Contributed Papers

Amazonian Nature Reserves: An Analysis of the Defensibility Status of Existing Conservation Units and Design Criteria for the Future

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Abstract: *Many tropical nature reserves are woefully understaffed or exist only on paper. Without effective implementation, tropical reserves cannot count on in situ enforcement and consequently are subject to a wide range of invasive threats. Weak institutional structures are aggravated by reserve designs that facilitate rather than discourage unlawful human activities. Taking into account severe financial and institutional constraints, we consider the current status of forest reserves in lowland Amazonia. We ask how the criteria by which reserves are delimited may affect the efficiency with which the contained areas are defended. In a GIS analysis, we found that 40 to 100% of the area of all existing nature reserves in Brazilian Amazonia are directly accessible via navigable rivers and/or functional roads. Such access greatly facilitates the illegal harvest and conversion of forest resources in a region where each guard is responsible for protecting an area larger than the State of Delaware. Cost-effective defense of large areas can be achieved through appropriate delimitation of reserves along watershed divides and by efficient deployment of limited infrastructure and personnel. Given current and probable future levels of financial resources allocated to reserve maintenance in Amazonia, any new nature reserves in this region should be designed and situated so that their defensibility is maximized. Defensibility criteria should complement site considerations based on biological criteria, such as presumed centers of diversity and endemism.*

Las Reservas Naturales Amazónicas: un análisis del estado relativo de protección de las unidades de conservación existentes y del criterio de diseño para el futuro

Resumen: *Muchas reservas naturales tropicales se encuentran desastrosamente atendidas o existen sólamente en papeles. Sin una implementación efectiva, las reservas tropicales no pueden contar con una implementación in situ de la ley y en consecuencia estan sujetas a un amplio espectro de amenazas invasoras. Las estructuras institucionales débiles se ven agravadas por diseños de reservas que facilitan más que desalientan las actividades humanas fuera de la ley. En este estudio, consideramos el estado actual de las reservas de bosques en las tierras bajas de la Amazonía, tomando en cuenta las severas restricciones financieras e institucionales. Nos preguntamos cómo el criterio por el cual las reservas son delimitadas puede afectar la eficiencia con la cual las áreas contenidas son defendidas. A través de un análisis de SIG, encontramos que entre un 40 y un 100% del área de todas las reservas naturales existentes en la Amazonía Brasileña resulta directamente accesible por medio de ríos navegables y/o rutas funcionales. Este tipo de acceso facilita la recolección ilegal y la conversión de recursos forestales en una región dónde cada guardia es responsable de proteger un área mayor que el Estado de Delaware. Una defensa de grandes áreas, eficiente desde un punto de vista de costos, se puede lograr a través de una delimitación adecuada de las reservas a lo largo de las líneas divisorias de aguas y mediante un empleo eficiente de los limitados recursos de infraestructura y personal. Dados los niveles de los recursos financieros presentes y probablemente futuros,*

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dedicados al mantenimiento de las reservas en Amazonía; cada nueva reserva natural en esta región debe ser diseñada y localizada de tal forma que su defensa sea maximizada. Los criterios de defensa deben complementar las consideraciones del sitio basadas en criterios biológicos, tales como presumibles centros de diversidad y endemismo.

Introduction

Tropical-forest nature reserves are experiencing mounting human encroachment, raising concerns over their future viability even in remote areas. Long-term maintenance of nature reserves in economically marginal areas of the tropics is particularly problematical because protection is based on severely restricted funding from politically and administratively weak governments. Many tropical forest reserves consequently operate on skeletal budgets, are chronically understaffed, lack the most basic infrastructure, and cannot count on effective institutional support to enforce conservation legislation. Such frailties render reserves susceptible to a wide range of illegal activities—hunting, fishing, logging, mining, land clearing—carried out by both individuals and corporations. Worse, the frequent inability of guards, who are often unarmed and lacking authority to make arrests, to prosecute violators leads to a general disregard of reserve boundaries and regulations. Once it is observed that the responsible authorities are unable to intervene, large-scale invasions by colonists, poachers, loggers, and miners may ensue and jeopardize the reserve's biological resources.

The Amazon basin consists of some 7.05 million km^2 of lowland tropical forest in contiguous parts of Brazil, Peru, Ecuador, Colombia, Bolivia, Venezuela, and the Guianas (Irion 1978). The location of nature reserves in this region has been profoundly influenced by biogeographic analyses purporting to locate centers of diversity and endemism for a number to plant and animal taxa (Haffer 1969; see also Prance 1977, 1982; Whitmore & Prance 1987). Reacting to newly available biological information, Wetterberg et al. (1976) produced the first comprehensive proposal for establishing conservation areas in Amazonia and recommended 30 high-priority areas for preservation. Proposed conservation areas coincided with centers of endemism identified by overlaying distribution maps for birds, lizards, butterflies, and woody-plants (Haffer 1969; Vanzolini 1970; Prance 1973; Brown 1975). Recently, this approach was reinforced and expanded by an international workshop ("Biological priorities for conservation in Amazonia," Manaus, Brazil, January 1990), which proposed 94 priority conservation areas for the Amazon Basin (Conservation International 1991). Many criteria were incorporated in the analysis, including phytogeographic regions, centers of biodiversity and endemism, and types of soils and climate (Rylands 1990*a*). The resulting map is available to planners, politicians, and conservationists.

The maps prepared by these conservation plans have led to the establishment of nearly 20 new nature reserves. Among the first were 10 in Brazilian Amazonia resulting directly from the proposals by Wetterberg et al. (1976, 1981; see reviews in Padua & Quintão 1984; Foresta 1991). More recently, the Manaus Workshop sparked the creation of eight ecological stations, which were decreed by the Brazilian State of Amazonas to coincide with proposed high-priority conservation areas (C. Miller, personal communication). Moreover, a comprehensive environmental blueprint entitled "Ecological and Economic Zoning of Amazonia," which has been carefully considering proposals from the Manaus Workshop, is being prepared by Brazilian government agencies. When implemented, the blueprint is likely to have sweeping implications for Amazonian conservation, both within and outside Brazil.

The biogeography of a limited number of taxa has been the primary consideration in identifying priority areas for conservation in Amazonia. Criteria of efficiency and effectiveness of protection have hardly entered the planning process (see Foresta 1991:131). Ignoring such practicalities in the design of new reserves is risky. The job of procuring and keeping resources to implement and maintain a reserve may pale before the physical threats that may have to be repulsed.

We urge that henceforth criteria of defensibility be incorporated into the process of designing and selecting future Amazonian nature reserves, so as to discourage and deter external pressures. We suggest that, in addition to biological considerations, reserve design in Amazonia should take into account the realities of low-budget implementation and weak or nonexistent enforcement of conservation policy. We do not propose any specific areas for protection, such as those recommended on the basis of intrinsic biological criteria (see Terborgh & Winter 1983; International Council for Bird Preservation 1992). Rather, we focus on the pragmatic issue of how to design and locate reserves to minimize implementation costs and maximize defensibility against existing and future external threats.

We begin our analysis with an overview of the numbers, sizes, and types of conservation units in Amazonia. We next consider practical design criteria, such as reserve configuration and location of boundaries with respect to avenues of access, especially roads and navigable rivers. We then suggest criteria for maximizing the defensibility of protected areas given the assumption of meager investments in infrastructure and human resources. Finally, we propose some practical guidelines for designing future Amazonian reserves.

