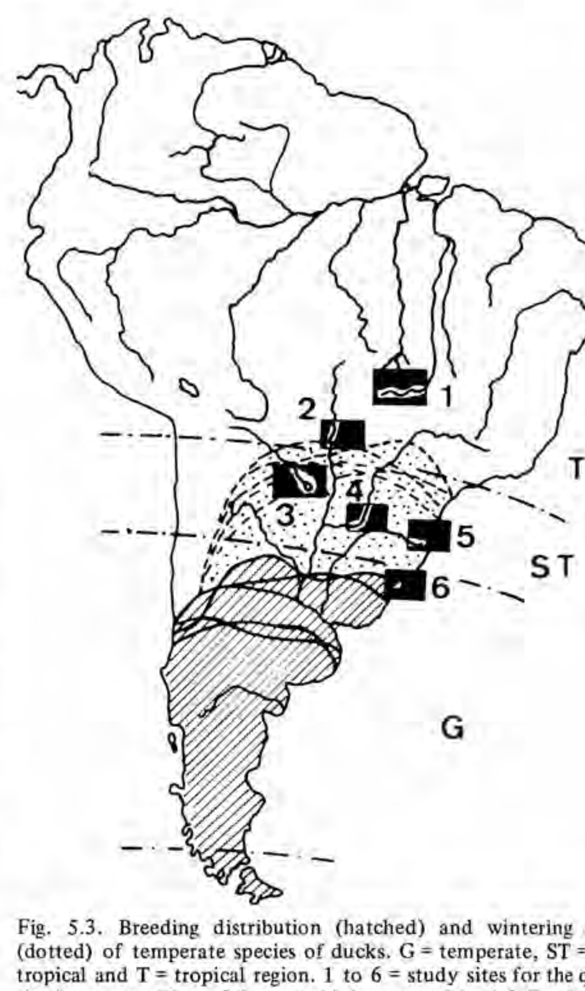

Fig. 5.3. Breeding distribution (hatched) and wintering areas (dotted) of temperate species of ducks. G = temperate, ST = subtropical and T = tropical region. 1 to 6 = study sites for the quantitative composition of the waterbird communities (cf. Fig. 5.5).

1977). Even under good conditions the standing crop rarely exceeds 10 g/m². Our studies in temperate aquatic systems revealed a feeding-type specific level of standing crop necessary for the balance of gains and losses during feeding. Figure 5.4 shows that the level for sustained yield lies quite high for diving ducks. They need a biomass-density of more than 100 g/m² because of the high energetic costs of diving. Dabbling ducks can forage quite successfully in a food supply of 10 to 100 g/m² whereas fishes which use the same prey items thrive even with values below 10 g/m². Of course these limits must not be viewed definitive under all conditions but they provide size classes for the energetic levels of the different species (Lindeman, 1942 called it the trophic-dynamic aspect of ecology).

In any case warm-blooded birds and mammals need much more energy for basic metabolism, especially for keeping body temperature constant which means warming or cooling at any time. This energy expenditure is not necessary for poikilothermic animals like fishes or insects. This is the reason why they can use scarce food resources more efficiently than warm-blooded animals. Their superiority is enhanced under the tropical rainforest conditions where water and heat energy are not limited but mineral resources become critical. Therefore, fish should be the better exploiters in the competitive system for macrozoobenthic prey.

In fact, species richness, diversity and also the density of fish are critical in the Amazonian land–water-interactive systems (Goulding, 1980). Fish competition, especially the exploitative competition (Miller, 1967), may become the limiting factor for duck distribution and abundance (Reichholf, 1975), because fish can keep the standing crop well below the value necessary for birds for energetic reasons. The fish have no need to overcome the uplift and buoyancy a diving duck has to cope with. So mineral cycling through the fish chain may even enhance the transfer process, as has been pointed out by Fittkau (1982) for the fish-eating caimans, and its highly important linkage into the energy flow in the main food chains.

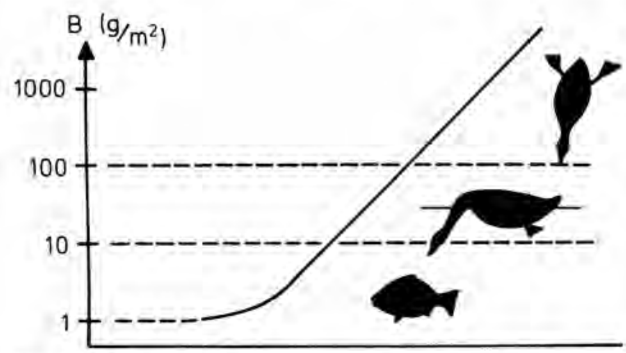

Fig. 5.4. Model of the basic energy levels necessary for a sustained yield for fishes, dabbling and diving ducks in units of invertebrate standing crop.

For similar reasons, it should be predictable that high fish density and/or diversity should allow a diverse array of fish-eating birds. This is the case, but with an important restriction: the diversification of adaptational types occurs in the herons and storks but not in the diving birds. Obviously the 'watch-and-wait' tactic is more appropriate and less energy demanding than active hunting under water. For the latter group, the high speed of fish in warm waters, the turbidity of waters rich in fish, and the competition by crocodiles and predatory fish may be critical.

Consequently the aquatic bird community of Amazonia is mainly a 'fishing-community', which means that the birds operate in comparably high positions in the total food web. In temperate or sub-arctic South America, as well as in the high Andine lakes and rivers, the aquatic bird community is predominantly composed of primary or secondary consumers and therefore centered at much lower levels in the food web (Fig. 5.5). This position makes them less sensitive to environmental change than holders of high positions ('top-predators').

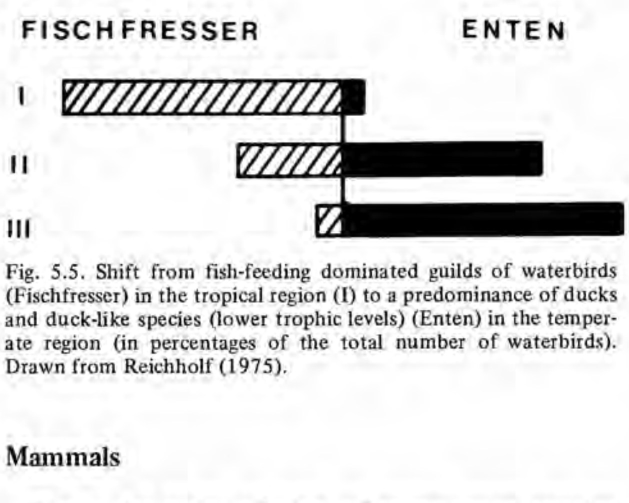

Fig. 5.5. Shift from fish-feeding dominated guilds of waterbirds (Fischfresser) in the tropical region (I) to a predominance of ducks and duck-like species (lower trophic levels) (Enten) in the temperate region (in percentages of the total number of waterbirds). Drawn from Reichholf (1975).

Mammals

From the point of view of energy most species of medium size or bigger mammals are in the same position as the primary and secondary consumers among the aquatic birds. They need much food rich in energy, too much often with respect to the productivity of tropical lowland forests. Again the situation is not unique for the Amazon, but most clearly visible there because of the huge landmass and uniformity of the area. Yet even structurally diverse and geologically richer areas in the south-east Asian tropics provide quite low values of mammalian diversity and density (Marshall, 1979). The detailed analyses of Fleming (1979) and Keast (1969) underline this result for tropical lowland South America. The comments of Hershkovitz (1969) are noteworthy. The Amazon valley is one of the most important physiographic features of South America and was and remains the largest focus for mammalian colonization during the Quarternary period. The Valley is not, strictly speaking, a discrete zoogeographic province. It has few terrestrial species of its own and no native genera except possibly the uacaris (Cacajao), which may yet prove to be of upland origin. Even the fluviatile fauna is a small part of a vastly larger and widely disseminated fauna.

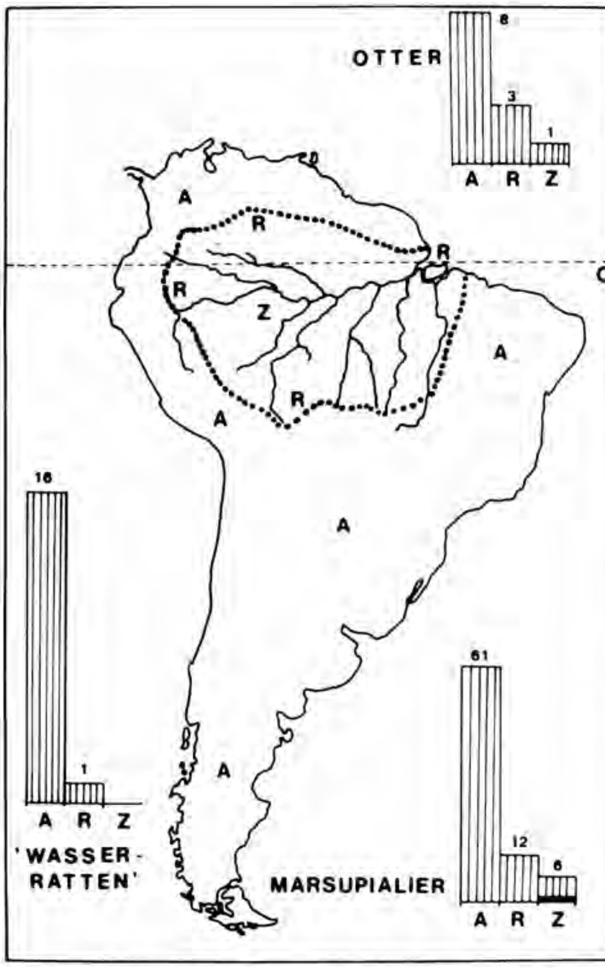

Fig. 5.6. Pattern of distribution of otter species (Lutrinae), aquatic and semi-aquatic rats (Wasserratten) (Rodentia) and marsupials Central (Z), Marginal (R) and extra-Amazonian (A) regions of South America. Central Amazonia is obviously low in species numbers. Numbers are numbers of species within the groupings.

Distribution Patterns

Much of our recent knowledge about the distribution of birds and mammals in Amazonia we owe to the studies of Haffer (1974, 1979) and Hershkovitz (1969) (Fig. 5.6 and 5.7). Three main results support my hypothesis, firstly a number of species show allo- or parapatric pattern of distribution thus forming a superspecies-complex. This may be one important reason for high number of 'species' in Amazonia for forest birds and mammals. These superspecies-complexes show quite distinctive lines of contact zones, and one may easily plot centers of endemism around the margins of Amazonia. These three basic results must have consequences for conservation strategies and this is discussed at the end of this paper.

My recent studies in the rich avifauna of Eastern Africa (Reichholf, 1980) showed that some sort of a chequer-board-parapatry accounts for much of the overall richness in avian species there; a type of pattern rarely found in temperate regions. The species turnover (per unit of field work or area) is so high that the increase of species number with area follows a much steeper slope than would be expected by the exponent of continental species-area-curves (Macarthur and Wilson, 1967). The value comes close to that for islands which could mean that habitat selection in tropical avifaunas is more 'island-like' and results in a more patchy distribution than in temperate regions.

It is the larger birds which separate their niches predominantly by food selection or feeding technique. The medium sized and especially the smaller (passerine) species separate in space in woodlands, but generally tend to some sort of micro-geographic parapatry. It is, therefore, quite difficult to sort out a 'typical' section of a larger area which looks uniformly enough to the eyes of an ecologist from temperate regions.

Consequences for Conservation

Judging from the state of the present knowledge, which has been put together in a concise form here, I have to put the question: Is there any prospect of a sound strategy of conservation? Or more precisely, is it possible to identify precisely the areas most important for the conservation of the tremendously rich species pool of Amazonian birds and mammals?

I would like to follow Haffer when he proposes to concentrate the interest onto the 'centers of endemism' or 'distribution centers' (Haffer, 1974) on the one hand and onto the 'zones of contact' between the centers of endemism on the other. Conceptually a strategy based on these basic features should be efficient, especially if it is amended with a network of refugia in between containing the 'typical array' of species with wider distribution. But how should this system work in practice? Do we know enough about the more than 1500 bird species of Amazonia or the much less thoroughly studied mammals? Most of the quantitative work, which provides a basic

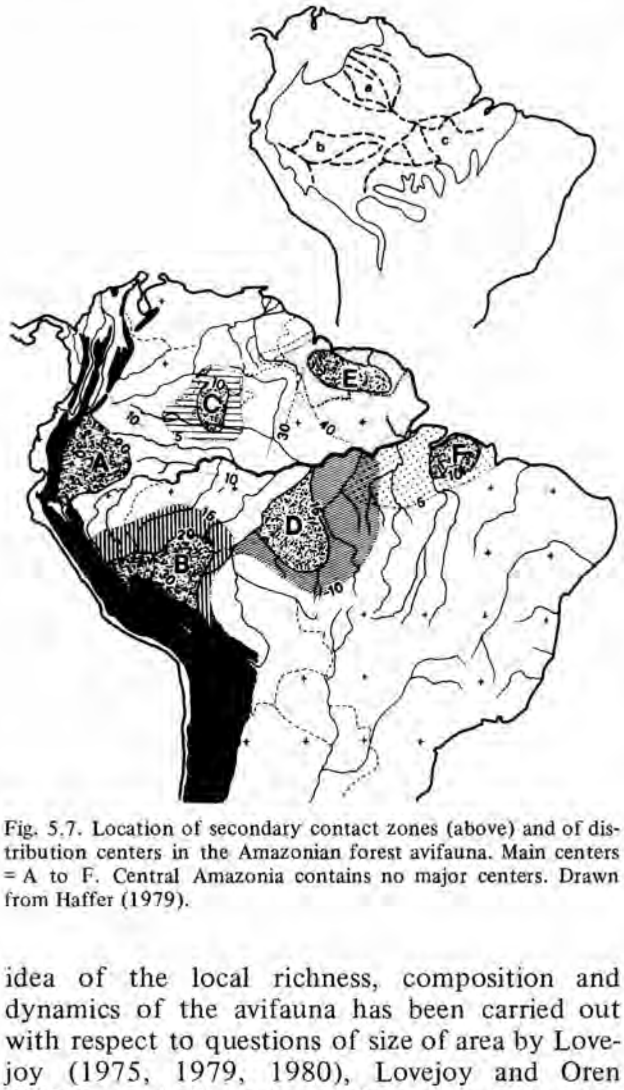

Fig. 5.7. Location of secondary contact zones (above) and of distribution centers in the Amazonian forest avifauna. Main centers = A to F. Central Amazonia contains no major centers. Drawn from Haffer (1979).

idea of the local richness, composition and dynamics of the avifauna has been carried out with respect to questions of size of area by Lovejoy (1975, 1979, 1980), Lovejoy and Oren (1981), and Wetterberg, Prance and Lovejoy (1981). For a significant community of Amazonian mammals no such studies at all exist to my knowledge. Taking the bird studies, the 'minimum-size-project' near Manaus may provide some basic data about the possibilities to conserve an appropriate array of species within a confined area of Amazonian rainforest, but according to Haffer (loc. cit.) the sites are not adequately situated in the centers of endemism or along major contact zones. Many more comparable studies are badly needed. They must include other parts of Amazonia and especially the marginal areas which are under the most severe threat of destruction. They may preserve an even more important part of the avifauna.

