Ecological Determinism on the Orinoco Floodplain

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Floodplains of large rivers are among the most productive of ecosystems; they are also among the first to be altered by economic development and population growth. Floodplains are vulnerable not only to direct agents of change, such as agriculture and settlement, but also to changes in the hydrology or quality of water in the rivers to which they are connected. Thus, even floodplains not yet cleared or diked may show drastic ecological change caused by shifts in flooding regime, sediment transport, or nutrient budgets as a result of human activities upstream.

Because the floodplains of large rivers are vulnerable to a diverse array of anthropogenic influences, their natural functions cannot be observed or documented in any region of dense population or where natural resources and agricultural potential have been exploited extensively. Nearly all of the major floodplain rivers in the Northern Hemisphere, and many in the Southern Hemisphere, have been leveed or impounded for navigation, agriculture, power generation, or flood control (Power et al. 1995, Vitousek et al. 1997). Only large rivers of the far north and in some parts of the tropics now offer a view of large floodplains as they existed before human intervention (Cushing and Cummings 1995). Information on the ecological characteristics of these few floodplains is the only practical means of understanding the natural functioning of floodplains, and is probably the most useful basis for planning the restoration or protection of floodplains.

All large floodplains give the impression of great ecological complexity. The combination of constant physical change, which is driven by the rise and fall of the river, spatial heterogeneity of vegetation reflecting varied depth and duration of inundation, and longitudinal gradients of floodplains projects intractable multidimensionality. Closer inspection shows, however, a surprising degree of order and repetition in the physical and chemical environment, which in turn suggests the possibility of order and predictability in the biotic components of the system. The most feasible candidate for a test of this idea is a large floodplain whose physical characteristics remain essentially natural.

This paper summarizes a search for order and simplicity in ecosystem characteristics of the Orinoco River floodplain in South America. The main underlying hypothesis

A 15-YEAR STUDY OF THE ORINOCO FLOODPLAIN SHOWS THAT THIS PRODUCTIVE AND BIOTICALLY DIVERSE ECOSYSTEM IS FUNCTIONALLY LESS COMPLEX THAN IT APPEARS. HYDROGRAPHIC AND GEOMORPHIC CONTROLS INDUCE A HIGH DEGREE OF DETERMINISM IN BIOGEOCHEMICAL AND BIOTIC PROCESSES

for the work is that geomorphic and hydrologic factors on the floodplain have strong, deterministic influences on most major ecosystem characteristics. The testing of this concept, which has extended over 15 years, has covered five major themes: annual site-specific patterns in biogeochemistry and population dynamics; heterogeneity of processes among sites; control of community structure in top-level consumers (fishes); functioning of food webs and energy flow; and reciprocal biogeochemical relationships between the river and its floodplain. The Orinoco floodplain work shows that much of the apparent complexity in

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this ecological system can be resolved through chains of cause and effect that are pervasive and predictable over the system as a whole.

Overview of the Orinoco floodplain

The Orinoco River of Venezuela and Colombia is one of a small number of tropical rivers whose floodplains can still be studied under more or less natural conditions at scales up to hundreds of kilometers. The Orinoco ranks third by discharge among world rivers (38,000 m^3/s; the discharge of the Amazon is 5–6 times larger and that of the Zaire is only slightly larger). The watershed of the Orinoco extends over 1.1 million km^2 (Figure 1). To the north and west of the main stem,its headwaters rise in the Andes and
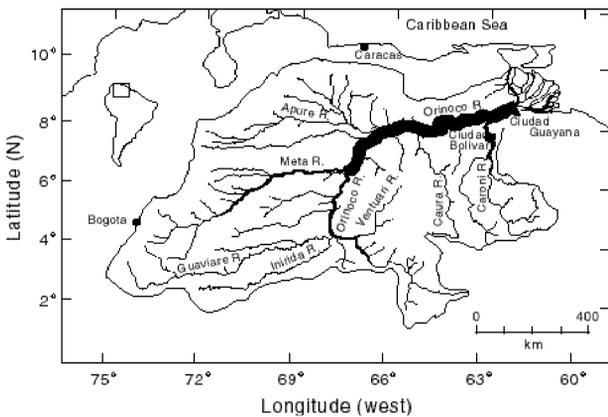

Figure 1. Map of the Orinoco River watershed.