Methods and Definitions

Data on Amazonian parks were obtained from published and unpublished reports of Amazonian natural resource agencies (see Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renovaveis [IBAMA] 1990; Dias et al. 1991) and international nongovernmental organizations (Rylands 1990*b*, 1991; World Conservation Monitoring Centre 1992). Uniformly scaled maps of reserves were prepared for the Amazonian region of each Amazonian country using a digitizing table (Kurta XLC 3648) and a desktop Geographic Information System (GIS; Strategic Mapping 1990) to obtain measurements of total areas and perimeters. GIS-derived area measurements, when regressed against the areas of 50 reserves for which data were available, accounted for 99.8% of the variation, affirming the accuracy of the GIS procedure.

In a separate analysis based on high-quality 1:250,000 maps, available only for Brazilian Amazonia (Projeto Radam Brasil [RADAM] 1973–1981), we classified the geographic positions of existing reserves in relation to the total length of the watershed in which they are found. Watershed length was calculated using digitized linear measurements (broken down into 10-km segments) of the principal open-water fluvial course draining a reserve, from its headwaters to its final confluence with the Amazon (Solimões) River. Meandering of river channels was ignored because the maps we used indicate pronounced differences in river linearity across Amazonia. Reserves were then assigned to one of four position categories along the principal watercourse (lower, central/lower, central/upper, and upper), depending on where their geometric centers fell with respect to watershed length.

In the context of Brazilian Amazonian reserves, we also measured accessibility to illegal incursion as a function of nonlinearized lengths of navigable rivers (open water visible from space) and roads traversing or forming the boundaries of reserves, as resolved by the best available maps for the region (Defense Mapping Agency 1966–1989; RADAM 1973–1981; Institut für Angewandte Geodäsie 1986). Our measure of accessibility assumes that extraction of forest products (game, timber) in Amazonia is limited by transportation and that most rivers and roads within reserves are accessible to unauthorized intruders. We further assume that visitors will be willing to walk up to, but not more than, 10 km from the nearest navigable river or road to extract forest products, and accordingly we designated as accessible all such portions of reserves. The 10-km criterion is based on our own field experience and information obtained from tribal and nontribal Amazonians (Terborgh et al. 1986; Peres 1990). For instance, a 10-km walk is often reported as the maximum hunting radius for highly profitable game, such as tapirs (*Tapirus terrestris*) in unflooded (*terra firme*) forest (Bodmer et al. 1990; personal communication). Moreover, 10 km matches the recommended strip width for proposed buffer zones to be placed around Amazonian conservation units (Wetterberg et al. 1976; Decree 99.274/6th June 1990, National Environmental Council).

One potential weakness of our measure of accessibility is that it overlooks the large variation in human densities around reserves and associated differences in intensity of land use and intrusion pressure, all of which are subject to change over time. The 10-km criterion applied here is likely to be conservative because it neglects the potential for canoe traffic at high water on myriad forest streams that course underneath a closed canopy and hence are invisible in the RADAM side-scanning images.

Our classification of conservation units follows that of IBAMA, the Brazilian Institute of Environment and Renewable Natural Resources (Nogueira-Neto & Carvalho 1979; Instituto Brasileiro de Desenvolvimento Florestal 1988; Dias et al. 1991; IBAMA 1991), with some slight modifications. We wish to emphasise the distinction between strict nature reserves and other types of conservation units that legally permit various forms of resource extraction. Here, *nature reserve* means areas set aside for absolute or nearly absolute protection of representative biotas and ecosystems. Nature reserves, including national parks, biological reserves, and ecological stations, are established for nonconsumptive purposes, are strictly protected by law, and impose severe restrictions on human activities.

Production reserves, comprising national forests, extractive reserves, and game reserves, are defined as conservation units subject to forest and game management and are intended for sustainable production of timber and nontimber products. State or federal concessions to extract resources may be granted either to private interests, such as timber companies, or to communities of nontribal Amazonians operating independently or through cooperatives.

Indigenous reserves are distinguished in a third category because they exist on a substantially different legislative basis (Davis & Wali 1993). Indigenous reserves in Brazil are typically administered by an independent government agency, the National Indian Foundation. The category includes both indigenous and anthropological reserves (Brazil), indigenous reserves and *resguardos* (Colombia), and designated Amerindian lands (Guyana).

Results and Discussion

The Conservation System in Amazonia

An extensive network of 459 nature, production, and indigenous reserves is designated on paper for all Amazonian countries, although many of these have yet to be formally decreed (World Conservation Monitoring Centre 1992). Reserves are widely distributed across the region, although many important gaps remain (Fig. 1). Nearly half (47%) of all designated reserves are smaller than 1000 km^2. Conservation areas between 1000 and 10,000 km^2 account for another 41%, and those larger than 10,000 km^2 account for the remaining 12% (Fig. 2). Nature reserves have an average area of 4765 km^2 (sd = 7815 km^2, range = 0.1–57,740 km^2, n = 117) and in general tend to be larger than production forests (mean = 3626 km^2, sd = 5823 km^2, range = 0.4–37,900 km^2, n = 94) and indigenous reserves (mean = 4003 km^2, sd = 9870 km^2, range = 0.5–83,380 km^2, n = 248).

One quarter (117 of 459) of all Amazonian conservation units are nature reserves, and theoretically have comprehensive protection. These account for 41% of the region's total acreage under some form of institutional protection. The remaining conservation units include 94 production and 248 indigenous reserves, which respectively account for 15% and 44% of all non-private land with some degree of protection.

Extensive systems of indigenous reserves are retained primarily by Colombia and Brazil. Over 18 of the 38 million hectares of Colombian Amazonia are allocated to indigenous groups. In Brazil, approximately 20% of the Amazon area consists of indigenous reserves under the jurisdiction of the National Indian Foundation. The future value of these areas for biodiversity preservation is debatable, as several Brazilian tribes have already begun a process of outright liquidation of their resource capital (Redford & Stearman 1993). Resource depletion has taken the form of large land concessions granted to logging companies and goldminers and small-scale leases of forested land for a variety of exploitative uses (Economist 1993). If indigenous areas are to serve as stable strongholds of biological diversity, current practices will need to be replaced by enforced limits on the rights of indigenous peoples and colonists (Peres 1994).

Conservation planning is well developed on paper in all Amazonian countries other than Suriname and Guyana, but in practice nature reserves often lack adequate protection. For example, only 10 of 30 nature reserves in Brazilian Amazonia employ even one local guard (Rylands 1991). Although IBAMA maintains an extensive network of administrative outposts in small towns, the locations of these offices are often far from the nearest reserve. Current staffing results in an average of one park guard per 6053 km^2 of nature reserve. To put this in perspective, the density of guards in the 367 units of the U.S. National Park Service is more than 70 times greater (Table 1).

Understaffing is a consequence of a low governmental priority placed on conservation needs. Low priority results in severe financial constraints, aggravated by inflated administrative structures and competition with politically stronger government sectors (see Foresta 1991 for historical review of political commitment on conservation in Amazonia). Apart from the financial and staffing limitations of park agencies, Amazonian park guards lack power to arrest violators and receive little or no backing from local police forces. Even if all these hurdles are surmounted, enforcement efforts are pursued in a procedural vacuum without the benefit of legal precedents. Enforcement of protective legislation is therefore almost nonexistent, and the nature reserves of Brazilian Amazonia are consequently experiencing a wide range of anthropogenic threats to biodiversity (Table 2).