An area as big as Amazonia evidently allows some experimental studies on the faunal changes connected with different types of refugia systems, e.g., larger continuous plots, smaller interconnected or scattered plots and/or 'stripes' versus 'points'. Little is known about the critical sizes of really isolated forests plots below which the number of species begin to drop sharply according to the species–area-relationships. Above what size would be attained the constant increase of species numbers with area?

We should at least in principle understand the basic pattern of distribution and abundance before these patterns are changed. In the present situation we have to consider quick strategies as a more than urgent necessity. A sub-optimal strategy will be better than none.

Summary

The tropical rainforest, especially in Amazonia, holds the world record for species diversity and richness. This broad generalization applies for many groups of organisms, e.g., trees, insects, frogs and passeriform birds. There are also several important exceptions: large mammals, aquatic mammals and birds, snails and freshwater mussels. The availability of certain minerals (Co, P, N and trace elements), competitive interactions between higher taxa and difficulties with the thermal balance in more sizeable homoiotherms account for the paucity of species and/or population density of these groups within the generally overwhelming tropical life form diversity. This is exemplified by the antitropical trends of ducks and other aquatic or semi-aquatic birds. High fish diversity and—at places and at times—also high density may inhibit the build-up of a macroinvertebrate biomass suitable for exploitation by ducks. Biomass density must exceed about 10 g/m^2 for dabbling ducks and 100 g/m^2 for diving ducks.

In another respect the distributional patterns of many of the tropical lowland species of birds and mammals differ profoundly from those of temperate regions.

This is the high degree of microgeographical segregation of closely related species which leads to the predominance of parapatry or allopatry and to the formation of extensive superspecies complexes. Overlap of areas of occurrence and true sympatry are comparatively rare, which either expresses phylogenetically recent split-ups of the once contagious gene-pools or secondary

contacts after the Pleistocenic events (shrinking and expanding of the forests and formation of refugia and dispersal centres). Marginal areas, therefore, tend to be richer in species than the central parts. This complicated situation makes species-conservation even more difficult, because it seems virtually impossible to sort out 'typical' sections of the rainforests for sanctuaries. The consequences for conservation strategies should be discussed seriously, especially in combination with the minimum-size studies.

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6. Flow of Nutrients in a Large Open System: The Basis of Life in Amazonia

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Introduction: Personal Background

My experiences of Amazonian life date back some twenty years to the time when Amazonia was economically forgotten and politically not even discovered. As a scholarship-holder of the CNPQ I had been an employee of the INPA for three years. As there was no electricity in Manaus at that time and as a consequence neither ventilator nor air-conditioning in my laboratory, I preferred to work as much as possible in the forest. My most important discovery, I should like to call it an ecological experience, was that man cannot, or only with enormous difficulty, survive because of food shortage in that large region which I call Central Amazonia, in view of the geochemical formation. I spent enough time among caboclos, the settlers at the river bank in the forest, to recognize that their poverty was not a result of their mentality but rather of their impossibility to earn their living on their rossas with only the resources they were given.

In the middle of the last century the administration of the federal state Amazonas was in Barcelos, about 400 km up the river from Manaus. The officials received the 'pirarucu seco' from Careiro, the island in the Varzea of the Amazon close to Manaus, though they lived on the bank of a big river and with a hinterland rich in waters. The reason for the removal of the administration to Manaus was the insufficiently guaranteed supply to the officials, I have been told. It was very impressive but not so delightful to learn in Manaus that the capital of the state with about 100 000 inhabitants at that time could not live on a hinterland of 1.5 million square km, but had to be supplied by imported meat and other food which sometimes failed to come.

At that time people were convinced that depending on food of foreign countries or other states of Brazil was caused by the bad structure of the Amazonian economy. I am convinced that the insufficient exploration and the extremely small population of the interior Amazon Region (like the deserts of the world in the lack of people) results from the heavily leached soils of the terra firma of Central Amazonia, which were formed in the tertiary.

Consequently, it is not for an economic-political problem that Amazonia—although the largest tropical rainforest area of the world—does not contribute significantly to the world timber trade, or that the genuine caoutchouc only makes a small percentage of the world production. Even now, man is exposed to the extreme ecological reality which creates this situation. The economical profit in Amazonia is so low because of the extremely poor nutrient resources of the landscape. The Ford rubber-plantation, the Transamazonica-experiment and most recently the Ludwig Jari project were bound to fail for ecological reasons (Fig. 6.1).

Today we know that the enormous diversity of species in flora and fauna of Amazonia is not based on a great fertility of that region. Some time ago I formulated the hypothesis that the diversity of species of the Amazon Region means an adaptation to cope with the lack of nutrients, that the highly developed floristic diversity is perhaps the most important strategy of the rainforest to use the nutrients in the most effective way. High diversity does not only intensify the effectivity of the recycling but also—as I try to show in the following example—even makes possible the gathering of nutrients offered to the forest by the rainwater. This allochthonous source of minerals may be critical for the continuation of life in Central Amazonia.

Structure of Central Amazonian Stream and Forest Ecosystems

The Amazonian Region, especially Central Amazonia, is a highly mature landscape shaped under tropical conditions. A mature tropical

Fig. 6.1. Road built across the Amazon Basin, Brazil (Photo credit: WWF/Michael Freeman).

landscape means a levelled area with plains of sedimentation where the soils have already developed to kaolinitic oxysols or sandy podsols. In addition the fauna and flora have evolved quite completely in a long-lasting process of adaptation to the increasing geochemical poverty (Fittkau, 1981). There is no continent other than Amazonia where the process of maturing could be accomplished over such an extensive area without being heavily disturbed. So it is to be expected that the tropic ecological regularities must be especially evident there.

Examples from two different ecosystems of the 'terra firma', which are spatially and functionally connected with each other, will be considered to make an ecological sketch of the nutrient flow in Central Amazonia according to present knowledge. The examples are the 'forest' and the 'stream' draining a 'terra firma' forest.

There is an essential difference in the basic structure of the ecosystems 'terra firma forest' and 'terra firma stream'. The forest is an autotrophic ecosystem, which gets its energy by primary production. The river is a heterotrophic system, which gets its energy, not taking into consideration the kinetic energy of running water, from organic material built up in the forest from where it comes into the river. In the river ecosystem the essential macroscopic structural units are animals, in the forest those are represented by plants. Besides these structural units there is in both systems a microbiological component, bacteria and fungi, which seems to have tremendous importance for all functions of the systems, but due to the present insufficient analysis they are not included in the consideration presented here. A comparison between forest and stream should emphasize that despite the basically different elements, plants in the forest, animals in the river, both systems are governed in structure and function by the same ecological principles.

Landscape Ecological Prerequisites in Central Amazonia

According to Fittkau (1971) and Fittkau *et al.* (1975a, b), Central Amazonia is not only a geographical region but also an ecological or biogeochemical region, whose biotic configuration is influenced in an unusual way by abiotic and ecological factors (Fig. 6.2).

Central Amazonia is situated in an ancient zone of tectonic instability (Fittkau, 1974). Since the Precambrian the crystalline continental block of this area shows a variable subsidence and has partly incorporated sediments of the shields of Guayana and Brazil. These continental sediments were, before being deposited, already extensively weathered and washed out. The soils, latosols or oxysols, formed on and by these sediments consists, therefore, almost only of kaolinitic clays or sandy podsols and have hardly any nutrient reserves (Klinge, 1976a, b; Irion, 1976, 1978; Sanchez, 1976).

The areas surrounding Central Amazonia are usually more favoured and especially towards the periphery of this region in the headwater areas of the tributaries, the geochemical situation improves further (Furch and Junk, 1980). This is especially true for the western border area, which is formed of relatively recent sediments from the Andes and from which it still gets additional supplies. The uniformity of Central Amazonia is interrupted by the andine and preandine rivers flowing through this area and depositing nutrient rich sediments, which in this area are according to Schwabe (1942), ecologically strange ('umraumfremd').

The chemistry of the surface waters has been used as an indicator for the geochemical situation of the different Amazonian ecological regions. Especially in Amazonia, close relationships between the chemistry of waters and soils have been demonstrated (Sioli, 1950, 1954, 1965). From numerous water analyses, summarized in Table 1, it is concluded that all waters originating from Central Amazonia are very acid and demonstrate a conspicuous low conductivity, which is always below 10 μs_{20}. Characteristic for the entire geochemical region is the low content of Ca, which is found below 20 μg per liter, below the commonly used limits of evidence. The low content of Ca is also characteristic of the Central Amazonian terra firma oxysols, which is also well below the limits of evidence (Table 2). The Ca content of soils, rivers and plant biomass (Fig. 6.3) is far below the world average (Furch, 1976; Furch and Klinge, 1978; Furch *et al.*, 1982).

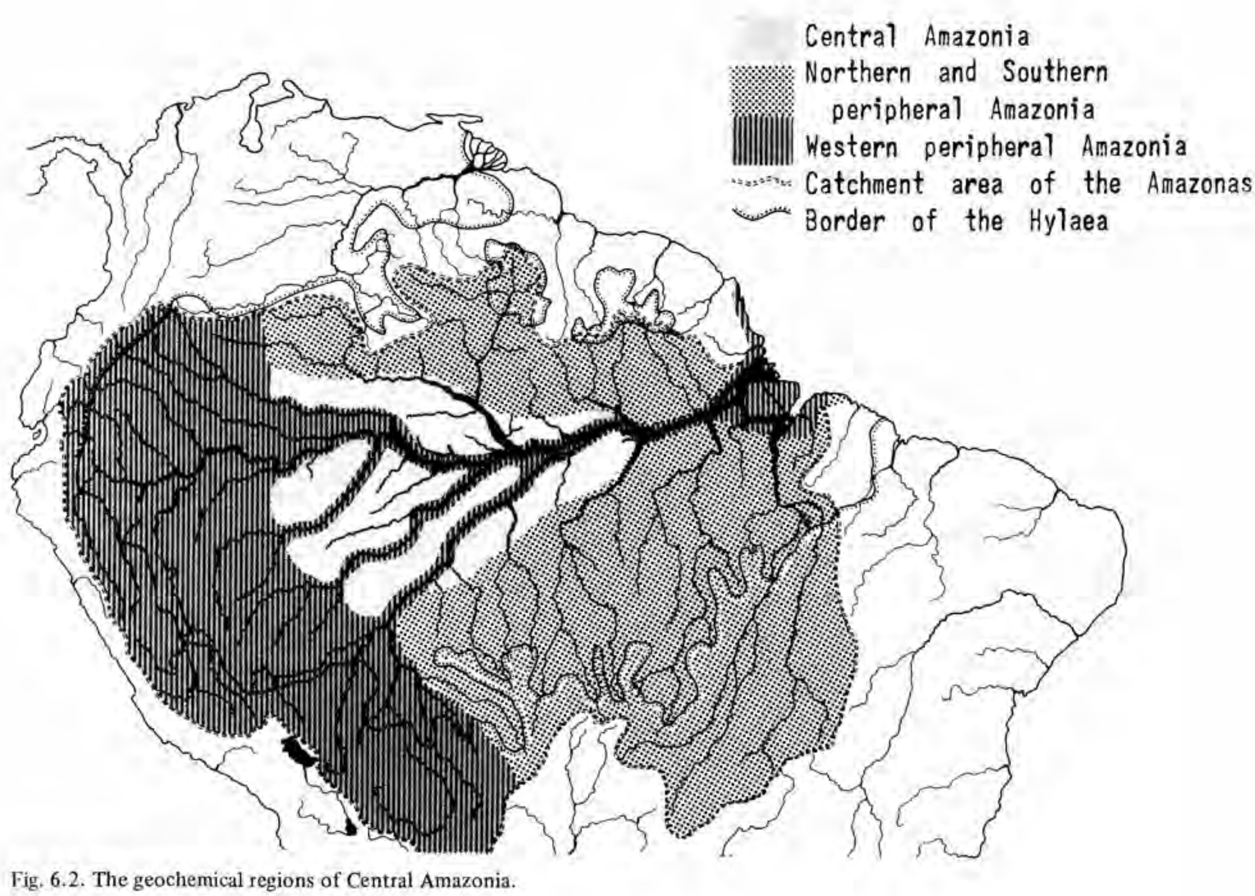

Fig. 6.2. The geochemical regions of Central Amazonia.

TABLE 1

Chemistry of Central Amazonian rivers and streams from the region of Manaus. Average values taken from 34 samples from 24 different places.

μS 20	pH	SBV mval/l	Na mg/l	K mg/l	Ca γ/l	Mg mg/l	P/tot. γ/l	Si mg/l
5–10	3.7–4.5	0–0.02	0.2–1.2	0.08–0.5	20	0.01–0.05	2.5–10	0.6–2.0

TABLE 2

Distribution of nutrients in kg/ha in parts of the Central Amazonian rainforest ecosystem (after data of H. Klinge).

	N	P	K	Ca	Mg	Na
Living plant biomass	2986	66	498	50.7	257	239
Dead plant biomass	293	2.8	9.3	21.2	17.4	3.1
Mineral soil 0–100 cm	8924	147	58	0	23	50
Rain/year, Manaus	10	0.28	–	3.6	3.0	–

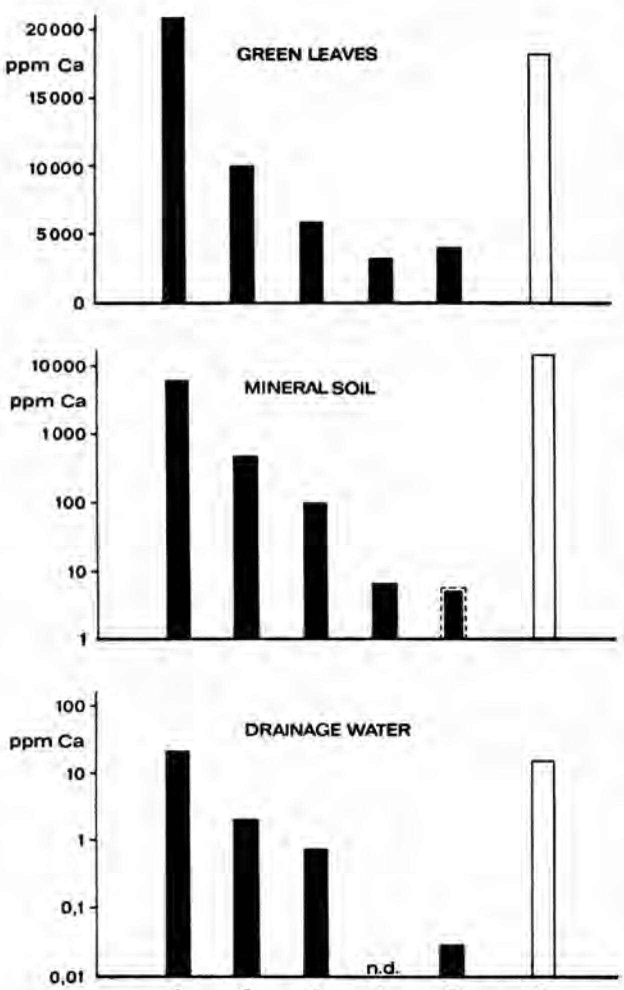

Fig. 6.3. Calcium in green leaves, mineral soil and drainage water of five forest ecosystems of Northern South America (after Furch and Klinge, 1978). 1 = Tropical moist forest, Panama; 2 = Montane forest, Puerto Rico; 3 = Tall Amazon Caatinga, Venezuela; 4 = Evergreen rainforest, Columbia; 5 = Seasonal evergreen rainforest, Central Amazon; 6 = World average.