flow across alluvial plains. Tributaries in this portion of the drainage enter the main stem as "white waters," that is, waters that contain large amounts of dissolved and suspended solids produced by rapid weathering in the Andes (Figure 2; Saunders and Lewis 1989). In contrast, waters originating from the east and south flow largely from Precambrian shield, which has been weathered so extensively that it yields only small amounts of suspended and dissolved solids (Lewis and Saunders 1990). Most waters of
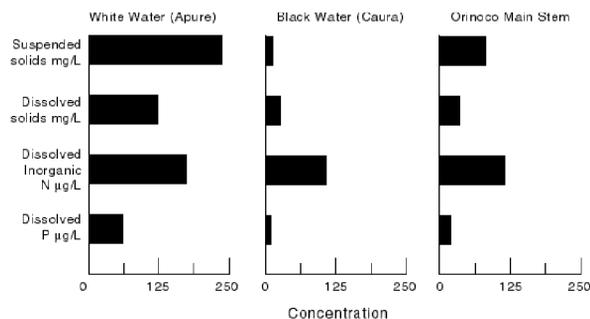

Figure 2. Contrasts in dissolved and suspended load between black waters (e.g., Caura River), and white waters (e.g., Apure River) that make up the mixed waters of the Orinoco main stem.

the shield are darkly colored by dissolved organic matter of terrestrial origin. These are the so-called black waters of the Orinoco drainage. Because it receives both white-water and black-water tributaries, the Orinoco, like many other large rivers,is a mixture of contrasting water types (Lewis and Saunders 1989).

Although much of the Orinoco watershed is settled, especially to the north of the main stem, the extent of anthropogenic change in the river and its floodplain is still small. The Orinoco drainage has no large population centers that might affect the river. The hydrologic regime of the Orinoco is essentially natural (Figure 3). Although the Orinoco has immense hydroelectric potential, there is only one large dam in the watershed (on the Caroni River; Figure 1). Also, most of the native vegetative cover of the Orinoco drainage is intact.
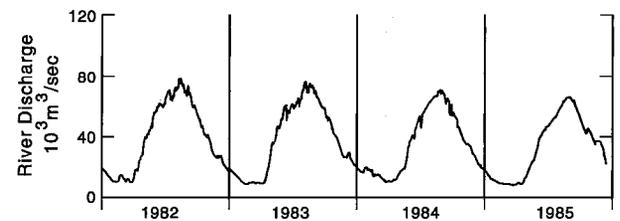

Figure 3. Hydrograph of the Orinoco main stem at Barrancas,near the Orinoco delta.

The Orinoco has a fringing floodplain that extends along the river and more or less parallel to it, approximately 600 km from the delta to the confluence of the Meta River with the Orinoco main stem (Figure 1). The fringing floodplain is made up of 2300 basins, each of which includes an uncanopied depression (i.e., floodplain lake;the mean area of these lakes is close to 20 ha) and surrounding floodplain forest (Figure 4; Hamilton and Lewis 1990a). The annual hydrologic cycle defines two seasons on the floodplain: inundation, when the river is connected to the floodplain, and isolation, when the two are not connected. When flooding reaches its maximum extent, 79% of the floodplain area is flooded forest and 21% is uncanopied area, of which approximately half is open water and half is macrophyte mats. Water extends over the entire floodplain only briefly (approximately 3 months per year); much of the inundation season consists of the filling and drainage phases, during which the water depth and extent of flooding vary (Figure 5; Hamilton and Lewis 1987). Water retracts progressively from the forested portion of the floodplain as the river level drops. By the onset of isolation, the waters have retreated primarily to the lakes, which decline in volume during isolation but persist until the next inundation.

Topographic and hydrologic features add structure to the floodplain at the interbasin scale. The Orinoco is flanked by a natural levee that is approximately 10 m high and contains gaps through which water can flow before it