A lack of financial and political will can lead to abandonment of conservation units as soon as conflicts with larger economic interests arise. Some examples of this include central-government decisions to overrun existing reserves with road construction and settlement projects throughout the southern flank of Brazilian Amazonia (Fearnside & Ferreira 1984); plans to exploit 12 established conservation areas in Bolivia; and encroachment of national parks by petroleum and mining companies in Ecuador (World Conservation Monitoring Centre 1992). In several of the worst cases, nature reserves have suffered from unencumbered disturbance to such a degree that they have been legally downsized or degazetted within a few years of establishment (World Conservation Monitoring Centre 1992).

Many of the human threats confronted by nature reserves could be reduced if reserves were designed and located to maximize their defensibility under difficult financial conditions. In practice, reserves can be protected from hunters, loggers, miners, and other illegal intruders by physical inaccessiblity as well as by strategic deployment of personnel.

Reserve Area versus Perimeter

Circles minimize perimeter length per unit of enclosed area and have consequently been proposed as optimal shapes for reserves (Wilson & Willis 1975). The size of existing nature reserves in Amazonia is a good predictor

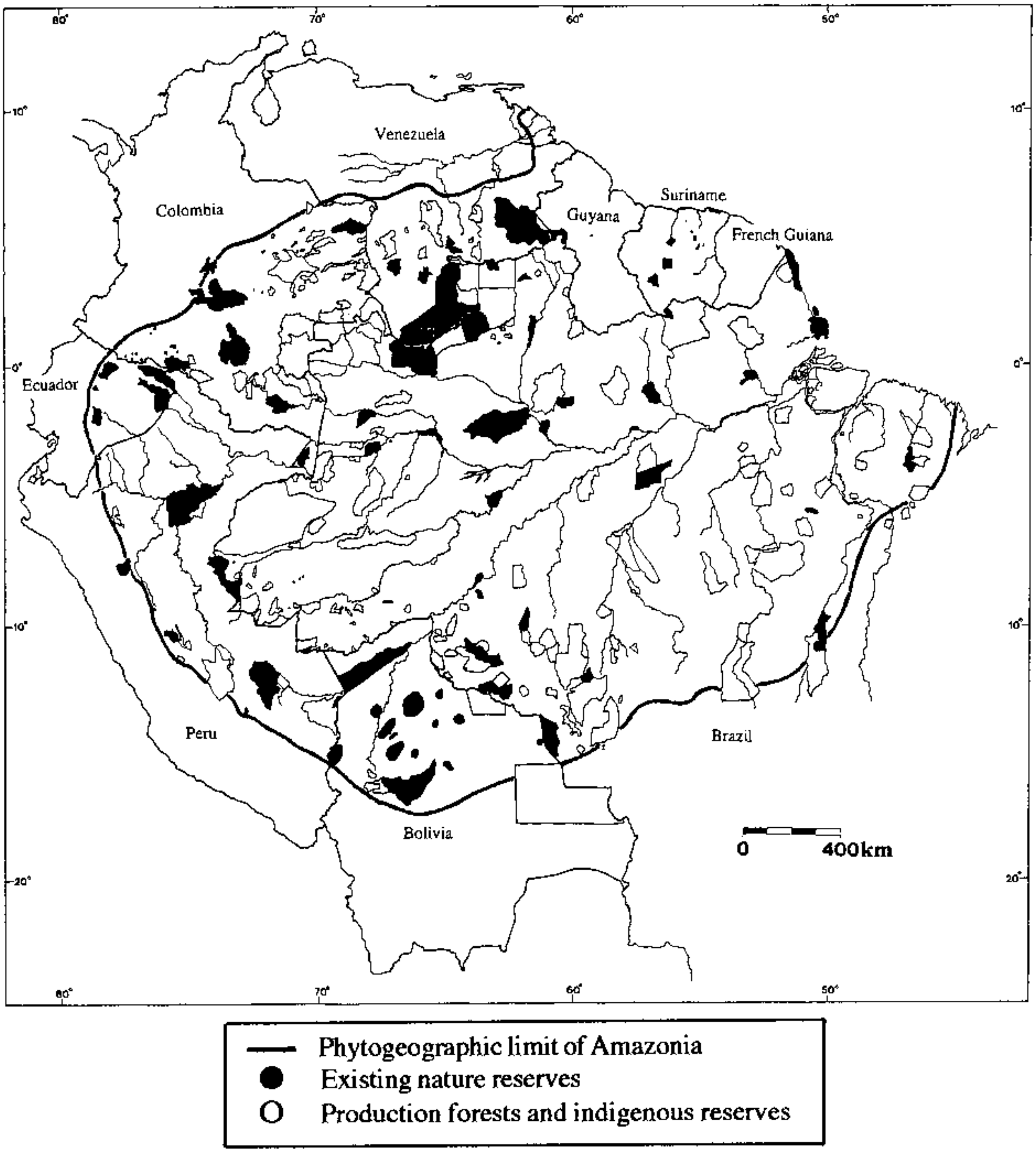

Figure 1. Geographic distribution of conservation units in all nine Amazonian countries. The peripheral solid line indicates the phytogeographic (rather than political) limit of Amazonia. Boundaries between contiguous conservation units may not be shown in every case.

of perimeter length, explaining 90% of its variation (r = 0.951, n = 63). The same is true for top-priority conservation areas proposed by the Manaus Workshop (r = 0.955, n = 62), even though the size range of these areas is nearly six-fold greater than that of existing reserves (Fig. 3). A considerable expenditure on patrolling and surveillance efforts would be required should reserve perimeters be equally accessible.

Accessibility of Brazilian Nature Reserves

Taking advantage of high-quality RADAM maps available only for Brazil and employing the 10-km criterion described above, we found that a mean of 75 ± 19% of the areas of existing nature reserves in Brazilian Amazonia are accessible to intruders entering by foot from included or adjacent rivers and roads. This parameter fell

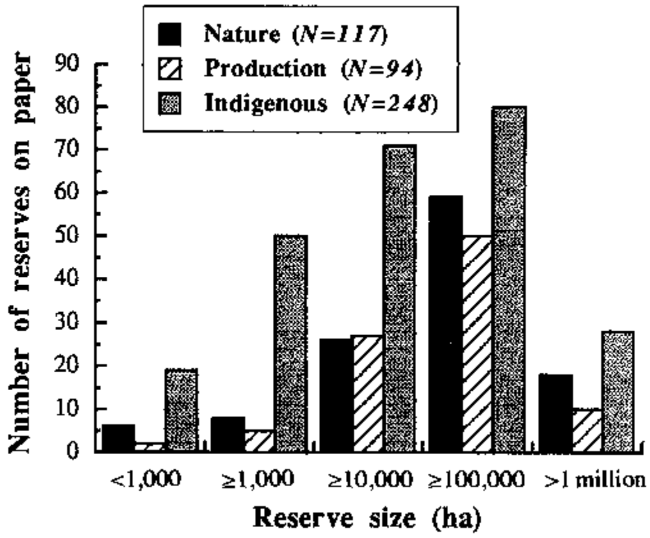

Figure 2. Size distribution of all nature, production, and indigenous reserves in the Amazon basin. N indicates the total number of reserves in each category (see text for definitions).

between 40% in the least accessible to 100% in the most accessible reserves (n = 29, Fig. 4). All existing reserves, including those relatively far from settlements, are therefore accessible to entirely accessible. Reserve size explains 98% of the variation in area of accessibility ($r = 0.99$, $n = 29$, $p < 0.01$). There is little decrease in relative accessibility with reserve size. Larger reserves, given their present design, encompass greater numbers of rivers and permit access to commensurately greater areas. But the absolute amount of inaccessible "core habitat," beyond the practical limits imposed by physical distance, clearly increases with reserve size. We view large core areas as indispensible to safeguarding populations of important biotic elements, such as top predators and preferred game and timber species.