Structure of the Terra Firma High Forest

The structure of the Central Amazonian rainforest is characterized by an unusually high richness of species of trees and treelike plants (Brünig and Klinge, 1975; Klinge, 1973; Klinge and Rodrigues, 1968a, b, 1971). Near to Manaus, Klinge found about 500 different species on a plot of 2000 m^2.

As already emphasized the quantitative proportion of the fauna of the forest ecosystem is very low (Fig. 6.4). According to our data, estimations and calculations faunistic elements are represented by only 210 kg/ha fresh weight, which is less than 0.02% of the total living biomass of the ecosystem (Fittkau and Klinge, 1973).

About half of the biomass of the Central Amazonian rainforest is represented by mites, collembolans and numerous other arthropods and worms. A great proportion is represented by termites, ants and many other insect groups while vertebrates are in terms of weight of minor importance. Larger mammals, like monkeys and pigs, which live in groups, prove to be omnivorous nomads. Especially significant is the fact that phytophagus animals, in spite of the rich offer of plant material in the terra firma forest hardly occur in the area. Like the vegetation, the fauna is characterized by a high variety of species. In fact, it is easier to find 30 beetle or butterfly species than 30 individuals of the same species.

Structure of the Terra Firma Streams

In the river ecosystem, animals and the microbiological component are the major living structural element. Only a negligible percentage of the biomass is represented by a few algae, especially red algae (Batrachospermaceae). However, they do not noticeably contribute to the total amount of nutrients within the whole system. It is not the lack of light, but the non-availability of nutrients in the stream water, which seems to limit the development of primary production (Fittkau,

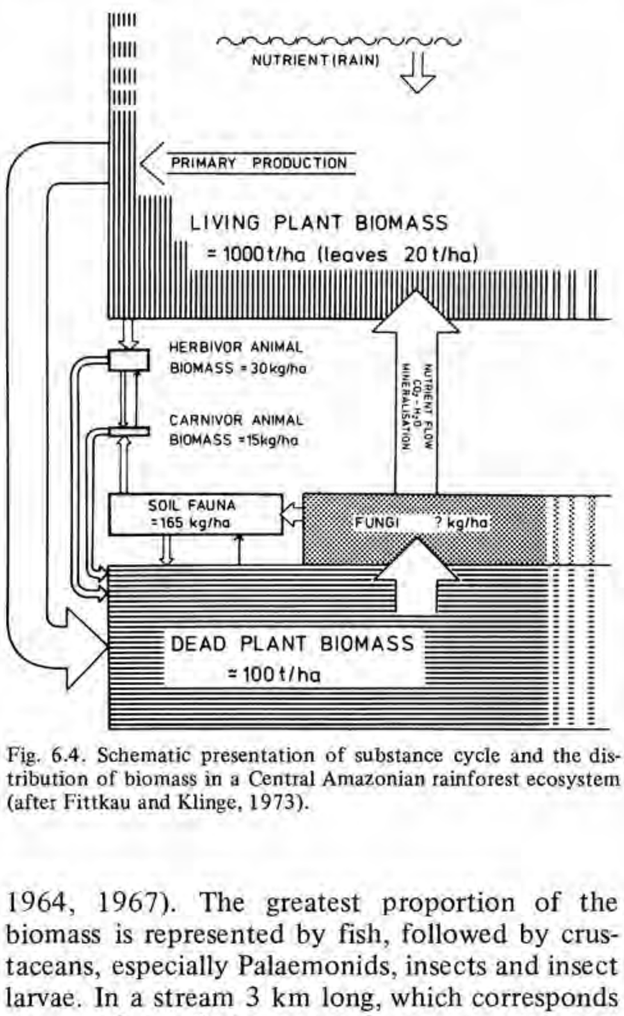

Fig. 6.4. Schematic presentation of substance cycle and the distribution of biomass in a Central Amazonian rainforest ecosystem (after Fittkau and Klinge, 1973).

1964, 1967). The greatest proportion of the biomass is represented by fish, followed by crustaceans, especially Palaemonids, insects and insect larvae. In a stream 3 km long, which corresponds to a surface of about one ha, one can expect about 500 animal species: 50–80 species of fish, about 40 aquatic water bugs, the same number of aquatic beetles, and further the larvae of 150–200 species of chironomids. Extremely rich in species are also the poorly known mites and ephemerids, trichoptera and dragonflies, whose larvae also belong to the river fauna.

Diversity of Central Amazonian River and Forest Ecosystems

As in the forest, the diversity of the stream system decreases if certain environmental conditions deteriorate. This is the case when the solid substrate of the river is reduced and dead wood material becomes scarce. As a result not enough water is dammed and there is inadequate opportunity for the attachment of species of running water which usually obtain their food by filtering. In the forest, this situation occurs when areas with latosols border areas with podsols. The hydrographic conditions on sandy soils are less constant and favourable than on clay soils. The gradual broadening of the river has a negative influence upon diversity which is explained by the increasing amount of water carried by the river and which simultaneously brings about a deterioration of the initially highly variable substrate, and the stream bottom is gradually transformed into a layer of sand.

Within forest and stream numerous species may be divided easily into a relatively few discrete types of life forms. The well balanced coexistence of similar or similar behaving species does not fit into the niche concept developed for temperate zones. Obviously the humid tropical conditions, which show small, if any, seasonal variations, favour a different form of coexistence (Fittkau, 1973, 1976). (The genesis of species in Amazonia is a process we must ignore in this context, compare Brown, 1979; Haffer, 1974; Lowe-McConnel, 1967; Müller, 1973.)

From experiments made by Slobodkin (1964) we know that two hydra species can only be kept together when there is a hydra predator. Similarly, the density of individual species in tropical ecosystems seems to be regulated by a rather tense predator–prey relationship. If the density of prey species decreases due to an overabundance of predators, it may be possible that in the same habitat and with the same amount of food supply species diversity increases. Phytocoenoses are governed by the same rules as zoocoenoses. According to the definition of Janzen (1970) not only are animals considered to be predators of plants, but also viruses, bacteria and fungi. An ecosystem with a large number of species preying on plants or animals is viewed as a result of a long evolution. When there is a further increase of predator species, it is possible that the total amount of species of the system increases.

If the indicated tense predator–prey relationship regulates the species density of the ecosystems and thus their structure, why do we find a high or the highest density on the soils with an extremely low nutrient supply, or in a stream with a short supply of food?

Function of Central Amazonian Stream and Forest Ecosystems

The structure and function of an ecosystem are interdependent. Insights into the functions of the system should further allow conclusions on diversity and its possible dependency on food and nutrient supply. Since the structural elements and their functions are much easier to understand in a stream system, a stream will be used to demonstrate their possible relationship (Fig. 6.5). The food chain of the stream system is made up of allochthonous organic material which has its origin in the forest. This material can be separated into two components:

(a) material which will be immediately used by fish such as flowers or parts of them, fruits, seeds and especially animals;

(b) material which serves as food for the benthic fauna only after being microbiologically decomposed by bacteria and fungi, such material is leaves and woody material.

In the terra firma forest about 10 kg/ha of woody material and leaves fall to the ground (Klinge and Rodrigues, 1968a, b.). The same quantity is expected to fall into the stream, part of which is washed away and the rest is deposited in slow flowing sections of the stream and decomposed by bacteria and fungi. The resulting microbiological components mixed up with particles of organic matter of different origin, here called for reasons of simplicity detritus, form an essential food supply for such benthic fauna as worms, crustaceans, but especially insect larvae and adult insects. The detritus serves, where it is deposited in areas of still water, as food and partially as substrate for particle feeders. Many insect larvae filter this material from the running water with filter devices developed for this purpose (Sattler, 1963). Besides the allochthonous material fish may get from the forest system, a considerable part of the benthos serves as food for fish (Knöppel, 1970). On the other hand products of fish metabolism accepted directly or via microbiological decomposition, are an important source of food for the benthos. Some of the insect larvae terminate their life cycle inside the water and leave the ecosystem if not eaten. They are called emergents (Illies, 1973). Through deposition of the egg into the water, part of the emergents returns into the system as either food for fish, when the egg depositing animal is preyed upon, or as spawn.

The arrows printed on Fig. 6.5 indicate that parts of the dissolved and undissolved material, and even part of the benthos of the running water system, are permanently drifted away and redeposited elsewhere by running water. During drifting away detritus and other organic matter like organisms, leaves and wood particles may serve as food. Simultaneously there are permanent interchanges between dead and living materi-

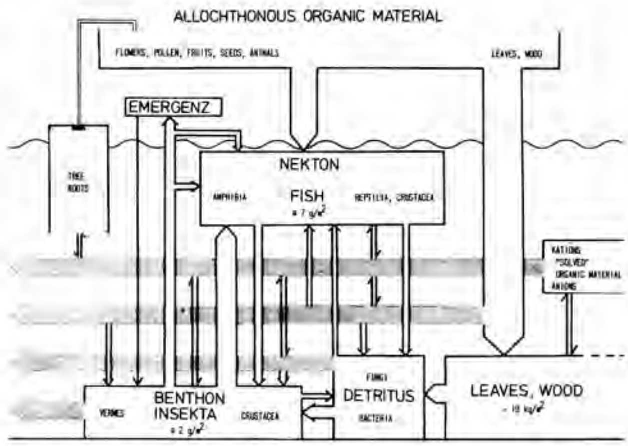

Fig. 6.5. Schematic presentation of the distribution of biomass and relationships in the ecosystem of a Central Amazonian rainforest stream.

al, which determine the chemical composition of the water. With the decomposition of leaves and wood, inorganic and organic material is set free into the water. The same holds true concerning all metabolic processes of bacteria, fungi, benthic organisms and fish.

At the same time vital components are absorbed by the body surface of organisms. Some trees on the river banks develop a dense system of roots right into the river, obviously in order to filter nutrients from the water. Presumably as the water of the river is almost or completely free of calcium, each Ca-ion is immediately absorbed by organisms.

The relationships which have been indicated demonstrate that the allochthonous food supply is optimally utilized if the morphology of the riverbed provides sufficient space for the microbiological decomposition of leaves and wooden material. Zones of calm water change with those where the water flows rapidly. In rapidly flowing water there should be sufficient solid substrate, such as rotting wood and roots, for the sessile organism to be able to hold back the drifting detritus.

Much benthos means abundant food for fish. Many fish guarantees the utilization of usable drifting allochthonous and organic material. This results in an additional amount of nutrients, which may be utilized by any part of the whole system including the bank trees, whose roots provided the important solid substrate for the benthos.

An increase of the biomass should further optimize the efficiency of the stream ecosystem and also its ability to keep food and nutrients within itself. The biological filter represented by such an ecosystem should improve in performance as its species diversity increases. The greater number of different species of similar or the same types of life forms living close to each other, the better is the guarantee that the efficiency of this filter is permanently reactivated. With increasing numbers of species the energy flow should approach a biological optimum and the biomass should attain the maximum. Increasing species diversity should at the same time lead to an increase in stability under the given conditions and thus influence the evolution of the stream biocoenosis.

Ecological System of the Terra Firma Forest

Like all ecosystems, the forest system is open and depends on light and heat energy, on water and nutrients. In comparison with the stream, the forest represents, in an extremly reduced form, a similar flowing system. The rain provides nutrients, at the same time however, percolating water transports nutrients to the groundwater, which partially reappear in the surface streams. The soil contains little or no nutrient reserve to compensate for nutrient loss. For the continuation of an ecosystem in a situation of limited nutrient supply, it is essential to retain the nutrients in living and dead organic material for the benefit of the system and to utilize the external supply of nutrients exhaustively and economically. This means that the nutrient cycle should be as closed as possible (Herrera *et al.*, 1981; Jordan and Herrera, 1981).

One obvious means of nutrient economy is to exclude all faunistic elements from the nutrient cycle. The diverse phytophagus species are, considering the biomass, rather unimportant, even if one considers leaf biomass to be only 20 t/ha and herbivore biomass 30 kg/ha. The weights of termites, beetle larvae and ants are already included in Fig. 6.5. These groups have an important function concerning the decomposition of wooden material and litter. Termites and other wood consumers are controlled by numerous predator species from ants to highly specialized vertebrates with many feed back loops.

Another nutrient economy process is to produce seeds and fruits sparingly, which limits the food supply for such vertebrates as birds, rodents and monkeys. Furthermore, fruits and leaves through their evolution have substances with high molecular weights, preventing mechanical or chemical nutrient release when they are eaten (Janzen, 1974).

Before old leaves are shed as much nutrient as possible is withdrawn (Table 3) (Klinge, 1977). The material which composes the litter is very poor in nutrients, and only fungi are able to decompose it. Often these fungi are species which form a mycorrhiza, which enables them to make the produced nutrients directly available to the living vegetation (Herrera *et al.*, 1977; Herrera *et al.*, 1978, a, b; Stark and Jordan, 1978; Went and Stark, 1968).

Under these conditions the continuity of the ecosystem depends on its ability to retain the allochthonous substances, formed through remineralization, and to make use of the supply of allochthonous substances in the rain (Jordan *et al.*, 1979). The river filter system is efficient in retaining organic nutrients, in the forest inorganic nutrients are retained (Klinge and Fittkau, 1972). Forest efficiency also increases with growing species diversity. Furthermore the stability of a forest ecosystem increases with a growing number of species and consequently this has influenced forest evolution.

High Diversity as an Adaptation to an Impoverished Geochemical Habitat

The described ecosystem interrelations emphasize that the impressing diversity of life in tropical ecosystems may partially be viewed as an adaptation to geochemically impoverished habitats which have other important ecofactors for the optimal conditions of life. The richness of species of humid tropical habitats with a simultaneous high diversity is—contrary to common views—not a function of high food supply but obviously an adaptation to continuous limitation of nutrients and food scarcity under otherwise optimal conditions of life. This hypothesis formulated already earlier by Fittkau (1973), has been examined by Fränzle (1977) from an information theory point of view and has been confirmed inductively by numerous diversity analyses.

Tropical habitats, which are rich in nutrient and food supply, are generally unstable from a spatial and temporal viewpoint, and presumably do not permit the formation of high diversity. The structure and function of the Central Amazonian ecosystem rainforest and rainforest-stream seem to provide a possibility of identifying discrete general rules about the development of life on the earth. A superabundance of nutrient and food supply is usually of short duration. With the development of a diversity of life forms, the lack of food must have been of tremendous evolutionary importance. The lack of vital substances means selection, selection enforces adaptation and adaptation induces modification, which finally produces diversity and makes evolution.