reaches the crest of the levee. The waters of the Orinoco fluctuate by 10–15 m over the course of the year. At times of the very highest discharge, and typically for only a brief interval, the river passes over the crest of the levee, and in so doing deposits some of the heavier components of suspended load, thus maintaining the levee. Also, for extended intervals on both the rising and falling limbs of the hydrograph, the river enters the floodplain through openings in the levee. These gaps typically lead to tie channels that are connected to a floodplain lake and thence to other channels that reach one or more additional lakes downstream.
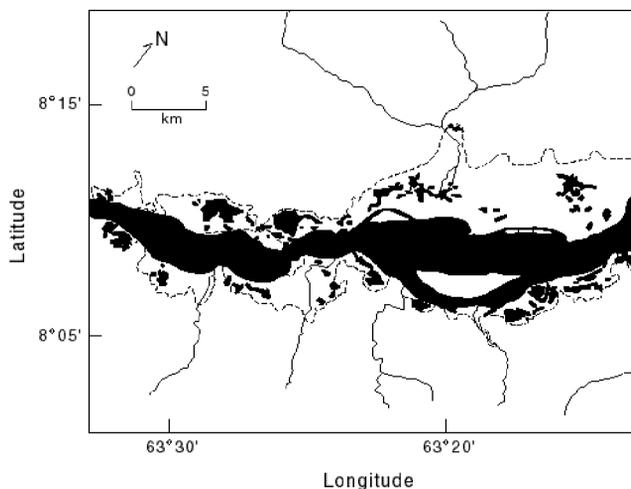

Figure 4. A portion of the Orinoco floodplain showing areas of permanent standing water (river channel and floodplain lakes; shaded area) and the maximum extent of seasonal flooding (dashed line).

The first phase of inundation is filling, during which the channels passing through the levee carry water onto the floodplain. After the water on the floodplain has come into equilibrium with the water in the river, however, water on the floodplain flows down the topographic gradient, parallel to the river but at much lower velocity. This down-gradient flow of water on the floodplain continues for most of the inundation season.

The down-gradient movement of water on the floodplain is regulated by transverse ridges approximately 10 km apart, extending from the upland adjacent to the floodplain (Hamilton and Lewis 1990a). These ridges divide the floodplain into segments. Water entering the floodplain through a channel at the upper end of a floodplain segment must exit the floodplain before reaching the lower end of the segment, which is effectively dammed at the bottom by a topographic rise.

The levee gaps, tie channels, connected lakes, and topographic rises dividing the floodplain into segments define the structure of the floodplain at a scale of 10–100 km (Figure 6). At this scale, the floodplain consists of hydrologic units that receive water from points up the gradient and discharge water back to the river from points down the gradient. Topography, in combination with the river hydrograph, causes water to be routed through these segments of the floodplain during the inundation season.
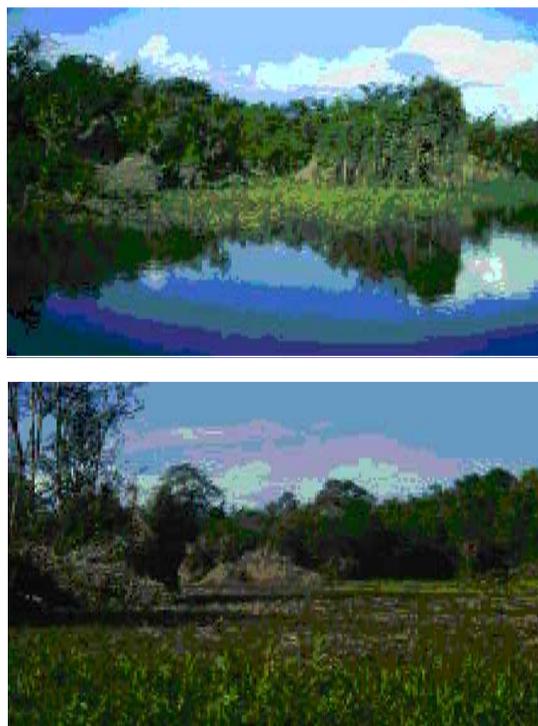

Figure 5. Photographs of the fringing floodplain at two stages in the seasonal cycle: (top) inundation, when water extends beyond large macrophyte mats into the forest, and (bottom) isolation, when basins are separated from each other and from the river.

Decline in the water level of the main channel eventually leads to separation of the river from its floodplain, thus initiating the season of isolation, during which most of the lakes become disconnected from each other and from the floodplain forest. The mean water surface area of the floodplain declines at least 50% through evaporation over
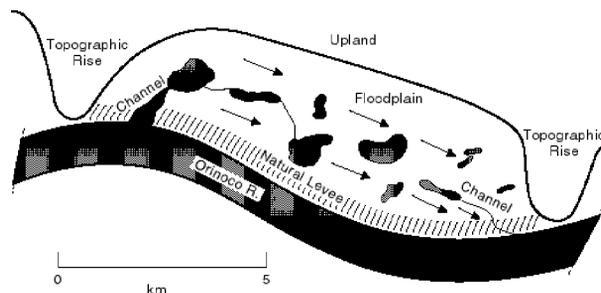

Figure 6. Diagrammatic representation of the topographic rises and interconnected basins that comprise the structure of the floodplain at the 100-km scale.

the isolation season, during which there is very little precipitation. Although infiltration of groundwater occurs, it is slow in the dense clays of the floodplain and does not offset evaporation (Hamilton and Lewis 1987).