Controlling river or road traffic in and out of a reserve would in principle require a guardpost with similar levels of staff and infrastructure for each access point. The cost of protection thereby increases linearly with the number of entrance and exit points. To examine this further, we determined the number of access routes in nature reserves of Brazilian Amazonia and conservation areas proposed by the Manaus Workshop for the entire region.

The number of rivers and roads providing potential access to conservation areas increases with their size and perimeter. This is true for both existing nature reserves (area: $r = 0.73$, $n = 30$, $p < 0.001$; perimeter: $r = 0.77$, $n = 30$, $p < 0.001$) and proposed priority conservation areas (area: $r = 0.42$, $n = 69$, $p < 0.001$; perimeter: $r = 0.37$, $n = 69$, $p = 0.002$). These results confirm that even the largest lowland Amazonian reserves and designated priority areas, given their present configurations, are highly vulnerable to incursion. Size alone is an ineffective defense because commensurately greater resources are not allocated to protect larger reserves. In Brazilian Amazonia, for instance, there is no relationship between the size of nature reserves and the number of guards ($r = 0.27$, $p = 0.14$, $n = 30$) or total personnel employed ($r = 0.05$, $p = 0.79$, $n = 30$). We therefore propose that new Amazonian reserves should, as much as possible, be delimited so as to gain the benefit of passive protection.

Table 1. Comparison of the level of personnel and resources allocated to defense of nature reserves in Brazilian Amazonia and in the United States.

	Brazilian Amazonia[a]	*U.S.A.*[b]
In situ park guards deployed[c]	23	4002
All nature reserve personnel[d]	65	19,000
Number of nature reserves	29	367
Protected area (km^2)	139,222	326,721
Park guard-to-area ratio	1:6053	1:82
Park personnel-to-area ratio	1:2142	1:17
Reserves equipped with at least one (%):		
Park guard	31	100
Administrative building	45	100
Guardpost	52	100
Motor vehicle[e]	45	100

[a] *Includes all federal National Parks, Biological Reserves, and Ecological Stations and Reserves (Instituto Brasileiro de Desenvolvimento Floretal 1988; IBAMA 1990; Rylands 1991).*
[b] *Includes all National Park System units (U.S. National Park Service, personal communication).*
[c] *Includes all seasonal and full-time law-enforcement officers and rangers.*
[d] *Includes all seasonal and full-time parkguards, technicians, caretakers, drivers, and urban-based administrators.*
[e] *Includes aluminum canoes with outboard engines, jeeps, and trucks.*

The Upper Watershed Reserve Model

Passive protection can be maximized by drawing boundaries along watershed divides, wherever practical. Watershed divides represent the least accessible points in the landscape and therefore, as boundaries, provide passive protection to the greatest possible degree. Second, locating boundaries along topographic divides protects intact watersheds and their aquatic resources. A complete watershed in a roadless landscape, no matter how large, can be controlled at a single point—where the contained stream exits the zone of protection (Fig. 5). By concentrating personnel at that point, effective protection of the entire watershed can be achieved at minimum expense.

However, most Amazonian nature reserves are either bisected and/or bordered by navigable rivers in the legal public domain. From a defensibility standpoint, such reserves suffer from multiple disadvantages: (1) every river that traverses a reserve calls for at least two guard-

Table 2. Categories of current threats to biodiversity faced by 29 federal and one state nature reserves in Brazilian Amazonia.

	National Parks[a]								*Biological Reserves*[b]							
Types of Threats	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*
Preventable with Improved Design																
Encroachment by squatters	•	•	•	•	•	•	•		•	•	•	•	•	•	•	
Slash-and-burn agriculture												•	•	•		
Subsistence/commercial hunting	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Other commercial uses of wildlife					•	•			•			•	•			
Commercial fishing					•				•	•	•	•	•			
Selective logging	•	•	•	•	•				•	•	•	•	•	•	•	
Indian reserves within boundaries	•	•	•	•	•			•						•		
Indian reserves along boundaries	•	•	•	•	•		•	•		•		•	•	•	•	
Gold mining	•	•	•	•	•						•					
Mining (bauxite, cassiterite)				•					•	•				•		
Agrochemical/mercury pollution	•	•		•					•		•			•		
Livestock conflicts	•	•	•		•				•		•		•	•		
Deforestation	•		•	•	•				•	•	•		•	•		
Tree monocultures											•					
Soil erosion			•											•		
Episodic wildfires	•								•		•		•	•		
Heavy river traffic	•	•		•		•	•		•	•		•	•			•
Land-tenure problems	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•
Unpreventable with Improved Design																
Inadequate management	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Road-building operations	•	•	•	•			•			•			•			
Adjacent land development	•		•	•					•	•			•	•	•	•
Hydroelectric development									•	•						•
Military activity				•												

	Ecological Stations (or Reserves)[c]													
Types of Threats	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*
Preventable with Improved Design														
Encroachment by squatters	•	•			•	•	•		•	•	•			•
Slash-and-burn agriculture		•		•		•								
Subsistence/commercial hunting	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Other commercial uses of wildlife					•									•
Commercial fishing			•					•			•			•
Selective logging		•		•		•		•			•			•
Indian reserves within boundaries		•												
Indian reserves along boundaries	•		•			•			•					
Gold mining		•	•			•					•			
Mining (bauxite, cassiterite)														
Agrochemical/mercury pollution			•							•	•			
Livestock conflicts					•	•			•					
Deforestation			•			•		•		•	•			
Tree monocultures														
Soil erosion														
Episodic wildfires			•			•	•			•				
Heavy river traffic	•	•		•				•		•	•		•	•
Land-tenure problems						•				•	•			
Unpreventable with Improved Design														
Inadequate management	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Road-building operations											•			
Adjacent land development										•		•		
Hydroelectric development							•				•			
Military activity														

[a] *National parks: 1—Araguaia, 2—Amazônia, 3—Pacaás Novos, 4—Pico da Neblina, 5—Cabo Orange, 6—Jaú, 7—Serra do Divisor, 8—Monte Roraima.*
[b] *Biological reserves: 9—Rio Trombetas, 10—Jarú, 11—Lago Piratuba, 12—Abufari, 13—Guaporé, 14—Gurupí, 15—Tapirapé, 16—Uatumã.*
[c] *Ecological stations: 17—Anavilhanas, 18—Iquê, 19—Maracá, 20—Rio Acre, 21—Maracá-Jipioca, 22—Caracaraí, 23—Jarí, 24—Juami-Japurá, 25—Niquiá, 26—Coco-Javaes, 27—Cuniã, 28—Sauim-Castanheiras, 29—Jutaí-Solimões, 30—Mamirauá (state ecological station).*
Modified from Rylands 1990b, 1991.