TABLE 3

Different contents of nutrients (ppm) in fresh and shed leaves of trees of the terra firma forest in the area of Manaus. Values after data from Klinge and Rodrigues, 1968b; Klinge, 1976b.

	N	P	K	Ca	Mg	Na
Fresh leaves	18000	500	4000	3500	2500	1500
Shed leaves	15–16000	300	2000	2000	2000	800
Difference*	2–3000	200	2000	1500	500	700

*The difference may be caused by either washing out or reabsorption by plants.

Superabundance reduces the process of selection and limits the formation of biological diversity. Diversity is known to be reduced in eutrophic systems (Odum, 1971; Thienemann, 1918, 1920; Utschick, 1976).

Summary

The Central Amazonian rainforest covers a large lowland plain with geochemically extremely poor and acid kaolinitic oxysols and/or sandy podsols. The unusual deficiency of nutrients in this landscape is clearly demonstrated by the poorness of electrolytes in the running waters draining the area. Their content of metallic ions is only twice as high as that of the Amazonian rainwater. So one could call them properly 'rainwater' streams and rivers.

Central Amazonia can be characterized generally by the virtual absence of calcium in the soils and waters. Another basic feature is shown by the structural and functional properties of the main types of Amazonian ecosystems: the rivers and the forests. That is the origin and processing of the nutrients. Whereas the communities of the streams and rivers receive their food supply directly or indirectly from the forest and build up a predominantly 'consumer-based community', those of the forest (which are of the tropical lowland rainforest type) rely heavily on the influx of the allochthonous nutrient support brought by the rain. But in this 'producer-based community' the basic property too is the withdrawal of nutrients imported or released within the system. The specific function of the extremely high species diversity obviously lies in reduction or minimization of nutrient losses which would be caused by metabolism or decay of animals and plants. The communities in the rivers and the forest likewise act as highly efficient 'nutrient-traps'. But maximal diversity is restricted to areas where the streams flow straight and change frequently between lotic and lentic habitats or where the forest cover is on well aerated and drained soils.

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7. History of the Brazilian Forests: An Inside View*

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Seeing Nature in Brazil

An understanding of reality is only possible with historical vision. It is through an understanding of the present as it developed from the past that we will try to introduce ideas which could be useful in the formulation of the future. It is important to realize this and how this country has been identified with the earthly paradise.

Columbus was among the first Europeans to be struck by the continual spring and agreeable climate, where (quoted by Buarque de Holanda, 1977) "the good and soft smell of the flowers and trees was the sweetest thing in the world". The scientific names of the banana, *Musa paradisiaca* and *M. sapientum* still carry this notion, the latter with reference to the tree of knowledge of good and evil.

The image of paradise linked together religion and greed. The legends described the areas around Paradise as full of monsters, like the fierce female warriors known as Amazons. They were first situated in the Caribbean. As the region became better known they were placed further away, until Orellana definitively put them in the forest which has kept their name until this day.

All early descriptions, by travellers and scientists, referred to the very large size of the country, the exuberance of its nature, and fed the myths which have lasted even to our own time, of an immeasurably grand virgin land, inexhaustible. Here is a telling poem by Gonçalves Dias (1928):

Our sky has more stars
Our valleys have more flowers
Our forests have more life
Our life has more love.

The discoveries in the New World: the gold and silver of the Aztecs and Incas, gained through the destruction of their empires, inspired a greedy outlook and voyages that led to the beginnings of capitalism. The silver mines of the Andes produced the legend of Eldorado, located in the North of the Amazon region, which might have led the three world powers to conquer the Guyanas. Always the goal has been to take the greatest economic profit from new lands, giving the least possible in return. It is important to remember that Brazilian history developed under the shadow of capitalism.

To be sure, there is in Brazil a tradition of observing nature, and modelling one's life accordingly. Here is a part of a rhapsody by Guimaraes Rosa (1963):

– Near plenty of water is happiness.

– The butiti (palm tree) wants everything blue: it never goes away from its water, because it wouldn't have a mirror.

– Study this senhor: The buriti (palm tree) lives on the banks of the rivers. It drops its seeds on the footpaths and the waters carry them away along the riverside. Thus we find the buriti lined up following the river far more exactly than if someone had planted them there.

– All palm trees, so smooth and so close together, just like the huts (choupa) of the Indians. I am sure that it was seeing such palms that the bugres (Indians) came up with the idea of how to make their huts...

– It was a month when the macuco (birds) still flew singly.

– The part (of the cerrados) with more trees increases as one heads for the headwaters... Overhead, one could see long bands of araras flying through the air, looking like a blue or red cloth spread over the loins of the hot wind.

*The author attended the meeting of the IUCN Commission on Ecology and the Symposium on the Ecological Structures and Problems of Amazonia at São Carlos, SP. He delivered a lecture on conservation work with regard to Amazonia and the Atlantic Forest, and afterwards conducted an excursion to the latter with several members of the Commission on Ecology.

His thesis for the degree of Master of Landscape Architecture, "Toward a History of the Brazilian Forests", (University of California, Berkeley, USA, 1979, 114 pp.), aroused the interest of COE members. As it contains a number of elements highly relevant to the subject of the Symposium on Amazonia, I was happy to prepare, with the author's permission, this abridged version of the (unpublished) thesis, for inclusion in the Proceedings.

Dr M. Jacobs

We now come to the history of exploitation of the land. Several means can be distinguished whereby it assumed the character of a spiral degradation.

The Brazil Wood Cycle

Exploitation of brazil wood came first. It began in 1503 and lasted to the 19th century, as a result of the almost complete extinction of the species and the discovery of synthetic dyes. The harvest during the first three decades is estimated at 3000 metric tons annually; from there it continually grew and was considered in Portugal an inexhaustible mine.

Brazil wood or dye-wood, first named *Caesalpinia echinata* and nowadays *Haematoxylum brasiletto* (Leguminosae) and the source of a brick-red dye, gave its name to Brazil. In the beginning the country was known as Ilha de Vera Cruz, Terra de Santa Cruz, Terra dos Papagaios (land of the parrots). The present name comes from braza meaning braised wood, as for extraction of the dye the heartwood was crushed before it was cooked. Dye-wood was the only extractive industry that was worth developing at the time. The trees were abundant in the strip of rainforest along the Atlantic coast, from where they were extracted at increasing distances.

"The aborigines, urged on by the demand of our merchants, prepared huge deposits of wood, which piled up along the coast; but since they did not know how to conserve their riches, they cut them down haphazardly. Many times, in order to avoid the work of cutting them down, they would even set fire to the lower part, and the fire would spread throughout the rest of the forest." Piracy and smuggling became so extensive that land grants or *capitanias* were soon given out by the government, giving its owner, the *capitao*, full rights to all products, but prohibiting the use of fire. "This economic cycle... did not bring any benefits to the land, and only served to carry out the devastation of the forest to the point of the effective elimination of these precious species. Behind it were left only some areas of secondary forest, grasslands, huge areas of erosion, or some lands which were later incorporated into the sugar plantation." (Page 49 of the thesis).

The Sugarcane Cycle

Sugarcane cultivation began early in the 16th century and had its high point in Brazil in the first half of the 17th century. The rapidly growing custom of drinking tea, coffee, and chocolate was one of the principal factors in increasing sugar consumption. Between 1600 and 1700, Brazilian sugar dominated the world market. This lead to the occupation of the northeast part of Brazil by Holland from 1630 to 1661, to break the Brazilian monopoly. The plantations, or *engenhos*, were situated along the coast because of the qualities of its land and its greater proximity to Europe. In Bahia, in 1711, there were 146 plantations, in Pernambuco 246 and in Rio de Janeiro 136.

When the Portuguese arrived, they adopted the slash and burn method of the Indians. Abundance of forest without developing other agricultural systems made them look for new lands further in the interior; thus rarely would two generations pass without a plantation changing location or owner.

Firewood was needed to maintain the furnaces in the sugarcane industry which ran around the clock for 7–8 months; with every harvest each engenho used up to 2560 wagon loads. By decree of 1682, a minimum space of $1^1/_2$ league was required between the engenhos. Altogether, sugarcane cultivation left us a North-east despoiled of its very rich forests, impoverished soils, and miserable and servile population, possessing only its popular culture and the humility and humanity which only many generations of suffering can teach.

The Occupation of Territory by Livestock

Livestock served the various needs for transportation within the engenhos, as well as being a source of food. Lack of means to enclose the animals led to farming the remote areas. In 1701, the Portuguese government decreed that livestock breeding was prohibited less than 10 leagues from the coast. Given the conditions of transport and water supply, the corrals were established near rivers, e.g., up the São Francisco River, hence up the Parnaiba, and to the sertoes of Minas Gerais, Goias, and Mato Grosso. Other levies left São Paulo heading for Minas and for the South. In 1711, 500 corrals were counted in the sertoes of Bahia and 800 in those of Pernambuco, with a total of c. 1 300 000 head. Activities were concentrated in the caatingas and cerrados, where the savannas only needed to be burnt annually to 'strengthen' the range. No book better describes 'how a desert is made' than *Os Sertoes* (1947) by Euclides da Cunha.

Hides were the only export product of this activity. They were also used to wrap the packages of tobacco that were sent to the Court, and there were many domestic uses. The Gold Cycle brought a need for transportation, by mules from the corrals. This was an important factor in populating the sertoes.

The Gold Cycle

It was only at the end of the 17th century that expeditions of bandeirantes from São Paulo (who were hunting down and imprisoning Indians) were to find the metal. The main focus of exploitation then shifted from the Northeast to the Central-South, and the occupation of the centre of the country took place. An estimated 300 000 Portuguese immigrated, a large number for the time. The influx resulted in restrictions in Portugal to avoid further depopulation, and in Brazil in two famines, which caused the people to disperse and to make new discoveries.

In addition to panning the bottoms of the rivers to wash gold, they looked for the metal on the banks, for which the riparian vegetation was cleared. In their anxiety to discover gold the miners carried out large-scale burnings, devastating extensive zones of forest. One can still see the traces of their work, in Minas Gerais, Goias, Mato Grosso and Bahia.

All this fortune, which made possible a century of wealth in Portugal, ended up with the Holy See and in the coffers of England. In Brazil, it left only a very fine layer of gold leaf on magnificent carved wood baroque altars. Also left was what could not be carried away: slaves and mule teams, which later would ease the cultivation of coffee.

The Rubber Cycle

The Indians already knew how to grow the *Hevea brasiliensis* that so surprised Columbus on one of his voyages. The cycle was started about 1890, after development of the motorcar with its inflated tyres. Rubber exploitation involved much of the Amazonian forest. It was carried out through tapping under a work system of semi-slavery. Tappers collected the product along the Amazon River, resulting in a first experience of wealth, which was squandered before long, however. Its apogee lasted till about 1920, when the Hevea seeds, previously smuggled to Kew Gardens and then sent to Singapore, were planted commercially in Malaya. Brazilian rubber could not compete with this, and fell into decline. There was a re-animation during the Second World War, there it ended. Rubber trees growing in more recent times can be seen in Fig. 7.1.

Fig. 7.1. 1960 photo of Rubber trees, *Hevea brasiliensis* (Photo credit: Dr E. J. Fittkau).

The Coffee Cycle

Coffea arabica was first brought from its oriental home to the North of Brazil. It began with a few caboclos carrying out subsistence farming on virgin lands, using the rudimentary methods from the natives. After some years of burning and enlarging the clearings, the lands would be taken by a group of people who declared themselves owners and had some capital accumulated from other plantations. Then the entire area of the plantation would be burned; the same type of landscape can still be seen along the frontiers of the land in a forest region (Fig. 7.2). Immediately, planting began, and building of facilities for drying and storage of the coffee, the house for the senhores, and the shelter for the slaves.

It was commonly accepted that only forest areas were sufficiently fertile for coffee. Erosion was rapid. Without any care or attention, forests were destroyed without concern, even in the highlands. Coffee was planted without any other ideas than immediate profit. The negligence can be seen in the very placement of the plants: in straight lines following a slope—no arrangement could be more favourable to erosion. "The result of all this was disastrous", wrote Prado Junior in 1945, "a few decades were enough to produce rapidly falling incomes, weakening of the plants, and the appearance of destructive pests. Then came the full sinister cortège of decadence: impoverishment, successive abandonment of cultures, demographic rarefication."

Large-scale cultivation began at the beginning of the 19th century, on the slopes along the Rio Paraiba do Sul. Rarely were more than two generations of coffee planted. At the first signs of exhaustion of the land, new forests were cut for new plantations, and the process continued repeating itself. The devastation caused by coffee's violent passage over the hills of the Paraiba Valley can still be seen in the continually worsening erosion. Its end result is still shown by the large number of plantations and cities abandoned after rapid depopulation. In the State of São Paulo, according to a study by Morae Victor (1975), the area of natural forest in 1800 amounted to 81.8%, in 1907 to 58.0%, in 1920 to 45.0%, in 1935 to 26.0%, in 1952 to 18.0%, in 1962 to 13.7% and in 1973 to 8.3%.

Standards for accumulation of capital were never applied to agriculture. Everyone wanted to extract excessive benefits from the soil without large sacrifices or, as our oldest historian said "they wanted to avail themselves of the earth, not as senhores, but as exploiters, only to take its fruit and to leave it destroyed" (Buarque de Holanda, 1971).

Fig. 7.2. Clearance by fire of slopes in Central Amazonia (Photo credit: Dr E. J. Fittkau).

Modern Times

The principal characteristics of the present process of occupation of territory is the speed with which it is taking place. Growing industrialization, demographic expansion, increased aggression on the part of national enterprises, and participation of foreign companies—such is the present panorama.

The forests of the Central-South have practically disappeared. The mountains in the State of Minas are rapidly losing their native vegetation cover—in spite of legislation to the contrary—to feed the furnaces of the steel industry. The foothills of the Serra do Mar are being devastated by land speculators, who are destroying the very sources of tourist attraction which provide the basis for their sales. Thus one sees some of the most beautiful landscape of the country being diluted and lost because of an activity which should be concerned to zealously preserving the environment. Tourism in the Central-South has become an activity with a moving frontier: it destroys here, and soon passes on to continue destroying further along.

All such events—as well as the large-scale burning of cerrado—take place within a context of economic growth, between 1968 and 1974 of over 9% of the GNP. Most of this growth benefits people with the highest income.

The government's ideal of national (territorial) integrity, together with the mirage of a Brazilian economic miracle led to the attack on the Amazon forest. The government provided the main financial incentives, which benefit the larger enterprises while being hard on the people. Thus we are leveling the largest forest on this planet, without even knowing the consequences of this act, cutting trees in long straight lines, showing a complete lack of sensitivity to the natural factors involved in the division of the land. This penetration is being carried out with a technology alien to the native culture, resulting in the beginning of a loss of the cultural patrimony of the adaptation of mankind to the forest. As Souza put it in 1978: "The Amazon is still one of the homelands of myth, where there is still unity between thought and life, in constant interaction of stimuli and affirmation. The Amazon will be free when we finally recognize that this nature is our culture: that each tree cut down is like a word censored; and each polluted river is a torn page. The struggle for the Amazon is part of the general process of liberation of the oppressed people."