The physical features of the Orinoco are common to many other floodplains. The mainstem Amazon floodplain, for example, is strikingly similar (Junk 1997). Thus, linkages among hydrology, geomorphology, and ecological processes on the Orinoco floodplain are likely to be found elsewhere as well.

*Figure 7. The fringing floodplain at two stages of inundation: early inundation (top), with turbid water and newly developing aquatic plants (*Paspalum repens*), and post-peak inundation (bottom), with clear water and well-developed macrophyte mats (*Paspalum repens*).*

Events at the basin scale: Annual succession

Hydrographic change on the floodplain is both drastic and predictable, and thus is likely to force changes in biotic and biogeochemical processes. The importance of disturbance associated with flooding is well recognized (Junk 1997), but substantial hydrographic change extends beyond the flood to the retraction of waters from the floodplain and subsequent evaporative reduction in volume of floodplain waters. Thus, successional processes should be linked directly or indirectly to hydrographic change and, if so, they should be predictable.

Individual floodplain basins, which consist of a lake and surrounding floodplain forest, show considerable biotic and biogeochemical diversity but have in common an annual sequence of physical, chemical, and biotic changes. The sequence of events begins as basins are inundated with river water. As the river water first enters the floodplain (the filling phase of inundation), it is turbid, has low transparency, and contains nutrients in sufficient quantities to promote rapid growth of autotrophs (Figure 7). During this phase of inundation, the margins of floodplain lakes expand into the surrounding floodplain forest and merge with the waters of adjacent basins.

As inundation proceeds, the waters of the floodplain change rapidly (Figure 8). The rapidly deepening water column decants 95% or more of its suspended load (Hamilton and Lewis 1987). As a result, floodplain waters become transparent and thus offer ideal optical conditions for the use of nutrients by phytoplankton, which might be expected to develop intense blooms at this point in the seasonal cycle. But blooms do not occur until later, when the river has separated from the floodplain. This apparent paradox is explained by the constant movement of water through dense mats of macrophytes that develop quickly from propagules remaining from the previous period of inundation. Macrophyte mats provide invertebrates—which in the Orinoco commonly reach abundances approaching 100,000 individuals per m^2 (Lasi 1993)—with substrate and protection from predation by fish. These dense populations of consumers (probably with the assistance of some physical processes) strip planktonic organisms, which originated in open water, from water passing through the macrophyte beds; in this way water clarity is maintained and development of an algal bloom prevented (Hamilton et al. 1990, Lasi 1993).

As the margins of individual floodplain lakes expand, they cover vast amounts of organic matter remaining from the desiccation of macrophyte mats that developed during the previous season of inundation, as well as litterfall that accumulated under floodplain forest canopies following the last inundation. These two major reservoirs of organic matter do not decompose during the dry season because rainfall is insufficient to support microbial metabolism. Intense decomposition begins as soon as the floodwaters inundate the organic matter. Oxygen demand is augmented by respiration of a growing mass of new macrophyte roots (cf. Hamilton et al. 1995). The result is a strongly heterotrophic character for floodplain waters over most of the inundation season, as illustrated by the subsaturation of floodplain waters with oxygen (Figure 9).

The dominant macrophyte of the floodplain is *Paspalum repens*, an aquatic grass that is also abundant in the Amazon floodplain (Junk and Piedade 1997). During inundation, *Paspalum* elongates from roots with sufficient speed to keep pace with the rising water. The result is formation of macrophyte mats very early in the inundation phase, and expansion of the mats until the inundated area begins to shrink.