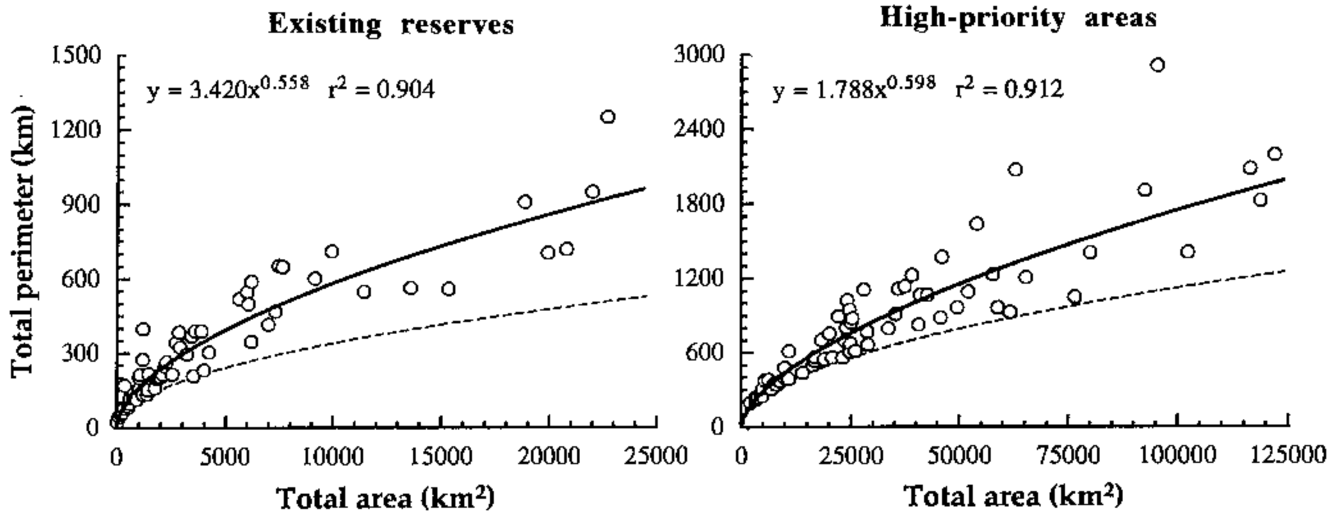

Figure 3. The relationship between total area and total perimeter of existing nature reserves and proposed high-priority conservation areas (combination of the two highest priority levels as proposed by the Manaus Workshop [Conservation International 1991]) in Amazonia. Dashed lines represent the theoretical curve showing the lowest possible increment in perimeter length/expected if reserves and priority areas were shaped as perfect circles.

posts (Fig. 5a); (2) inhabitants of legal settlements on a bank opposite a reserve boundary have direct access to the reserve (Fig. 5b); and (3) even frequent fluvial patrols by guards would be ineffective in averting illegal (and undetectable) activities farther inland (Fig. 5).

An upper watershed approach to reserve design in Amazonia would simultaneously protect distinct biological assemblages in successive interfluvia and address the issue of species complementarity within reserve networks (Pressey et al. 1993). Also, locating Amazonian reserves in headwater regions would help maintain the spawning grounds of many migratory fish species (Ribeiro 1983; Goulding et al. 1988) and preserve a supply of potable water for downstream residents. Headwater regions often contain more topographic diversity than downstream areas and thus may include a greater variety of aquatic and terrestrial habitats. The watershed approach would protect riparian corridors and their hydrologic regimes, the latter being critical to maintaining the complex dynamics of landform mosaics, plant succession, and associated biodiversity (Salo et al. 1986; Kalliola et al. 1992; Puhakka et al. 1993; Naiman et al. 1993).

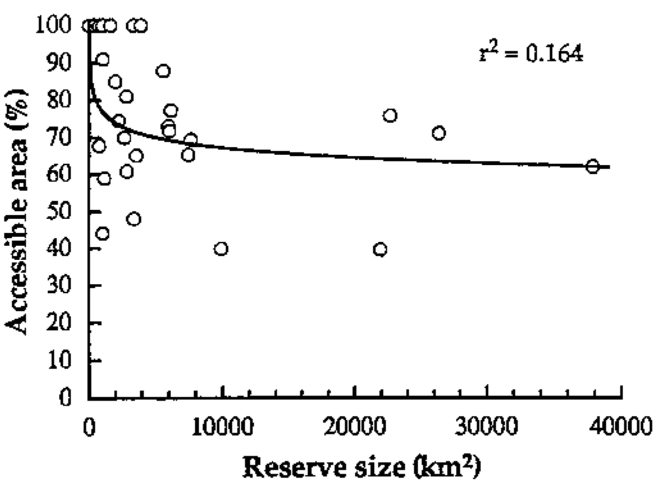

Figure 4. The relationship between the size of 29 Brazilian Amazonian reserves and the proportion of the total reserve area that is accessible on foot, assuming a 10-km radius from the nearest point along navigable rivers and/or functional roads.

Biodiversity Gradients along Watersheds

If future Amazonian reserves are to be situated in headwater regions, it becomes important to consider how biodiversity is distributed along the length of river basins in both the aquatic and terrestrial realms. In the aquatic realm, zonation of riverine fish faunas is strongly differentiated with respect to stream order (Horwitz 1978; Goulding et al. 1988; Ibarra & Stewart 1989), as is the hydrological regime. Frequency of flooding and sediment concentration increase upstream, while amplitude and duration of flooding increase downstream. The richness of Amazonian fish communities increases downstream (Ibarra & Stewart 1989), an observation that is supported by a clear correlation between water discharge and species diversity (Garutti 1983). In particular, a number of large-bodied, aquatic vertebrates, including the Amazonian lung-fish or pirarucú (*Arapaima gigas*), giant river turtle (*Podocnemis expansa*), and pink dolphin (*Inia geoffroensis*) rely heavily on

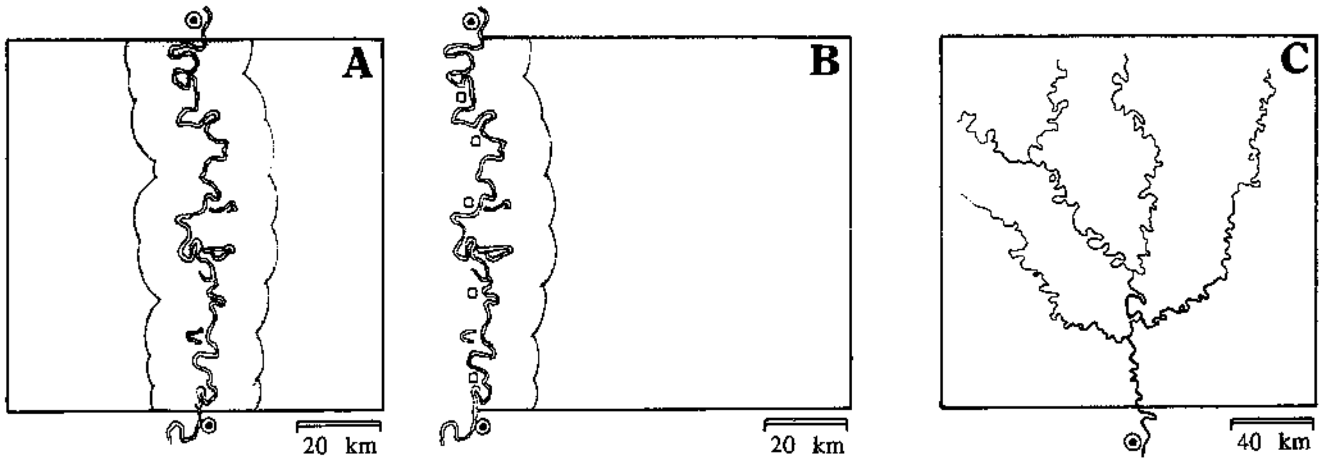

Figure 5. Hypothetical case scenarios in which Amazonian nature reserves are bisected (a) or bordered by a navigable river (b), or, alternatively, incorporate an entire upper watershed (c). Shaded areas, which are considered susceptible to uncontrolled access by illegal harvesters of forest products, represent sections of reserves bounded by arcs with a 10-km radius from the nearest point along rivers. Dotted circles indicate boat inspection outposts located upriver and downriver from reserve boundaries. Small squares indicate households within extractive communities legally settled on the opposite bank of established reserves (b).

whitewater flooded forests (*várzea*) and are often missing in headwater regions. Moreover, many fish species of downstream pelagic habits make lateral migrations into *várzea* and *igapó* (Ribeiro 1983; Cox-Fernandes & de Merona 1988; Goulding et al. 1988). These are also expected to be missing in headwater regions.