The Forest and the Law

Legislation with regard to the vegetation goes back to early dates. In 1605 there was a royal decree to protect the forests containing brazil wood, to regulate exploitation. This same purpose underlay a decree of 1797, in which the Portuguese Crown declared as its own all the forests and trees along the coast. Three years later the Governor General commented on its redundance, given the already complete destruction of these forests. A document of 1808 (the year of foundation of the Royal Botanic Garden of Rio de Janeiro), which opened Brazilian ports to international trade—one of the marks of independence—permitted free commerce in most things, but not in wood. Coming to the 20th century, we find a document of 1917 which recommends the creation of a forest code. This First Forest Code appeared in 1934, from which the following summary is extracted:

Chapter I

– The forests of the country are a good of common interest to all its inhabitants.

– The measures (of this Code) are also to be applied to the other forms of vegetation, when such should be recognized and useful.

Chapter II

– The forests are classified as: (1) protective—when they serve to conserve water, avoid erosion, stabilize dunes, guarantee the defense of the frontiers, guarantee health, or protect sites of special natural beauty and rare specimens of fauna and flora; (2) *remanescentes* (remaining)—national parks, as well as state and municipal ones; (3) model—artificial forests for future growth; (4) income—the remaining forests (remanescentes).

– It is the responsibility of the Ministry of Agriculture to classify the various regions in accordance with this code, and towards its effects.

– Private forest considered as remanescentes will be alienated to public ownership.

– Any tree whatsoever may, due to its exceptional characteristics, be declared immune from cutting, and the proprietor shall be idemnified.

– Forests are free from taxes, and the value of the land on which they stand shall not increase.

– Protective forests give freedom from taxes to the land they occupy.

– Urban properties with exceptional trees will have a reasonable reduction in taxes, as long as the trees are properly cared for.

Chapter III

– It is prohibited to cut the existing forests along the bank of rivers, lakes, and highways, in regions with sparse vegetation.

– It is prohibited to devastate the vegetation on the slopes of hills which surround (frame) picturesque sites and landscapes in the urban centers and their surroundings.

– No owner of lands covered by forests may cut more than $^3/_4$ of the existing vegetation.

– The steel industry and transports which use vegetable carbon are obliged to maintain sufficient forests to support their indispensable needs.

– In the Northeast, it is prohibited to cut any vegetation within a radius of 6 kilometers from the heads of water courses.

– It is prohibited to cut the trees in a band covering 20 meters on each side of highways, except to preserve the road or open a view to landscape.

The Code went on to point out measures, and to create a Federal Forest Council to spread throughout the country forestry education and conservation in general. However, its execution was very defective. In the State of São Paulo, for instance, where the destruction of forests was progressing most rapidly, only in 1943 was something done to apply the Code. The rule it contained to save 25% of the forests on private land was sabotaged by dividing the property into a forested and a non-forested half. As the forested half then was suddenly forested for 50%, half of this forest could be cut under the law. This process was repeated over and over. Low salaries led to corruption. Moreover, designation of forests as protective or remanescentes was neglected by the Ministry of Agriculture. Innumerable decrees were ignored by the bureaucracy, unknown to the people, and thus for all purposes were nonexistent.

The Forest Code of 1966 perfected the one of 1934. It created some protection for slopes of more than 25°, and completely prohibited cutting on slopes steeper than 45° or on lands more than 1800 m above sea level. Once again implementation was the weak point.

The same is the case with regard to another element which could have an important role in conservation, namely the Brazilian Navy. The Constitution guarantees access for all to a band 33 metres wide extending along the coast, which is the property of the Navy. It gives the right of passage across all property in order to reach this band. The fluvial and coastal islands also belong to the Brazilian Navy. But all these rights are neglected, whereby the population is losing a most valuable potential for recreation. This situation calls urgently for reversal.

Hypotheses, Considerations, and Proposals

By way of conclusion, five '*hypotheses*' are formulated (and elaborated in the original text). They are the following:

1. The relationship colonizer–vegetation has always been a predatory one.
2. The relative lack of knowledge about tropical nature makes this predation worse.
3. There are sufficient laws to guarantee preservation of this vegetation, if they were applied.
4. The Brazilian culture is in great part a consequence of its secular existence in relation to tropical vegetation. The preservation of this nature is intimately related to the preservation and evolution of this culture.
5. The Brazilian people, who are the legitimate owners of the Brazilian forests have historically received almost nothing from its destruction.

From these hypotheses we proceed by way of four *considerations*:

6. There is obviously a relation between the use of larger amounts of land and population growth. However, this relation is not necessarily one of the clearing of virgin forests. It seems evident that in the recent history of Brazil the clearing of forests was not tied to population growth, since the use of these new lands was principally oriented toward production for export.
7. We have already seen that there is almost no concern with the maintenance of native forms of vegetation. And very rarely has such concern been seen in work focused on hydrographic basis or regional problems, which are the adequate ecological scale in which they should be treated.
8. Another important conclusion is that the destruction of vegetation is, at its base, a consequence of relations among people, rather than simply coming from the relation of man with nature.
9. Finally, it is important to remember that the preservation of the natural vegetation forms should not be intended to block economic development. On the contrary, it should be seen as a search for a balanced way to rationally use these riches, keeping in mind the goal of its greater productivity, necessary reserves for the future, and the culture and well being of the community. In fact, the preservation of a reasonable amount of areas covered by native vegetation is one of the dimensions of development.

From here we proceed to fourteen *proposals*. First the 9 general ones:

10. The Brazilian people must have access to accurate information about the present reality of the devastation of native forms of vegetation.

11. The government must be transformed into the representative of the will of the Brazilian people in all matters, in order that the people shall have the power to decide on the primitive vegetation to be preserved.

12. Deeper research on the natural elements within the Brazilian territory should be carried out.

13. Since the process of destruction of the native vegetation forms is dynamic, it requires dynamic formulae and strategies to fight it. This struggle and review of strategy must be carried out at a velocity which is at least proportional to, or greater than, that of the potential destruction.

14. The preservation of vegetation should be seen as part of work focusing on the regional level, and on hydrographic basins, since these are the most complete environmental units produced by nature.

15. Study, research, and replanting of native vegetation should be immediately begun in all areas which have been excessively devastated.

16. All those who are working, at whatever level, to preserve natural vegetation should join forces as much as possible.

17. In general, the Brazilian population never learned to plant trees. A fundamental step to be taken is to discuss the importance of vegetation in all schools, at all levels. These discussions should be carried out in simple, direct, objective language.

18. It is necessary to find an effective way of establishing parks that really will preserve the native Brazilian vegetation. This would also enable the preservation of all those parks which have already been decreed but whose areas continue to be destroyed.

Finally the 5 ones with respect to the Amazon forest (in abbreviated form):

19. An occupation of this last large forest of Brazil should be carried out giving full attention to the integrity of the environment.

20. It is necessary to set aside reserves belonging to the Union, States, or municipalities, and provide them with sufficient policing power, rather than assuming that 50% of the forests will be saved.

21. An occupation of Amazonia should be carried out at a rate compatible with the studies necessary to safeguard it.

22. A large and undivided reserve in the Brazilian part should be established and maintained, with well-marked and publicized boundaries. This would give the next 2–3 generations the time to determine its destination. Exploitation of minerals should be allowed in rigidly determined areas.

23. While the responsibility for the use of Brazilian Amazonia rests with the Brazilian people, it will be necessary to control the multinational corporations in their home countries as well.

And here is a lyrical proposal:

24. The law must provide that only music composers—and only they—be allowed to have birds from our forests in their houses.

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8. The Science of Amazon Conservation

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A major problem in preparing an adequate conservation plan for the ten percent of the earth's biota thought to occur in the Amazon Basin is the minimal amount of knowledge about the natural history of the region. The least known of the earth's terrestrial biological formations, the majority of its species are unknown to science, and of those that are the details of their distribution and ecology are scantily known. Even the best recorded groups, such as the butterflies and birds, still produce surprises: for example, in 1969 I netted a pair of black-chested pygmy tyrant flycatchers (*Taeniotriccus andrei*) at Belem. This proved to be the first record of the species east of Santarem, some 625 km to the west.

Since the Amazon forest is not uniform in species composition throughout the basin, this rudimentary state of knowledge presents a challenge in choosing appropriate locations for national parks and other conservation areas. The current situation to the selection problem rests on an approach of analyzing the geographic distributions of well-known groups, such as birds (Haffer, 1969; Haffer and Simpson, 1978). In a series of publications Haffer (1969, 1970, 1974, 1978a, 1978b) noted that the distribution of species of forest birds of the Amazon included some which were relatively restricted and occurred in clusters —clusters of endemism. With insights derived from present rainfall patterns and information about past climates, he interpreted these clusters of endemics as representing those parts of the basin where rainforest persisted during periods of the Pleistocene when conditions were so cold and dry as not to allow a continuous forest cover. According to this view, new species and races of birds evolved during these periods of isolation, and when conditions once again favored forest cover over most of the basin, some of these did not spread throughout for a variety of reasons. The distributions of such birds, viewed today, in a sense represent ghosts of these past so-called Pleistocene refugia.

While this interpretation is generally accepted, it is far from proven fact. Fortunately, from the conservation point of view, it is not necessary to accept this interpretation of these geographic patterns in order to realize that such clusters of endemic species are indeed logical sites for parks and reserves. These species will only be conserved by establishing protected areas which include the areas in which they occur.

The current plan for a system of conservation units is based on this approach (Wetterberg *et al.*, 1976) and was accepted after discussion by the second meeting of the Intergovernmental Technical Group on Protection and Management of Amazon Flora and Fauna in August 1977. Maps of refugia as defined for birds (*vide* Haffer), butterflies (Brown, 1976), and reptiles (Vanzolini, 1973), as well as phytogeographic regions (a somewhat similar analysis) based on five families of woody plants (Prance, 1977) were superimposed. Those areas with the greatest degree of coincidence of 'refugia' as defined for the four taxa were given highest priority for conservation, and where there was the least degree of coincidence (i.e., a refugium for only one group) the least priority was given. Interestingly, some organisms seem to have more refugia than others, and not surprisingly, some of these do not coincide with all those for groups with fewer refugia. This is probably because a group such as butterflies which requires a small area could persist in a smaller forest patch (refugium) than could, for example, birds (Oren, 1982). This has important implications for conservation (Lovejoy, 1982).

As reassuring as the possibility of such an approach may be in the face of limited biological knowledge, it is nonetheless a doubtful assumption that conservation areas based on refugia defined for birds, two subfamilies of butterflies, reptiles, and only five plant families, will accommodate the rest (99 + %) of the Amazonian biota. It is the best we can do for the moment, but clearly there is a need to enlarge the data base on which such critical decisions depend.

At least two major efforts are afoot to do just this. The National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazonia, INPA) at Manaus has a joint effort with the New York Botanical Garden to enlarge the botanical data base. Existing data in the literature and herbaria have been assembled, and can be analysed once they are in a computer. At the same time, botanical expeditions are going to areas immediately threatened, or areas which have been largely neglected through remoteness, to fill in some of the blanks. Clearly there is a need for a Projeto Fauna to complement this Projeto Flora, although it is a much more difficult, an almost monumental task. Such a project was announced in 1981 by Brazil's National Research Council (CNPQ). Probably the first initiatives will be in western Amazonia where some of the funding will come from a research component of a World Bank loan.

Such an undertaking is so large as to require decades for completion, particularly in view of the limited trained scientific manpower available. Therefore it will be important to assess the results and their implication for conservation plans in five years or so. While in no way precluding the need for the larger and longer scholarly documents that should eventually emerge from such efforts, there is probably a need to consider preparation of preliminary atlases for some of the better known faunal taxa (e.g., various vertebrate groups and butterflies).

In the meantime, the reasonable thing to do is to proceed with conservation action based on current knowledge, as is happening. Since 1977 new protected areas have been established in Bolivia, Ecuador, Venezuela, and most notably, Brazil, totalling 118 300 km^2, an area larger than Austria (Wetterberg *et al.*, 1981). The Brazilian areas constitute close to 80 000 km^2.

The 1976 analysis of conservation priorities took note of the problem of what size parks and reserves should be. This is a problem all over the world because it is now widely recognised that an isolated fragment of once continuous natural habitat invariably loses species after isolation (Lovejoy and Oren, 1981). Habitat fragments go through an ecosystem decay process rather reminiscent of radioactive decay, progressively losing species in the process of approaching a simpler and somewhat stable state. This problem really calls into question whether any park or reserve in the world will ultimately fulfill the purpose for which it was originally established, as well as being of fundamental importance for almost any management goal for a habitat fragment.

The Amazon approach has been, once again, to use the best available information, namely Terborgh's estimate (1975), but also to work toward improving the state of knowledge about the problem. So while a minimum size of 2500 km^2 is being followed in the establishment of new areas, a major research effort is underway to study the problem. A joint US–Brazil effort involving the World Wildlife Fund-US and INPA is studying this problem taking an experimental approach (Lovejoy, 1980).

Brazil has a law that 50% of the land in any Amazon development project must remain in forest, and authorities of the Manaus Economic Free Zone (SUFRAMA) have agreed to arrange the 50% in the Distrito Agropecuaria north of Manaus to provide for the long-term study. On a number of cattle ranches (Fig. 8.1) researchers are being permitted to pick out a series of forest reserves while the forest is undisturbed but which will eventually be isolated. They will comprise a size series of reserves ranging from one to 1000 hectares in size, with replicates in each size class, plus one single large reserve in excess of 10 000 hectares and perhaps as much as 16 000. There are two 'controls' for the experiment. Firstly the data collected by studying the fauna and flora of the reserves while still part of an intact forest prior to isolation will provide a reference point. Secondly comparative data will be available from the single large area, which although most probably less than minimum critical size, will nonetheless be changing so slowly relative to the smaller reserves that it can essentially be considered mostly unaffected by the ecosystem decay function.

The purpose of the size series is twofold. One is to provide data to demonstrate whether forest patches of similar size tend to end up after species loss with similar species composition. The second is to provide a series of increasingly complex and more time consuming approximations of the species loss process. The smaller reserves will yield some quick and very simple insights into species loss and the larger reserves a slower but deeper understanding. Of course in addition there probably are certain factors which loom greater in importance in small reserves than larger ones. Further, the results of the research program (Fig. 8.2) are intended not only to make some approach to defining minimum critical size for Central Amazonian forest, but also to provide a basis for managing a reserve of lesser dimension to hold more and/or certain species which it otherwise would not.

Fig. 8.1. Cattle ranch near Manaus (Photo credit: Dr E. J. Fittkau).