Other macrophytes, including especially *Eichhornia crassipes*, the water hyacinth, are present as well. Both *Paspalum*
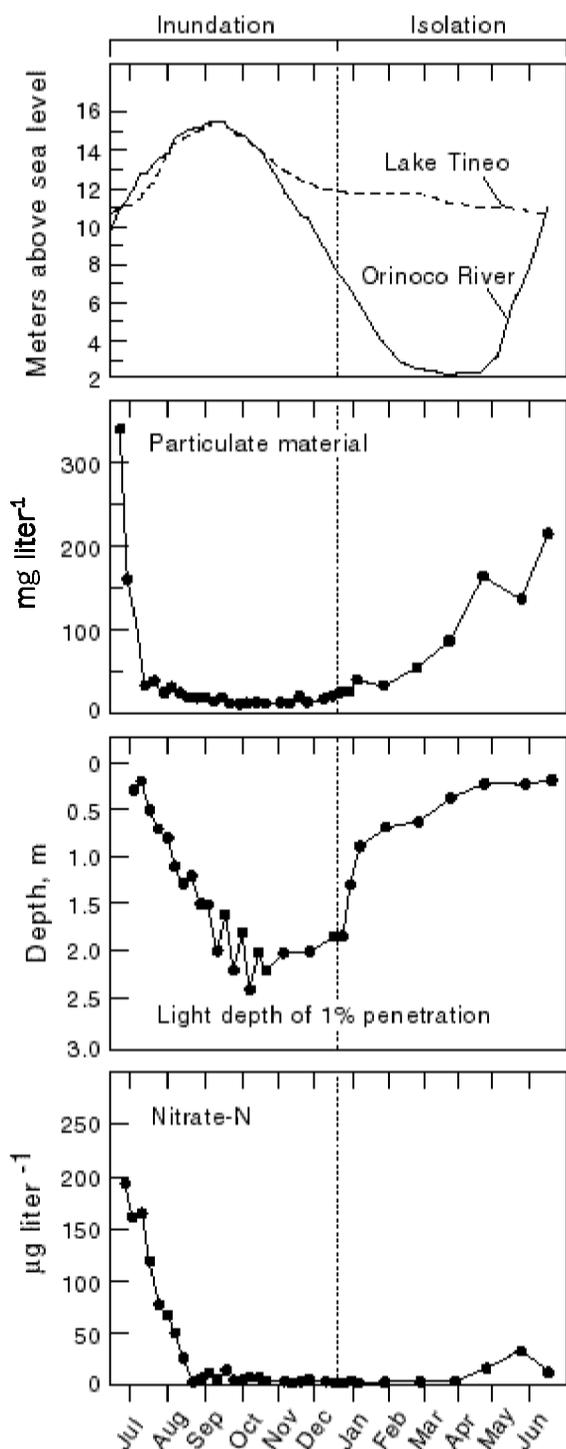
the constant movement of water on the floodplain leads to suppression of phytoplankton biomass, reduction and final cessation of down-gradient water currents on the floodplain lead to an increase of phytoplankton biomass (Figure 9). Consequences of the increase in phytoplankton biomass include suppression of transparency, appearance of large amounts of organic suspended solids, and depletion of free nutrients (Figure 8).
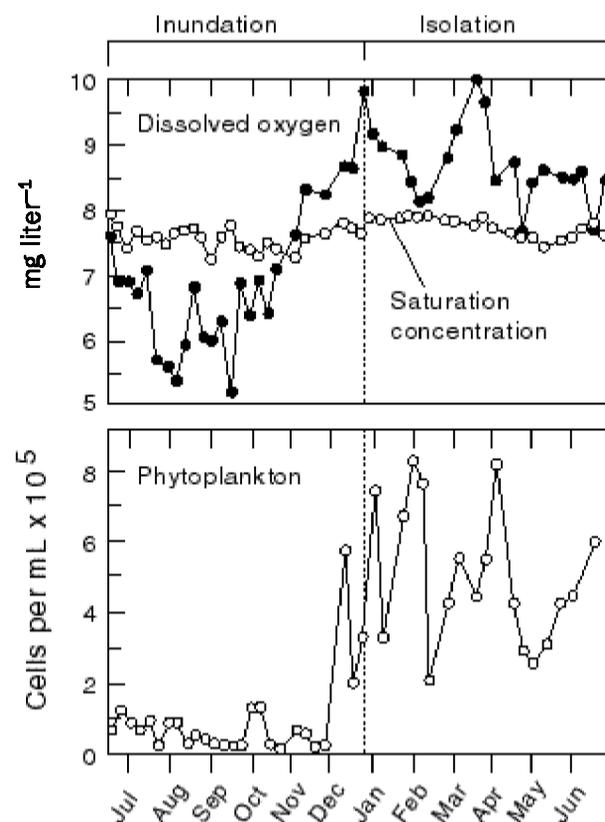

Figure 9. Metabolic changes on the floodplain during the annual cycle (Lake Tineo; Hamilton and Lewis 1987). Subsaturation of water with oxygen during inundation reflects high respiration and low abundance of phytoplankton. During isolation, phytoplankton supersaturate the water with oxygen.