On the other hand, recent fish collections in fast-flowing *terra firme* headwater streams in both the Guianan and Brazilian Shields appear to be extremely diverse and have yielded numerous undescribed and possibly endemic species (L. Rapp and Py Daniel, personal communication). The occurrence of unique elements in the aquatic faunas of both upstream and downstream sections of Amazonian rivers thus argues for the creation of reserves in both regions.

The ecological and evolutionary influence of rivers on Amazonian terrestrial biotas generally increases with distance from the headwaters, as rivers broaden to become more effective barriers to terrestrial organisms (Wallace 1849; Ayres & Clutton-Brock 1991; Capparella 1992; Haffer 1992; Peres et al. submitted). Greater duration and intensity of floods, lateral river-channel migration, and floodplain succession in lower river basins generally result in greater between-habitat (β) but not necessarily within-habitat (α) biological diversity along downstream sections of rivers. Headwater floodplains are more briefly and lightly flooded, and, accordingly, their associated forests are more similar to those of the adjacent upland (Puhakka et al. 1993).

Topographic gradients across Amazonia are extremely weak, as illustrated by the fact that ocean-going vessels routinely navigate more than 3000 km upstream. Consequently, the upper watersheds of major lowland Amazonian rivers contain most if not all of the terrestrial vertebrate alpha-diversity found in their central-lower catchment areas, a pattern that has been explicitly documented along the Rio Juruá for birds, primates, small nonvolant mammals, and frogs (Peres et al., unpublished data).

Flooded forest and river island species, however, may be excluded from or represented in low densities in headwater regions (Remsen & Parker 1983; Rosenberg 1990). The floras of downstream flooded (*várzea* and *igapó*) and unflooded forests are strongly differentiated (Prance 1979), and many plant species typical of downstream flooded forests may therefore be poorly represented in headwater sites. Junk (1989) estimates that roughly one fifth of the 4000–5000 Amazonian tree species are tolerant to periodic flooding of several weeks to many months, even though flooded forests account for only 4% of the region. A second set of reserves complementing those in headwater regions should thus be set aside to capture downstream biotas.

Conservation of Downstream Biotas

Clearly, the size, location, and design of nature reserves along Amazonian watersheds will explicitly have to take into account the countercurrent longitudinal biodiversity gradients in the terrestrial and aquatic realms. Downstream reserves should be designed partly for the purpose of conserving aquatic resources, with particular attention to the watercourse itself and its fringing *várzea* or *igapó* forests. Here, the approach of controlling whole watersheds at strategic entry points is not applicable, and other approaches will have to be developed. Greater investment in guards and other personnel for downstream reserves can readily be justified by the vital economic importance of aquatic resources to the human population of Amazonia (Smith 1979; Petrere 1982).

Watershed Coverage by Existing Nature Reserves

At present only three Amazonian national parks (Manu in Peru, Jaú in Brazil, and Canaima in Venezuela) encompass all or a substantial proportion of a major watershed. Other nature reserves tend to sprawl over two to several watersheds and to include only a minor fraction of any one. In Brazil, for instance, only one Amazonian nature reserve covers an area equivalent to at least one quartile of the length of its main watershed axis (Fig. 6).

From a fluvial perspective, the nature reserves of Brazilian Amazonia are more or less evenly distributed between headwater regions and the confluence of major tributaries with the Amazon River (Fig. 6). But the distribution of protected areas is very uneven across watersheds. Some major watersheds benefit from multiple reserves, while many others contain none. The existing array of nature reserves in Amazonia thus embodies weaknesses at two levels. First, there needs to be a better dispersion of protected areas across drainages, and, second, both upstream and downstream conservation areas should be designed to maximize passive defensibility and cost effectiveness of enforcement personnel.

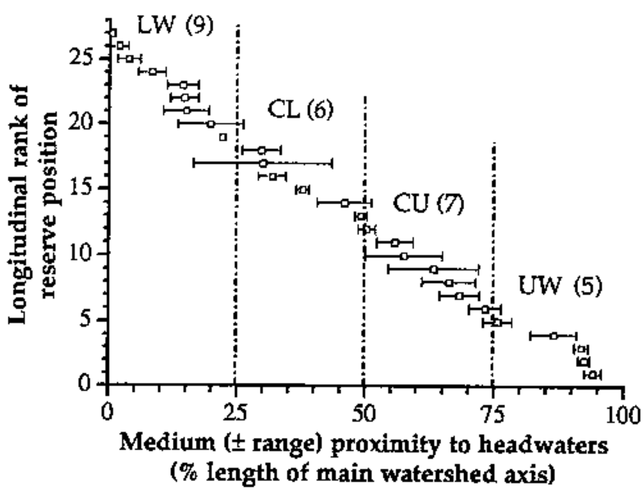

Figure 6. Relative distribution of Brazilian nature reserves ranked longitudinally in relation to watersheds of first-order tributaries of the Amazon River. Numbers (in parentheses) indicate the regional occurrence of lower (LW), central-lower (CL), central-upper (CU), and upper watershed (UW) nature reserves.

Proposed Priority Conservation Areas

The map prepared by the 1990 Manaus Workshop features several dozen high-priority areas for conservation action in Amazonia. These priority areas were intended to represent centers of endemism and diversity, but the evidence on which the areas were designated was often highly subjective, based on the personal experiences of participants. Available evidence on endemism and species density gradients in Amazonia is greatly weakened by heterogeneity of sampling effort, clustering of collecting sites, and large geographical gaps between sampling localities, any or all of which may account for apparent range discontinuities (Gentry 1986, 1989; Nelson et al. 1990; Oren & Albuquerque 1991). Large gaps between some high-priority conservation areas tend to correspond to subregions that received little or no previous sampling (Juruá river: Peres et al., unpublished data). Consequently, the Manaus Workshop map should not be taken as an unqualified picture of reality. Instead, it should be recognized as a good-faith effort to locate biologically important regions within Amazonia, with the understanding that the information upon which it is based will be subject to continuing revision.

To the degree that the Manaus Workshop map does accurately portray biologically distinctive areas within Amazonia, it should be noted that the locations of many of them, as well as those in previously published maps for individual forest-dwelling taxa, lie in the upstream portions of river basins (Prance 1982; Brown 1987). We therefore suggest that headwater reserves, if appropriately located and delimited, can satisfy both biological and defensibility criteria.

Costs of Implementing Reserves

Espírito Santo and Faleiros (1992) recently estimated at US$524 million the total cost of implementing the existing 99 National Parks, State and Federal Biological Reserves, Ecological Stations (or Reserves), National Forests, Extractive Reserves, and Environmental Protection Areas in the Legal Brazilian Amazon (a politically defined region of 5 million km^2). Included were the costs of land purchase, demarcation, management plans, infrastructure, and equipment. Maintenance costs, including staff salaries, were estimated at US$29.5 million for the first five years, and US$27.1 million for subsequent years.