A one and a ten-hectare reserve have already been isolated and have yielded new insights into the ecological dynamics of forest fragments (Lovejoy, Bierregaard and Schubart, 1982). It has been found that there is a major increase in the rate at which birds are netted in the reserve the instant the surrounding understory is destroyed. This may be due to truncated territories of some bird species resident in the reserve (i.e., no new individuals) but also probably includes an influx of birds from the surrounding devastated area. This overpopulation problem is superimposed on the basic species loss process. Within less than a year the capture rate in the one-hectare reserve had fallen to a level lower than prior to isolation, and species discovery functions (beginning with a series of successively later dates) calculated for the ten-hectare reserve indicated sampling of an increasingly impoverished bird community. In addition, the margins of the reserves were affected markedly by increased temperature and humidity fluctuation and showed an elevated susceptibility to tree blow down from increased exposure to wind. Both the influx and margin problems are of greater importance the smaller a reserve.

Amazon conservation, of course, must also take cognizance of the full variety of vegetation types, and particularly of the freshwater systems. Of special note in this regard is the remarkable relationship recently documented in considerable detail by Goulding (1980) about the relationship between many Amazon fish and the floodplain forests. Many fish swim into these forests at the time of high water and feed on fruits and seeds and other living matter which fall into the water. This transfer of nutrients from the terrestrial to the aquatic ecosystem permits a higher fish biomass than would otherwise be possible. This is of enormous significance in relation to the attraction of floodplain soils for agricultural development because of the annual deposition of silt. Any gain for agriculture through deforestation of the floodplain would be accompanied by a loss of fishery productivity. Since the Amazon fishery is a major source of animal protein (50%) for the Amazon populace this is a serious concern.

In additon there is a need for some parks or reserves of floodplain areas with accompanying portions of river to protect the associated fish community. These may be terribly difficult to design, and are not only important from the

Fig. 8.2. Minimum Size project—base camp (Photo credit: Dr E. J. Fittkau).

strictly biological point of view, but also are important in that they would in essence provide an undisturbed fish community so that the management of harvested and otherwise disturbed fish communities may be assessed.

Finally, much of the effort based on the above will fail unless cognizance is taken of the implications of the forest/rainfall relationship so elegantly illuminated by Salati and his colleagues (c.f. Salati, 1978; Salati *et al.*, 1978; Lovejoy and Salati, 1982). Through a variety of approaches, including isotopic analysis of rainfall across the Amazon Basin (which has an essentially unidirectional airflow from the Atlantic to the west), Salati *et al.* (1978) have demonstrated conclusively for the first time that forest can generate rainfall, and that in the case of the Amazon Basin, something of the order of 50% of the rainfall is generated within the basin itself and largely by the forest. This was the subject of a workshop at Piracicaba in November, which outlined the research necessary to define the precise dimensions of the Amazonian hydrological cycle so that appropriate land use recommendations can be made to avoid triggering an irreversible drying trend (Salati *et al.*, 1983).

The precise amount of Amazonian deforestation that has taken place is unknown and estimates of the current rate of forest loss are imprecise (Carvalho, 1981; Fearnside, 1982). Luckily it has not progressed to the extent that there have been many extinctions, or that the forest/fishery and forest/rainfall relationships have been destroyed. Consequently, there is still the opportunity to plan Amazon development scientifically so as to protect its incredible biological riches. There appears to be a good chance that this will actually happen.

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9. Conservation of Tree Genetic Resources: The Role of Protected Areas in Amazonia

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Introduction

The most important reason to conserve species of trees is to retain as much genetic diversity as possible. Different tree species are adapted to different conditions, susceptible to different diseases, and contain different substances of potential and actual use to man.

Compared to forests of temperate areas and even some other lowland rainforests, very little is known about the Amazonian forest; its composition, dynamics, geographic and genetic variation, nutrient cycles, productivity and economic potential.

Man's survival on earth may depend on genetic diversity of its plant cover. The larger the gene pool, the greater potential there is for utilization of the plants and for the survival and evolution of the entire system.

A disease can devastate an entire single tree crop, as has happened in a number of cases, for example coffee leaf rust (*Hemileia vastatrix*) of Brazilian coffee. Man needs other trees as alternative crops that are not susceptible to diseases already known. Many known species of Amazonia have not yet been adequately tested for potential uses such as wood, fibre, fuel, food, drugs and essential oils. The many undiscovered and only recently discovered species have not been tested at all.

Man is faced with worsening worldwide food and fuel shortages and will have to look, at least in part, for resources in the world's tropical vegetation to supply his needs. The fuel shortage will stimulate research towards new potential sources of tree biomass. There are a large number of, as yet, unexploited Amazonian plants which are rich in oil. Examples include the Babaçu palm (*Orbignya speciosa*) and a large tree of restricted natural range, *Acioa edulis*, described only in the last decade, and long used by local people as an oil source for cooking and soap-making. The latter tree is known so far only from the Rios Purus and Juruá and is typical of many other little known species of restricted local range which soon could be eliminated by widespread deforestation. Because of this restricted distribution of many species in Amazonia, and because of our present lack of knowledge about them, there is the real danger that widespread destruction of forest will destroy vitally important material and deny mankind both information and product before the world is even aware of their existence.

Tree Genetic Resources

Variation between species and species survival

The importance for preserving undiscovered species from extinction lies partly in their role in the ecosystem and mainly in their potential genetic resources.

In the ecosystem, different trees in the forest depend on each and are functionally linked with animals. A certain species of tree, not in itself of recognised importance to man, may provide food in one season for an insect species which in another season pollinates the flowers of a tree of importance. In order for the ecosystem to survive intact, there must be flowering trees throughout the year to feed the pollinators. There are certainly many other obligate interactions within the forest between the trees and other plants and insects (Figs. 9.1a and b), bats, rodents and birds, of which we at present know virtually nothing.

Potential genetic resources of unknown tree species are great. In Amazonia, where only 50 of some 2500 tree species are used, at least 400 species are thought to have some direct commercial value (Myers, 1980). This potential is not restricted to production of round or sawn timbers or fibre for pulp and paper. Although difficult to quantify for Amazonia there is little doubt that fruit including nuts, gums, tannins, oils, resins, bark fibres, latex, dyes and medicinal products such as produced by the different components of moist forests elsewhere (e.g., Jong *et al.*, 1973; Robbins and Matthews, 1974; Lea, 1976; Okafor,

(a)

(b)

Fig. 9.1. Insects from the rainforest of Peru: (a) tortoise beetle (*Tauroma aureicornis*), (b) male weevil (*Rhinastus latesternus*). (Photo Credit: Ken Preston-Mafham.)

1980) are equally as important in this region. Many of these forest products are gaining in economic importance with time (e.g., Grainger, 1980).

Any ecological programme for Amazonia must consider not only the untapped resources of lesser known species, but also the situation of several of the naturally occurring trees of economic importance such as Sôrva (*Couma* spp.), Brazilnut (*Bertholletia excelsa*) and Rubber (*Hevea braziliensis*). It is unfortunate, but understandable, that some of the most threatened species of the Amazonian tree flora are also some of the most well-known and profitable economically. Again, these species are important partly because of their role in the ecosystem and mainly because of their commercially important genetic resources. In the ecosystems, for example, some species such as Brazilnut depend on rodents to distribute their fruits by moving them and by chewing and weakening their hard seed coats as a prerequisite for germination. If the amount of forest conserved in a particular area is not enough to support the rodents then the trees will not regenerate.

A rush for quick and excessive short-term profit has led to the indiscriminate felling and loss of commercial genetic resources of several species. The classical example is Rosewood (*Aniba rosaeodora*) which used to be abundant in the forests of Central Amazonia but now has been almost eliminated (Goodland and Irwin, 1974). Mobile distilling factories were assembled at various places throughout the region and then all the trees in that area were felled in order to extract the rosewood oil which is rich in linalool. Better access in the last decade greatly accelerated the exploitation of Rosewood. All this has occurred despite the fact that the leaves contain more linalool than the wood and that plantations can be grown specifically for harvesting the leaves (Vieira, 1972) and these could be planted with more genetically appropriate stock to promote maximum oil yield. In addition there are other alternatives, such as species of *Croton*, which yield linalool and which grow in secondary forest.

Another tree indiscriminately felled, especially in the state of Pará, is Massaranduba (*Manilkara huberi*). These trees are felled to extract a few dollars worth of latex while perhaps over a thousand dollars of valuable timber is left to rot in the forest (Goodland and Irwin, 1974). This activity has severely reduced the incidence of this species.

Ucuuba (*Virola surinamensis*) much sought after in the plywood and veneer industries, was formerly a common tree in the igapó forests of Pará. The systematic felling and transport of large rafts of this tree to sawmills threatens its continued presence in Amazonia.

Geographic and genetic variation within species

It is evident that, in the past, the attention of conservationists has been focussed mainly on ecosystems and on species, especially on 'endangered species'. Problems peculiar to the conservation of within-species genetic diversity have often been neglected.

Man, in ignorance, has made many mistakes during millenia of domesticating food crop plants and animals. If he had studied the ecology of the native ancestral populations before he changed them and replaced them with domestic varieties, that knowledge would be very useful and satisfying to have today. If he had saved more of the geographic and genetic variability which was present in the ancestral populations, the modern breeder could effectively draw on such a reserve of variability to provide a better buffer against disease and insect pests and against other environmental insults which regularly wreak genetically-narrow, modern crop species.

Only with very few forest tree species have the wild origins of populations and plantations become confused and uncertain. With most commercial species, many of the stands are still growing in the regions and environments where they evolved, with little modifying effect by man. But even in the confused and uncertain situations commercial tree species today are very near their wild undomesticated beginnings compared with most food crop plants or domestic animals (Libby, 1973).

Some genetic variability within a species may be obtained by selection of geographic races (provenances) and more by selection among individual trees of a geographic race. Some may be released by recombinations of genes as domestication proceeds. Still more will be created by mutation, perhaps including techniques of directed mutation some time in the future. However it is the native populations which contain much variation that is potentially useful and it is there conservation of genetic resources must begin. Foresters, in company with ecologists and conservationists have the opportunity to study, conserve and preserve that original variability of forest trees before domesticated varieties replace much or all of it (Libby, 1973). Many animal and crop breeders envy this opportunity and it would be foolish and negligent to waste it.

Conservation of Tree Genetic Resources in Amazonia

While the risk of extinction of individual species may be great in some parts of Amazonia, the potential loss of a significant proportion of the total gene pool is a greater risk. For moist forest species, about which we know so little, the best method of preservation of gene pools is by conservation in situ on representative areas while recognising that action in this direction must inevitably affect the management and conservation of the related ecosystems and that in situ conservation of a given species or population should be complemented by ex situ conservation once problems such as shortness of periods of seed viability, irregular and infrequent flowering, susceptibility of relocated species to new pests and pathogens and so on are overcome. A lack of a dependable supply of seed for establishment of ex situ conservation stands could be overcome by research on vegetative propagation of the Amazonian species, for example.

Because of lack of biological knowledge of many forest trees and the difficulty of forecasting long-term changes in environmental conditions and human needs in Amazonia, 'conservation in perpetuity' is probably unrealistic and measures undertaken should be aimed to conserve genetic diversity over a period of some 500 years in the first instance. The time available during which an action programme must be implemented in Amazonia is very short, forest conservation must become effective within 5–10 years.

The Amazonian rainforest is not a uniform mass of vegetation as it is popularly perceived (Wetterberg *et al.*, 1981) and is capable of being divided up into phytogeographic regions. Phytogeographic regions served as a basis for a 1976 "Analysis of Nature Conservation Priorities in the Amazon" (The Amazon Analysis) which was published co-operatively by the Brazilian Forestry Research and Development Projects (PRODEPEF), the Food and Agriculture Organization of the United Nations (FAO) and the Brazilian Forestry Development Institute (IBDF). One recommendation of the Amazon Analysis was that each phytogeographic region should contain an average of at least six parks or other protected areas to be adequately represented, and, that their distribution be allocated proportionally according to the relative size of each region. Because of the geographic representation of these regions, they are much more likely to be effective in forest tree gene resource conservation than a single large reserve or randomly or systematically distributed smaller reserves. However there is still the fundamental problem of inadequate knowledge of which species occur where. Also, the ecotones or transition zones which separate adjacent ecosystems constitute important centres of genetic variability and of dynamic evolution. It is essential to conserve the generic wealth of these zones—a biological argument which reinforces the managerial convenience of including, wherever possible, more than one ecosystem within the same protected area (FAO, 1981).

If a given number of individuals is considered essential for a viable population gene-pool, then the density of individuals per hectare will determine the area of forest required. In Amazonian rainforest there are relatively fewer individuals of

Fig. 9.2. Manu River, Manu National Park, Peru 1974 (Photo credit: Dr H. Jungius).

each species per hectare than in temperate forests, therefore areas need to be larger.

Differences in breeding system have an important influence on the choice of in situ conservation strategy. In tropical rainforests, contrary to temperate forests, wind pollination is extremely rare, and dioecism much more frequent. Size of seed, and the palatibility of its fruit to birds and other animals affect the rate of seed dispersal and hence of gene flow.

The 1976 Amazon Analysis reviewed questions of minimum size, shape, existing and planned conservation units and general location of areas to be preserved, though research is continuing as to what is required for various purposes. For many species an effective system of areas managed for genetic conservation will find a place for both large and small areas.

The Role of Protected Areas in Amazonia in Conservation of Tree Genetic Resources

Many terms exist for various kinds of protected areas. Existing and planned conservation units in the Amazon include National Park (Fig. 9.2), Brazilian Forest Reserve (transitory designation), Wildlife Refuge/Reserve, Ecological Station, Nature Park, Natural Monument, National Reserve and Biosphere Reserve (Wetterberg *et al.*, 1981).

For purposes of genetic conservation of forest trees, it is sufficient to recognise four of the categories of protected areas described by IUCN (IUCN, 1978). They are: (1) The Strict Nature Reserve, (2) The Managed Nature Reserve, (3) The National Park and (4) The Managed Resource Area. The management objectives and criteria for selection and management of each, as set out in the IUCN publication, are reproduced in Appendix I.

The essential features of these four categories are:

(1) Strict Nature Reserve

Human disturbance kept to a minimum, allowing nature and natural evolution to take their course. Observational, but not manipulative, research and monitoring permitted, together with strictly controlled access for educational purposes. Controlled collection of limited quantities of seed permitted. Suitable to accommodate large numbers of both commercial and non-commercial species.

(2) Managed Nature Reserve

Deliberate human manipulation for research of management purposes permitted, provided that the basic objective is conservation. Suitable for conservation of particular species, populations or habitats which would eventually disappear in the absence of man's periodic intervention.

(3) National Park

A large area in which conservation is combined with public recreation and tourism. Often suitable for zonation for management purposes, with zones ranging from the man-made environment of camp sites and administrative buildings to undisturbed Strict Nature Reserves from which the public is excluded.

(4) Managed Resource Area

A large area in which the primary objective is sustained production of goods or services. For some species it may be possible to combine genetic conservation with production silviculture, for others zonation of the area and conservation in Strict Nature Reserves within it may be necessary.

It would be necessary to re-classify some of the Amazonian protected areas under the appropriate heading. As a supplement to these existing and proposed protected areas, the inclusion of an element of genetic conservation into the management plans of production forest areas could provide an additional simple but effective method of conserving genetic resources in some forest types, thus combining yield of forest produce with conservation of genetic diversity.