Phytoplankton populations of the floodplain are strongly dominated by blue-green algae (cyanobacteria). At temperate latitudes, blooms of blue-green algae are commonly taken as a symptom of anthropogenic eutrophication of waters, but the phytoplankton populations of the Orinoco floodplain are a reminder that dense blooms of blue-green algae occur naturally under some circumstances.

The blue-greens that become most abundant on the Orinoco floodplain are heterocystous, that is, they have the capacity for nitrogen fixation. Their dominance and persistence suggest that inorganic nitrogen is strongly

Figure 8. Annual cycle of a representative floodplain lake (Lake Tineo).

and *Eichhornia* have emergent photosynthetic tissues and thus contribute to underwater photosynthesis only through the periphyton that grows on their roots and stems near the surface, where light is available.

As the river begins to recede from the floodplain, the velocity of water flow on the floodplain declines. Because

limiting for the growth of autotrophs on the floodplain during late inundation and isolation, when the demands on nutrients are highest. In fact, nitrogen depletion (see Figure 8) indicates that phytoplankton populations are more likely to respond to additions of inorganic nitrogen than to additions of inorganic phosphorus.

Progressive shrinkage of floodplain lakes during the isolation season leads to a decline in mean depth of water, which in turn causes a variety of biotic responses. Changes in depth, volume, and biotic processes vary greatly from one basin to another, however.

Intensive studies of individual lakes show strong and predictable connections between hydrographic events at a given location on the floodplain and seasonal succession of ecological processes. Because the hydrographic sequence is repeated from year to year, hydrographic control introduces a strong element of interannual repetition. The basic sequence of events is also shared widely across locations, but geomorphic factors introduce an element of variation among basins that can be determined only from studies at the interbasin scale.

The interbasin scale: Variation among basins

Hydrographic conditions at specific sites on the floodplain are affected by geomorphology, that is, sizes, shapes and elevations of basins and tie channels. Thus, much interbasin variation should be explained by morphometric factors. Comparisons of basins in fact show strong morphometric control over interbasin variation.

Adjacent floodplain basins on the Orinoco floodplain show great similarity to each other as inundation reaches its peak, because the incoming river water rises enough to obliterate boundaries between basins and the rapid downgradient movement of water precludes the kind of interbasin divergence in chemistry and biota that can occur later. At the height of inundation, water quality is nearly uniform over scales of tens of kilometers, and aquatic organisms can move freely over the floodplain.

At the largest scales (more than 100 km), longitudinal gradients in the chemistry in the Orinoco main stem cause chemical differences among floodplain basins at the height of inundation. For example, waters entering the floodplain just below the large northern whitewater tributaries are likely to have the highest concentrations of dissolved and suspended solids (Figure 2). Thus, variability in the characteristics of the entering river water is a source of interbasin variation during the season of inundation, but only over great distances. The greatest differences among basins develop at smaller scales during the season of isolation, when the waters have retracted to uncanopied depressions (lakes), which may display great variation in chemical characteristics, suspended load, or plankton composition (Figure 10).

The greatest amount of variation among the floodplain lakes is explained by their morphometry and is most evident as flow between lakes slows or ceases (Hamilton and Lewis 1990b). At the beginning of the isolation season, most lakes have maximum depths between 4 m and 15 m. Among the deepest are the so-called channel lakes, which are the product of localized confinement of erosive flow on the floodplain. The shallowest lakes are dish-shaped topographic irregularities on the floodplain. Within a given lake category, variations in maximum water depth are influenced by the location of the lake with respect to the river level at the time of inundation: some lakes are at a higher elevation on the floodplain than others (Hamilton and Lewis 1990b).
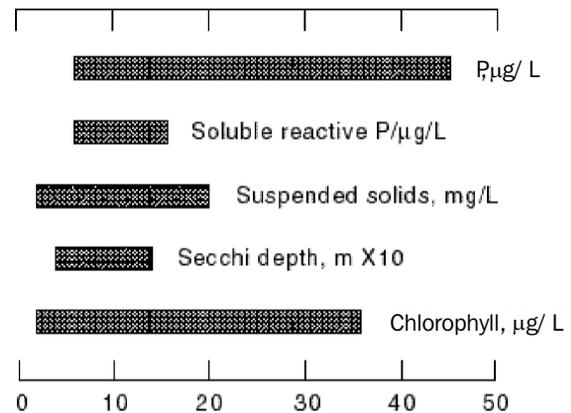

Figure 10. Range of biogeochemical and biotic characteristics among Orinoco floodplain lakes.