By far the largest component of the estimated cost (82%) was that for land acquisition. The complex land tenure system in Brazil is such that most Amazonian nature reserves are not entirely owned by the national or state governments: only 13 of 32 federal nature reserves in this region are wholly in the public domain (Espírito Santo & Faleiros 1992). Overall, private landholdings and claims amounted to 65% of the Legal Brazilian Amazon in 1990. States under strong development pressure are already at least 83% in private hands (Maranhão and Acre), if not entirely so (Mato Grosso and Tocantins). Clearly, the matter of land property rights looms as a major impediment to implementing the currently designated conservation system in Amazonia. Proposals to add to the existing system will have to take into account the rapidly rising cost of repatriating land from private ownership. The infinite green horizon seen by anyone who flies over the Amazon seems reassuring, but is an illusion. The reality is that much of the land is already under claim.

Recommendations

Our watershed reserve model calls for a two-tiered structure of Amazonian reserves targeted to both the upstream and the downstream sections of major watersheds. A system of large (>1 million ha), inviolate nature reserves encompassing the upper sections of intact drainage basins would permit maximum control over boat traffic at minimal cost in personnel and infrastructure and would be intrinsically more resistant to human incursion than nearly all existing reserves. Preference in locating new nature reserves should be given to drainages currently lacking them. On the south bank of the Amazon within Brazil, unprotected basins include the upper sections of the Teles Pires (Pará/Mato Grosso), Iriri (Pará), and Jutaí rivers (Amazonas), and some tributaries of the Juruá and Purús rivers (Acre). Networks of geographically clustered nature reserves could be interconnected by corridors running along headwater divides (Harris 1985). A similar linkage approach has recently been proposed for Venezuelan parks (Yerena & Romero 1992).

An additional system of nature reserves in central-lower watersheds should be established to complement those in headwater regions. Downstream reserves will be essential to safeguarding representative *várzea* and *igapó* habitats, as well as important commercial fisheries. Such flooded-forest reserves will assure the continued functioning of intact habitat mosaics with their high productivity and distinct biodiversity (Prance 1979; Junk 1989) and will preserve the lateral migration of downstream aquatic organisms as well as the seasonal movements of forest wildlife using both flooded and unflooded forests (see Peres 1993). Almost inevitably, downstream reserves will have to be located in areas of relatively high human densities and therefore cannot be expected to protect nature in pristine form. Effective implementation of such reserves may require greater local-community participation, a process currently being tested by the Projeto Mamirauá in the lower Japurá river (Polshek 1993; J. M. Ayres, personal communication).

Control posts should be located downriver of both headwater and flooded-forest reserves, either on the river bank or on floating docks in deep water at which boats could conveniently stop. Wherever practical, posts should be located within ready access of small towns, because it is difficult to recruit and retain competent personnel for duty in remote locations.

A new institutional approach to training and support of reserve personnel must be adopted if reserves are to be effectively defended in the future. Park guards in Amazonia are commonly recruited locally from the lowest social stratum. Accordingly, guards tend to be uneducated, poorly paid, and ill equipped. Such individuals are easily intimidated and hesitate to assert themselves to curtail unlawful activity. Effective enforcement of conservation policy depends entirely on the authority and respect given to guards. Therefore, it is imperative that guards be better trained and supplied with standard uniforms, weapons, and ammunition and be empowered to confiscate illegal materials and arrest violators.

Additional nature reserves are needed to increase the representation of fully protected areas in Amazonia and to fill some of the many large gaps between existing reserves. The existing system of nature reserves should be overhauled to the extent that large reserves can be redrawn, interconnected, and consolidated into comprehensive reserve networks. Small reserves should be retained unless the cost of maintaining them draws resources from more important reserves elsewhere.

Finally, we suggest that strict nature reserves should not be compromised by economic activities other than ecotourism if full complements of flora and fauna are to remain intact (Robinson 1993). A complementary network of production and indigenous reserves will assist in minimizing habitat fragmentation and maintaining biodiversity within the Amazonian landscape, but they should be designed to buffer and supplement rather than to replace an inviolate system of strictly protected nature reserves.

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Literature Cited

Ayres, J. M., and T. Clutton-Brock. 1991. River boundaries and species range size in Amazonian primates. American Naturalist 140:531–537.

Bodmer, R. E., N. Y. Bendayán, L. Moya I., and T. G. Fang. 1990. Manejo de ungulados en la Amazonía Peruana: Análisis de la caza de subsistencia y la comercialización local, nacional e internacional. Boletín de Lima 70:49–56.

Brown, K. S., Jr. 1975. Geographic patterns of evolution in Neotropical Lepidoptera. Systematics and derivation of known and new Heliconiini (Nymphalidae: Nymphalinae). Journal of Entomology (B) 44:210–242.

Brown, K. S., Jr. 1987. Conclusions, synthesis and alternative hypotheses. Pages 175–196 in T. C. Whitmore and G. T. Prance, editors. Biogeography and Quaternary history in tropical America. Oxford Science Publications, Oxford, England.

Capparella, A. P. 1992. Neotropical avian diversity and riverine barriers. Acta Congressus Internationalis Ornithologici 20:307–316.

Conservation International. 1991. Biological priorities for conservation in Amazonia. Map developed during the Workshop 90, Manaus, Brazil.

Cox-Fernandes, C., and B. de Merona. 1988. Lateral migration of fishes on a floodplain system in the central Amazon (Careiro Island, Lake of Rei) AM, Brazil: A preliminary analysis. Memoria Sociedad de Ciencias Naturales La Salle 48:409–432.

Davis, S. H., and A. Wali. 1993. Indigenous territories and tropical forest management in Latin America. Working paper. World Bank Policy Research, Washington, D.C.

Defense Mapping Agency Aerospace Center. 1966–1989. Aeronautical, relief, and hydrographic charts of South America. St. Louis, Missouri.

Dias, I. F. O., A. R. Gonçalves, M. Borges, and E. O. Meneses. 1991. Sistema de unidades de conservação federais do Brazil. Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA), Brasília, DF.

Economist. 1993. Brazil's less-than-noble Indians. The Economist, June 12, 327:54.

Espirito Santo, C. V., and A. A. Faleiros. 1992. Cost of implantation of conservation units in legal Amazonia. Funatura, Brasília, DF.

Fearnside, P. M., and G. L. Ferreira. 1984. Roads in Rondônia: Highway construction and the farce of unprotected reserves in Brazil's Amazonian forest. Environmental Conservation 11:358–360.

Foresta, R. A. 1991. Amazon conservation in the age of development: the limits of providence. University of Florida Press, Gainesville.

Garutti, V. 1983. Distribuição Longitudinal da Ictiofauna do Córrego da Barra Funda, Bacia do Rio Paraná. M.S. thesis. Universidade de São Paulo, São Paulo, Brazil.

Gentry, A. H. 1986. Endemism in tropical versus temperate plant communities. Pages 105–116 in M. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Gentry, A. H. 1989. Speciation in tropical forests. Pages 113–134 in L. B. Holm-Nielsen, I. C. Nielsen and H. Balslev, editors. Tropical forests: botanical dynamics, speciation, and diversity. Academic Press, New York.

Goulding, M., M. L. Carvalho, and E. G. Ferreira. 1988. Rio Negro, rich life in poor water: Amazonian diversity and foodchain ecology as seen through fish communities. SPB Academic Publishers, The Hague, The Netherlands.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165:131–137.

Haffer, J. 1992. On the "river effect" is some forest birds of southern Amazonia. Boletim do Museu Paraense Emílio Goeldi (Zoologia) 8:217–245.