An array of management strategies is available for in situ conservation of Amazonian forest genetic resources. The choice would depend on the level and intensity of forest management and utilisation being practised, and on the state of silvicultural knowledge of the forest system and species it contains. If nothing is known about some species, they should be preserved on an ecosystem basis.

Classification of known trees should be by species and be based on current utilization value, regeneration system and intensity of genetic management. Species not presently utilized would form a separate special category which, in Amazonia, would include the majority of forest tree species. For any reserve it is important to define the primary objects of management, whether it be to conserve the many unused and unknown, or the few long used and well-known species, or both.

Available options are illustrated in the flowchart in Appendix 2 (taken from FAO, 1981). The management of the appropriate genetic resources and protected areas are summarized in Appendices 3 and 4.

In deciding from this material appropriate strategies for reserves in Amazonia, a more enlightened attitude of administrators, foresters and conservationists to the untapped resources of the Amazonian forests is necessary if supplies of food, timber, fuel and other forest products are to be available for future generations.

Glossary of Terms

Dioecism: male flowers on one tree, female flowers on another.

Domestication: implies the collection of seeds or plants, ideally from the entire natural range of a species and, in time, the selection, propagation and breeding of variants best suited to the needs of man.

Gene pool: the sum of all genes in a given cross-breeding group of organisms. In the widest sense, natural forests are gene pools, in the narrower sense also seed stands, provenance collections, tree gene banks and arboreta.

Genetic resources: the reservoirs of genetic information accumulated for generations from the beginning of genetic diversity, by various reasons, and having survived against acute or chronic changes of evolutionary pressure at various locations are now a precious heritage of life on earth and of immeasurable value for future use.

Population: (1) genetically, a group of individuals which are related by common descent and which for convenience may be treated as a unit. (2) statistically, a group of observations (or the individuals on which the observations are made), which is homogeneous.

Provenance: The place in which any stand of trees is growing. The stand may be indigenous or non-indigenous.

Race: an intraspecific category, primarily a population or aggregate of populations, with characteristic gene frequencies or features of chromosome structure that distinguish a particular group of individuals from other groups of the same kind within formally recognisable sub-species or within species. The term sub-species is frequently used in the same sense as race. Any race is able to interbreed freely with any other race of the same species. Whenever different races of a cross-fertilising species occupy geographically separate territories they are said to be allopatric; those occupying the same territory are sympatric.

Races may become distinct species by reproductive isolation (with respect to the other races of the same species) and thus the formation of isolated gene pools.

Geographic races are subspecies occupying a geographic subdivision.

Ecological races are local races owing their most conspicuous attributes to the selective effect of a specific environment (ecotype).

Physiological races are races characterized by certain physiological, rather than morphological, characters.

Chromosomal races are races differing in respect to features of chromosome structure (cytotypes) or in chromosome number (polyplotypes).

Selection: natural selection acts to preserve in nature favourable variations and ultimately to eliminate those that are 'injurious' (Darwin). It is a consequence of differences between genotypes in respect to their ability to produce progeny and represents a process without purpose whose primary form ('Darwinian selection') takes place between individuals in a population. However, both competition and selection do occur between reproducible biological units of greater and lesser complexity than that of individuals.

Artificial selection, in contrast to natural selection, is a purposeful process with definite goals set by the breeder and means selection applied under a selected set of environmental conditions. It normally occurs with controlled matings of a few selected genotypes, and its goal is to change specific phenotypic characters of a population. Artificial selection applied to one character almost always leads to changes in others ('correlated response').

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Appendix 1

Categories for Conservation Areas
(Extracted from IUCN, 1978)

1. Strict Nature Reserve

Management Objectives

The objectives of a scientific reserve are to protect nature (communities and species) and maintain natural process in an undisturbed state in order to have ecologically representative examples of the natural environment available for scientific study, environmental monitoring, education, and for the maintenance of genetic resources in a dynamic and evolutionary state. Research activities need to be planned and undertaken carefully to minimize disturbance.

Criteria for Selection and Management

These areas possess some outstanding ecosystems, features and/or species of flora and fauna of national scientific importance. These areas are generally closed to public access, recreation and tourism. They often contain fragile ecosystems or life forms, areas of important biological or geological diversity, or are of particular importance to the conservation of genetic resources. Size is determined by the area required to ensure the integrity of the area to accomplish the scientific management objective and provide for its protection.

Natural processes are allowed to take place in the absence of any direct human interference. These processes may include natural acts that alter the ecological system or physiographic feature at any given time such as naturally occurring fires, natural succession, insect or disease outbreaks, storms, earthquakes and the like, but necessarily exclude man-made disturbances. The educational function of the site is to serve as a resource for studying and obtaining scientific knowledge.

Land use control and ownership should in most cases be by central government. Exceptions may be made where adequate safeguards and controls relating to long-term protection is ensured and where the central government concurs.

2. Managed Nature Reserves

Management Objectives

The purpose of these areas is to assure the natural conditions necessary to protect nationally significant species, groups of species, biotic communities, or physical features of the environment where these require *specific human manipulation* for their perpetuation. Scientific research, environmental monitoring and educational use are the primary activities associated with this category.

Criteria for Selection and Management

This type of area is desirable when protection of specific sites or habitats is essential to the continued existence or well-being of individual biotic species, resident or migratory fauna of national or global significance. Although a variety of (protected) areas fall within this category, each would have as its primary purpose the protection of nature, and not the production of harvestable, renewable resources, although this may play a role in the management of a particular area. The size of the area or in certain instances seasons in which special management is necessary, will be dependent upon the habitat requirement or specific characteristics of the species to be protected. These need not require vast areas but could be relatively small consisting of nesting areas, marshes, or lakes, estuaries, forest, or grassland habitats.

The area may require habitat manipulation to provide optimum conditions for the species, vegetative community, or feature according to individual circumstances. For example, a particular grassland or heath community may be protected and perpetuated through a limited amount of livestock grazing. A marsh for wintering waterfowl may require continual removal of excess reeds and supplementary planting of waterfowl food, whereas a reserve for an endangered animal may need protection against predators. These areas may be developed in limited areas for public education and appreciation of the work of wildlife management.

Ownership may be by the central government or with adequate safeguards and controls in which long-term protection is ensured, by lower levels of government, non-profit trusts or corporations or private individuals or groups.

3. National Park

Management Objectives

The management objectives of this type of area call for the protection of natural and scenic areas of national or international significance for scientific, educational, and recreational use. The area should perpetuate in a natural state representative samples of physiographic regions, biotic communities and genetic resources, and species in danger of extinction to provide ecological stability and diversity.

Criteria for Selection and Management

National parks are relatively large land or water areas which contain representative samples of major natural regions, features or scenery of national or international significance where plant and animal species, geomorphological sites, and habitats are of special scientific, educational, and recreational interest. They contain one or several entire ecosystems that are not materially altered by human exploitation and occupation. The highest competent authority of the country has taken steps to prevent or eliminate as soon as possible exploitation or occupation in the area and to enforce effectively the respect of ecological, geomorphological, or aesthetic features which have led to its establishment.

The resource is managed and developed so as to sustain recreation and education activities on a controlled basis. The area is managed in a natural or near-natural state. Visitors enter under special conditions for inspirational, educational, cultural, and recreational purposes.

The protected status of the area is adequately maintained directly by the central government or through agreement with another agency.

4. Multiple Use Management Area/Managed Resource Area

Management Objectives

To provide for the sustained production of water, timber, wildlife, pasture, and outdoor recreation and at the same time provide for economic, social and cultural needs over a long term. The conservation of nature is also an objective of this category primarily oriented to the support of the economic activities although specific zones may also be designated within these areas to achieve specific conservation objectives.

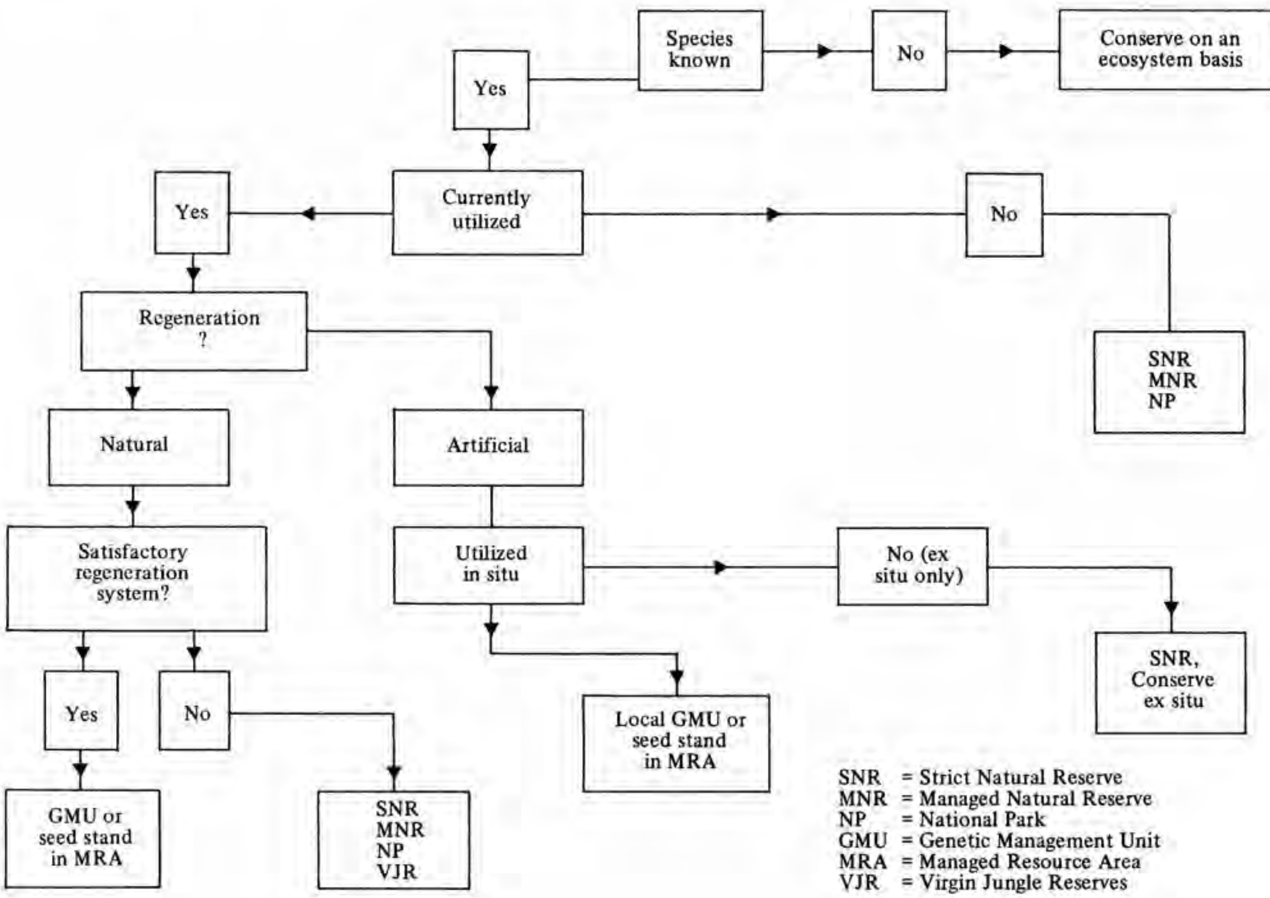
Criteria for Selection and Management

A large area, containing considerable territory suitable for production of wood products, water, pasture, wildlife and outdoor recreation. Parts of the area may be settled and may have been altered by man. Generally, these forest or other wildland areas do not possess nationally unique or exceptional natural features.

Planning to ensure the area is managed on a sustained yield basis would be a prerequisite. Land ownership would be under government control. Through proper zoning, significant areas could be given specific additional protection. For instance, the establishment of wilderness-type areas is consistent with the purpose of these areas as would be setting aside the nature reserves. Multiple use, in the context of a Managed Resource Area, is considered to be the management of all renewable surface resources, utilized in some combination to best meet the needs of the country. The major premise in the management of these lands is that they will be managed to maintain the overall productivity of the land and its resources in perpetuity.

Appendix 2

In Situ Genetic Conservation—Available Options
(Modified from FAO, 1981)



Appendix 3

Management of Genetic Resources and Protected Areas

(Modified from FAO, 1981)

Genetic resources management can be fully effective only if it is treated as an integral part of forest management and land management as a whole. The principle applies irrespective of which authority owns and manages a given area of land; this may be at national or federal level, at state, provincial or lower level, and the land manager may be the Forest Service, the National Parks Authority or university, company or private owners.

A clear case of integrated management occurs where the conservation of genetic resources can be combined with other management objectives on the same area, e.g., with sustained production forestry in Resource Management Areas or with tourism in National Parks. But the need for integrated management is no less when the conservation objective is the dominant one in an area, as in Strict Nature Reserves, since the value of the Strict Nature Reserve will be seriously impaired if the surrounding forest land is not well managed.

The management guidelines outlined below have been proposed by FAO (1981) for the four types of areas, (1) Strict Nature Reserves, (2) Managed Nature Reserves, (3) National Parks and (4) Managed Resource Areas. However, there would be considerable variation in detail from one management plan to another since every area possesses a unique set of conditions.

1. Strict Nature Reserves

These areas should ideally have a legal status over and above that of the Forest Reserves or National Parks in which they may be contained, but their establishment should not be deferred pending passage of the necessary legislation. They should be protected against human interference, but with provision for the following activities:

(1) Non-destructive scientific studies (e.g., sampling, measuring, monitoring).

(2) Controlled collection of reproductive material.

(3) Controlled access for education and training, including identification and labelling of individual trees as natural arboreta.

(4) Boundary maintenance including sign posting or planting with marker trees.

Especially note the following:

– *No* introduction of exotic plant or animal material into the reserve is permissible.

– *No* exploitation or removal of the forest resources (hunting, logging, mining, etc.) permissible.

– *No* collection of minor products, nor dead wood permissible.

– *No* management practices (e.g., thinning, cutting of creepers, removal of undergrowth, etc.) permissible.

Strict Nature Reserves should be protected by a buffer zone of sufficient area to prevent any outside influences and disturbances. The width of the buffer will vary according to the ecosystem and species to be conserved, but will generally be of a minimum of 100 m.

Strict Nature Reserves are appropriately located within National Parks, Managed Nature Reserves or Resource Management Areas which themselves constitute the necessary buffer zone. The Virgin Jungle Reserves of Malaysia, which cover some 20 000 ha or about 0.4% of the forest estate, provide a good example of this type of reserve (Putz, 1978). Rules concerning their management are shown in Appendix 4.

Another example is the system of Strict Natural Reserves in Nigeria, of which the one in Omo Forest Reserve has been designated as a Biosphere Reserve in the Unesco MAB programme. These reserves are surrounded by buffer zones. There are experimental plots—Investigation and Permanent Sample Plots—in which research is carried out on phenology, growth rate, nutrient cycling, biomass productivity, etc., in the buffer zones.

It should be noted that Strict Natural Reserves have not been established with the main purpose of conserving existing genetic resoucres, and will not be managed for this purpose. As a consequence, the ecosystem will evolve naturally, new species may become dominant and old ones will disappear in natural succession.

2. Managed Nature Reserves

These areas resemble Strict Nature Reserves in the desirability of special legal status and of a buffer zone, and in their use for non-destructive research, education and seed collection. No introduction of exotic plant or animal material is permissible.

The important difference from Strict Nature Reserves lies in the possibility, sometimes the necessity, for deliberate human intervention to favour the conservation of particular species, habitats or successional stages which might disappear if strictly natural conditions were to be maintained. Examples of management practices which may be required in Managed Nature Reserves are:

(1) Controlled burning to maintain fire-climax vegetation.

(2) Thinning, climber cutting, removal of undergrowth to favour survival and regeneration of particular individuals or populations.

(3) Enrichment planting to assist regeneration of particular local species and populations.

(4) Removal of predators, parasites, 'weed species', etc., to favour the desired species.

Harvesting and utilization of material removed in accordance with the prescriptions of the management plan may

Appendix 3 (continued)

be permitted in some circumstances, but production forestry is never the primary object of management in Managed Nature Reserves.

It is evident that the objects of management and the means of achieving them—*which* species are to be favoured and *which* operations are prescribed to that end—must be very clearly defined in the management plan if Managed Nature Reserves are to fulfil their purpose. The effects of management practises on species of secondary importance in the Reserves should also be closely monitored.

3. Genetic Resources within National Parks

On the overall management plan of the park, specific attention should be drawn to the fact that one of its objectives is genetic conservation, so as to ensure that this objective is not subordinated to other objectives of the park as a whole or of the specific areas inside the park to which it applies.

The following specific measures may be necessary to achieve the objectives of genetic conservation:

(1) Minimize human disturbance by limiting public access to the area.

(2) Avoid selective cutting and/or removal of particular phenotypes.

(3) Where applicable, permit intervention to maintain the desired successional stage and the integrity of the ecosystem.

(4) Permit non-destructive scientific studies and the controlled collection of reproductive material.

Since National Parks are commonly of substantial size, they offer the possibilities of zonation, e.g., they may contain Strict and Managed Nature Reserves from which the public is excluded, while the larger part of the Park area is freely accessible for tourism and recreation.

4. Genetic Resources in Managed Resource Areas

Unequivocal prescriptions should be inserted into the management plan for the area to ensure that the objectives of genetic conservation of the species under management is not subordinated to those of production forestry.

These prescriptions should include the following:

(1) Silvicultural treatment favouring the normal development of the full range of the species to be conserved should be applied.

(2) Logging should be carried out according to strict prescriptions to ensure renewal of the local populations of the constituent species while minimising damage to the habitat.

(3) Dysgenic selection through logging or removal of only the best species and phenotypes should be avoided.

(4) The area should be regenerated naturally or alternatively, by using seed or vegetative material collected within the reserve; the new generations should be derived from a representative and adequate number of parent trees.

(5) The area should be clearly demarcated, preferably by natural boundaries or permanent roads.

(6) A buffer should be maintained against contamination by pollen of non-local origin or, alternatively, reproductive material for artificial regeneration should be collected only in the central portion of the area where the local pollen source will predominate.

Other management practices can be applied to the area in accordance with local prescriptions for the species and sites in question. Restrictions on harvesting and production forestry should be limited to those, listed above, which are essential to conserve the integrity of the gene pool in the genetic management unit.

Survey, Monitoring, Research and Education

The following measures for survey, research and education are necessary in most regions but are urgently needed in the tropical rainforest if in situ conservation is to be fully effective:

(a) Need to support reconnaissance surveys of vegetation types with the purpose of preparing up-to-date vegetation maps and distribution maps of various species.

(b) A survey of endemic species to identify endangered species and their concentration within the various vegetation types, with the purpose of conserving them either in situ (within existing or new reserves) or ex situ.

(c) Taxonomic studies
  (i) intra-specific variation
  (ii) inter-specific variation

Preparation of practical plant taxonomic monographs for local use should be encouraged. Such monographs should deal with both the distribution of taxa and with intra-specific variation in forest ecosystems. The training of taxonomists should be encouraged, both in the field and in the herbarium.

(d) Initially (as soon as the reserve is established) a full list of all trees, shrubs, herbs, etc., should be prepared, and also herbarium specimens be documented. Subsequent inventory, depending on manpower and financial resources, should be carried out at regular intervals. This affords an opportunity of monitoring species frequency, mortality and growth rate.

(e) Areas of urgent research—breeding systems, population structures, phenology, fruiting, seed storage (most tropical forest tree seeds lose their viability very rapidly) and genecological studies.

(f) Universities running forestry courses in tropical countries should be encouraged to run postgraduate courses in conservation of forest genetic resources. They should also be given financial assistance and specialist staff as required.

(g) Attachment of personnel for training to countries with expertise and facilities in in situ conservation.

(h) Technical courses of 6 months–1 year duration should be organized for middle-level manpower.

Needs for International Action

A number of projects would be suitable for national, bilateral or multilateral financing and which would benefit the cause of genetic resource conservation:

Appendix 3 (continued)

(1) The preparation of a manual on methods of integrating the management of genetic resources in situ with forest and land management.

(2) The use of existing survey and inventory information to assess (i) the extent to which ecosystems, species and populations within species are conserved in existing networks of protected areas and (ii) the need for the establishment of supplementary protected areas to conserve the full range of within-species genetic diversity.

(3) The selection of few priority taxa or countries in which to assess existing surveys (and if necessary carry out new ones), which could serve for pilot studies providing models for later studies. In the tropics, the Dipterocarps in S.E. Asia and *Cedrela* spp. in Latin America would be suitable tropical pilot taxa, while developing countries which could contribute to pilot national surveys would include Malaysia, Indonesia, Nigeria, Chile, Costa Rica, Brazil and Peru.

(4) The organization of training courses devoted specifically to management of genetic resources. These could be located in the pilot study areas of (3) above.

(5) The injection of in situ conservation and management of genetic resources as an essential component of other training courses, both for scientists (e.g., tree improvement, forest management courses) and for planners and administrators (e.g., land use planning, economic development courses).

Appendix 4

Rules Governing the Virgin Jungle Reserves of Peninsular Malaysia

(Extracted from Putz, 1978)

3.1 Rules concerning the establishment of VJRs

3.1.1 Virgin Jungle Reserves (VJRs) should be located in Forest Reserves and surrounded by managed forest.

3.1.2 One or more VJRs should be established in every Forest Reserve representing all of the forest types present.

3.1.3 VJRs should be selected so as to be representative of the surrounding forests.

3.1.4 VJRs should be compact in shape, cover preferably 200 acres or more, and where possible have well defined natural boundaries.

3.1.5 VJRs should be reasonably accessible by road.

3.1.6 Proposals for VJRs will be forwarded to FRI by State Directors of Forestry. All proposed areas should be treated as VJRs until approved or rejected by the Director, FRI.

3.2 Rules concerning the maintenance of VJRs

3.2.1 All VJRs will have their own record books with copies at FRI and at the State and District Forest Offices. Sample Plot Forms 3 and 9 should be used in these records (these forms are reproduced in Appendix 2 of Putz, 1978).

3.2.2 VJR boundaries shall be inspected annually by the DFO and cleaned whenever necessary.

3.2.3 VJR signboards shall be posted at critical positions along the boundary and at intervals of not less than 30 chains.

3.2.4 When the compartments adjacent to the VJR are to be logged, trees along the common boundaries should be clearly marked with bright coloured paint.

3.2.5 Logging permits issued for compartments adjacent to a VJR must include the following clause:

> Nothing done under the terms of this permit may cause damage to trees in the Virgin Jungle Reserve in compartment... This forbids the dragging of timber through and the felling of trees into that compartment, the boundary of which is indicated on the attached plan.

3.3 Rules concerning the use of VJRs

3.3.1 No research plots of any kind will be demarcated in a VJR without the prior approval of the Director, FRI.

3.3.2 No cutting of any sort shall be made in a VJR apart from that required for the demarcation of boundaries, and around Ecology and Phenology Plots; such cutting, as far as possible, it to be restricted to monocotyledonous plants.

10. Preserved Areas in the Brazilian Amazon

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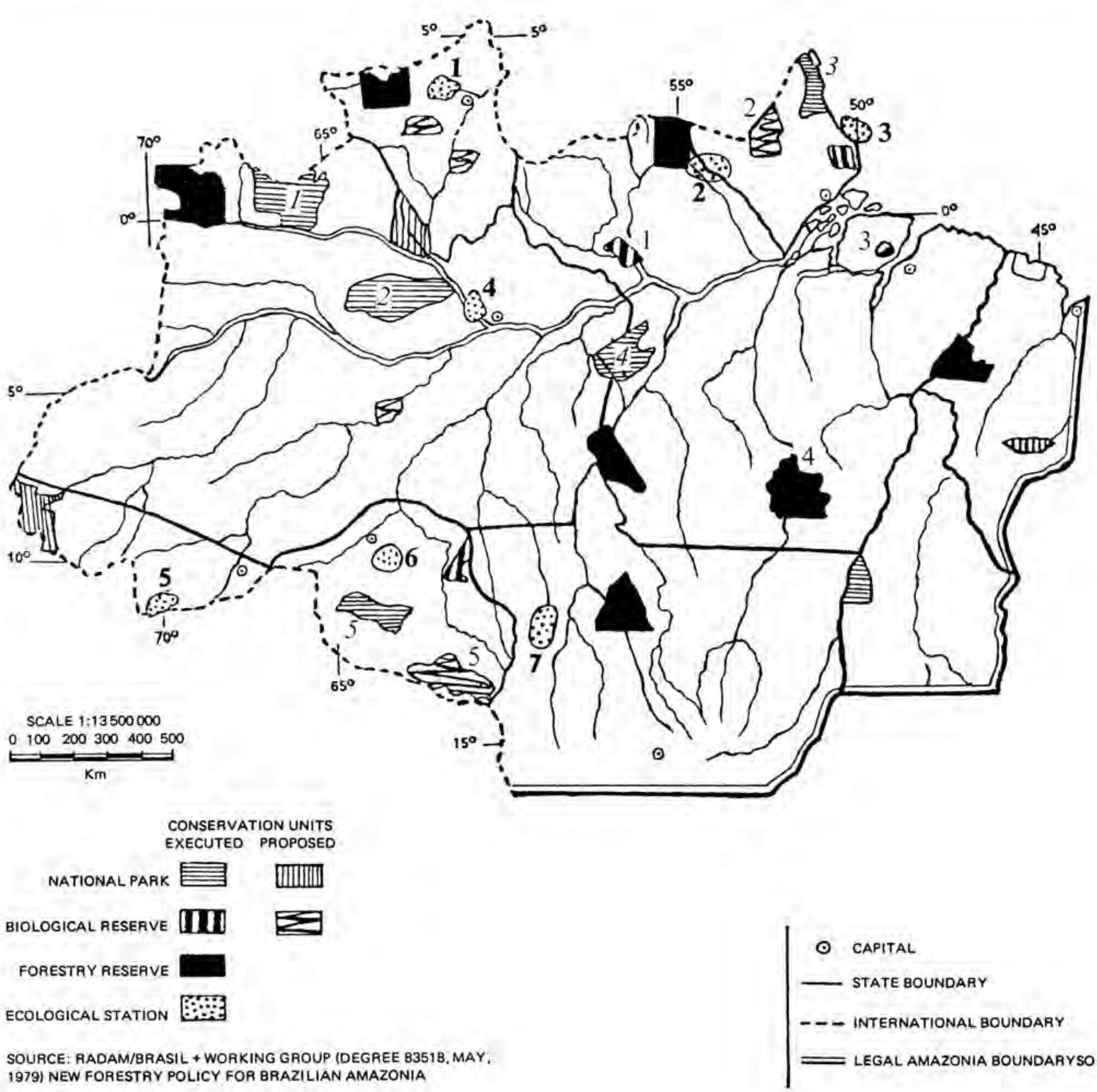
In Brazil, at the federal level, two Ministries are involved with preservation. The Ministry of Agriculture is responsible for the Brazilian Institute of Forestry Development (IBDF) which includes the National Parks Service. The Ministry for the Interior includes the Special Environment Agency (SEMA) and the National Foundation for Indian Affairs (FUNAI). Some state governmental entities create and preserve State Parks and Ecological Stations. National Forests can be created by the IBDF and in these areas forest exploitation can occur. The National Parks Service is also responsible for Biological Reserves. SEMA is responsible for Ecological Stations (Fig. 10.1) which are similar to National Parks but are selected to preserve good examples of all Brazilian ecosystems and connect them with Universities' Research Projects. Preference is given to transition areas which can preserve the highest diversity of species. They are also created to prevent the extinction of endangered species. Last year a new law was issued that allows SEMA to determine Environmental Protection Areas and to legislate over private property in regions of special interest.

Fig. 10.1. Ecological Station at Anavilhanas on the Rio Negro (Photo credit: Dr E. J. Fittkau).

Fig. 10.2 shows the positions of the preserved areas. Details of each preserved area is given in Table 1.



IBDF
NATIONAL PARKS

1 Pico da Neblina
2 Jaú
3 Cabo Orange
4 Tapajos
5 Paacas Novosé

IBDF
BIOLOGICAL RESERVES

1 Rio Trombetas
2 Oiapoque
3 Marajó
4 Xingu
5 Guaporé
? Jaru
? Lago Piratuba

SEMA
ECOLOGICAL STATIONS

1 Maracá-Roraima
2 Jari
3 Maracá-Amapá
4 Anavilhanas
5 Rio Acre
6 Rondonia
7 Iquê

Fig. 10.2. Sketch map showing the positions of preserved areas in the Brazilian Amazon. (Prepared by Prof. José Candido Melo Carvalho and Almirante Ibsen de Gusmão Camara.)

TABLE 1

Preserved areas in the Brazilian Amazon*

	Year founded	Area (ha)
IBDF National Parks		
Pico da Neblina	1979	2 200 200
Jau	1980	2 272 000
Cabo Orange	1980	619 000
Tapajos	1974	1 000 000
Paacas Novos	1980	765 000
Total		6 856 000
IBDF Biological Reserves		
Rio Trombetas	1979	385 000
Jaru	1979	268 150
Lago Piratuba	1980	500 000
Total		1 153 150
Oiapoque		
Marajo		
Xingu		
Guapore		
IBDF National Forests		
Gurupi	1961	1 674 000
Gorotiri	1961	1 843 000
Mundurucania	1961	1 377 000
Parima	1961	1 756 000
Rio Negro	1961	3 790 000
Pedras Negras	1961	1 761 000
Jaru	1961	1 085 000
Juruena	1961	1 808 000
Total		15 094 000
SEMA Ecological Stations		
Maraca Roraima	1977	92 000
Anavilhanas	1977	350 000
Iquê	1977	480 000
Total		922 000
Maraca Amapa		
Rio Acre		
Rondonia		
Jari		
Total		24 025 000

*Total area of the Brazilian Amazon = 4 800 000 km^2; total area of preserved areas = 240 250 km^2 (5%).

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