Harris, L. 1985. Conservation corridors: a highway system for life. ENFO 85–5. Florida Conservation Fund, Winter Park.

Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs 48:307–321.

Ibarra, M., and D. J. Stewart. 1989. Longitudinal zonation of sandy beach fish in the Napo river basin, eastern Ecuador. Copeia 1989:364–381.

Institut für Angewandte Geodäsie. 1986. Brasil: Areas indígenas e grandes projetos. Berlin, Germany.

Instituto Brasileiro de Desenvolvimento Florestal. 1988. Projeto Nacional do Meio Ambiente (PNMA)—Componente: Unidades de Conservação. Brasília, DF.

Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis. 1990. Programa Nacional de Conservação e Desenvolvimento Florestal Sustentado, Brasília, DF.

Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis. 1991. Legislação Ambiental Referentes a Parques Nacionais. Reservas Biológicas e Estações Ecológicas. Brasília, DF.

Instituto Nacional de Colonização e Reforma Agrária. 1990. Cadastro rural e situação jurídica dos imóveis rurais. Brasília, DF.

International Council for Bird Preservation. 1992. Putting Biodiversity on the Map: Priority Areas for Global Conservation (ICBP). ICBP, Cambridge, England.

Irion, G. 1978. Soil infertility in the Amazon. Naturwissenschaften 65:515–519.

Junk, W. 1989. Flood tolerance and tree distribution in central Amazonian floodplains. Pages 47–64 in L. B. Holm-Nielsen, I. C. Nielsen, and H. Balslev, editors. Tropical forests: botanical dynamics, speciation, and diversity. Academic Press, New York.

Kalliola, R., J. Salo, M. Puhakka, and M. Rajasilta. 1992. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. Journal of Ecology 79:877–901.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.

Nelson, B. W., C. A. C. Ferreira, M. F. da Silva, and M. L. Kawasaki. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. Nature 345:714–716.

Nogueira-Neto, P., and J. C. M. Carvalho. 1979. A programme of ecological stations for Brazil. Environmental Conservation 6:95–104.

Oren, D. C., and H. G. Albuquerque. 1991. Priority areas for new avian collections in Brazilian Amazonia. Goeldiana (Zoologia) 6:1–11.

Padua, M. T. J., and A. T. B. Quintão. 1984. A system of national parks and biological reserves in the Brazilian Amazon. Pages 565–571 in J. A. McNeely and K. R. Miller, editors. National parks, conservation and development: The role of protected areas in sustaining society. Smithsonian Institution Press, Washington, D.C.

Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. Biological Conservation 54:47–59.

Peres, C. A. 1993. Structure and spatial organization of an Amazonian terra firme forest primate community. Journal of Tropical Ecology 9:259–276.

Peres, C. A. 1994. Indigenous reserves and nature conservation in Amazonian forests. Conservation Biology 8:586–588.

Petrere, M., Jr. 1982. Ecology of the fisheries in the River Amazon and its tributaries in the Amazonas State (Brazil). Ph.D. thesis. University of East Anglia, Norwich, England.

Polshek, P. M. 1993. Projeto Mamirauá: An integrated conservation initiative. Newsletter **27**, Tropical Conservation and Development Program.

Prance, G. T. 1973. Phytogeographic support for the theory of pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. Acta Amazonica **3(3)**:5–28.

Prance, G. T. 1977. The phytogeograpic subdivisions of Amazonia and their influence on the selection of biological reserves. Pages 195–212 in G. T. Prance and T. S. Elias, editors. Extinction is forever. New York Botanical Garden, New York.

Prance, G. T. 1979. Notes on the vegetation of Amazonia. III. The terminology of Amazonian forest types subject to inundation. Brittonia **31(1)**:26–38.

Prance, G. T., editor. 1982. Biological diversification in the tropics. Columbia University Press, New York.

Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: Key principles for systematic reserve selection. Trends in Ecology and Evolution **8**:124–128.

Puhakka, M., R. Kalliola, M. Rajasilta, and J. Salo. 1993. River types, site evolution and successional vegetation patterns in Peruvian Amazonia. Journal of Biogeography **19**:651–665.

Radar Amazonas do Brasil. 1973–1981. Projeto RadamBrasil. Levantamento de recursos naturais. Vol. 1–18. Departamento Nacional de Produção Mineral, Ministério das Minas e Energia, Rio de Janeiro.

Redford, K. H., and A. M. Stearman. 1993. Forest-dwelling native Amazonians and the conservation of biodiversity. Conservation Biology **7**:248–255.

Remsen, J. V., Jr. and T. A. Parker, III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica **15**:223–231.

Ribeiro, M. C. L. 1983. As migrações dos jaraquis (Pisces: Prochilodontidae) no Rio Negro, Amazonas, Brasil. M.S. thesis. Instituto Nacional de Pesquisa da Amazonia (INPA), Manaus, Brazil.

Robinson, J. G. 1993. The limits to caring: Sustainable living and the loss of biodiversity. Conservation Biology **7**:20–28.

Rosenberg, G. H. 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru. Condor **92**:427–443.

Rylands, A. B. 1990*a*. Priority areas for conservation in the Amazon. Trends in Ecology and Evolution **5**:240–241.

Rylands, A. B. 1990*b*. Evaluation of the current status of federal conservation areas in the tropical rain forest of the Brazilian Amazon. World Wildlife Fund, Washington, D.C.

Rylands, A. B. 1991. The status of conservation areas in the Brazilian Amazon. World Wildlife Fund, Washington, D.C.

Salo, J., R. Kalliola, I. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka, and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature **322**:254–258.

Smith, N. J. H. 1979. A pesca no Rio Amazonas. Conselho Nacionalde Desenvolvimento Cientifico e Tecnologico and Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil.

Strategic Mapping. 1990. ATLAS-GIS Geographic Information System. Strategic Mapping, Inc., San Jose, California.

Terborgh, J., and B. Winter. 1983. A method for siting parks and reserves with special reference to Colombia and Ecuador. Biological Conservation **27**:45–58.

Terborgh, J., L. H. Emmons, and C. Freese. 1986. La fauna silvestre de la Amazonia: El despifarro de un recurso renovable. Boletin de Lima **8**:77–85.

Vanzolini, P. E. 1970. Zoologia sistemática, geografia e a origem das espécies. Instituto Geográfico de São Paulo. Série Teses e Monografias **3**:1–56.

Wallace, A. R. 1849. On the monkeys of the Amazon. Proceedings of the Zoological Society, London **20**:107–110.

Wetterberg, G. B., M. T. J. Padua, C. S. Castro, and J. M. C. de Vasconcellos. 1976. Uma Análise de Prioridades de Conservação da Natureza na Amazônia. Projeto de Desenvolvimento e Pesquisa Florestal (PRODEPEF). Série Técnica 8. PNUD-FAO-IBDF-BRA-45.

Wetterberg, G. B., G. T. Prance, and T. E. Lovejoy. 1981. Conservation progress in Amazonia: A structural review. Parks **6**:5–10.

Whitmore, T. C., and G. T. Prance, editors. 1987. Biogeography and Quaternary history in tropical America. Oxford Science Publications, Oxford, England.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages 522–534 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap, Cambridge, Massachusetts.

World Conservation Monitoring Centre. 1992. Protected areas of the world: a review of national systems. 4. Nearctic and Neotropical. The World Conservation Union, Cambridge, England.

Yerena, E., and L. Romero. 1992. Corredores de dispersion en los parques nacionales de Venezuela. Proceedings of the IVth World Congress of National Parks and Protected Areas, Caracas, Venezuela.