Lakes vary in size from less than 0.05 km^2 to more than 5 km^2, and in depth from 4–15 m at the height of inundation to 0.5–5 m by the end of isolation. Size and depth have a bearing on hydraulic residence time, which is shortest for small, shallow lakes connected to large tie channels and longest for large, deep lakes that are connected to small tie channels. In addition, size governs fetch (the distance along open water over which the wind blows), which in turn determines the maximum current velocity that will develop in a lake in response to wind of given velocity.

As water recedes from the floodplain just before isolation, lakes that are situated high on the floodplain may be separated from riverine influence earlier than others on the floodplain. Similarly, lakes with long hydraulic residence time (slow flushing) may effectively enter isolation before the actual separation of the river from the floodplain.

The cessation of flushing by the river leads to a succession of changes in floodplain lakes. Variations in placement and morphometry cause lakes to pass through these successional changes at different rates. Thus, the trajectories of ecosystem features, which include variables that are both biogeochemical (nutrient concentrations, organic carbon in suspension) and biotic (extent of macrophyte

growth, plankton abundance, fish community composition), differ among lakes (Figure 11).
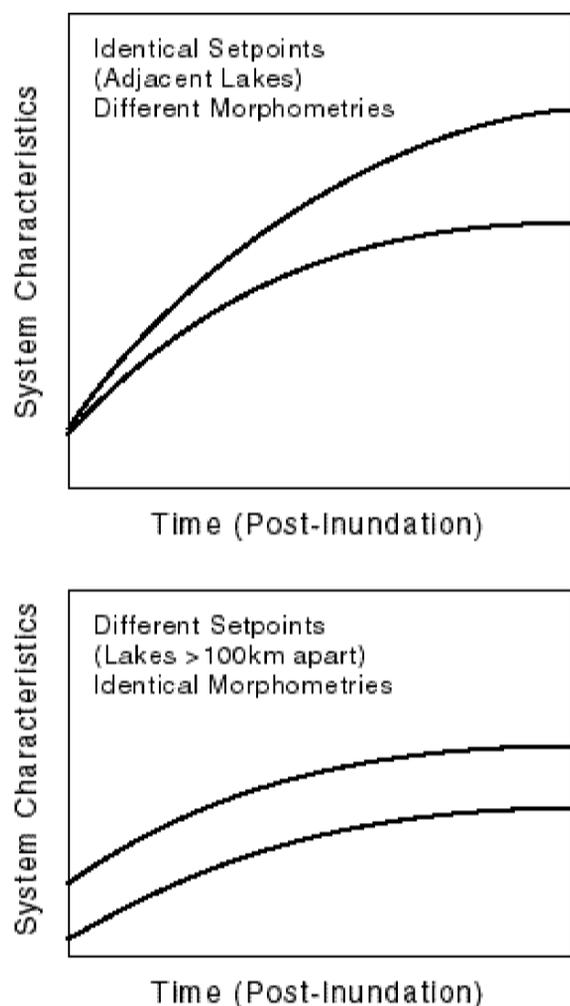

Figure 11. Illustration of the two main causes of variation among floodplain lakes. Setpoint (initial conditions at the time of inundation) is determined by position along the 600 km of the floodplain; basin morphology controls the progressive change in biogeochemical and biotic conditions from the setpoint after inundation.

In the course of seasonal succession, most lakes pass through a phase of phytoplankton biomass accumulation marked by strong predominance of blue-green algae, depletion of soluble nutrients (especially inorganic nitrogen), growth of zooplankton populations (Twombly and Lewis 1987, 1989), and diversification of the mat invertebrates (Lasi 1993). This phase is triggered by the weakening of down-gradient flow through macrophyte mats, where planktonic organisms are removed. Because of variations in morphometry and placement, lakes do not enter this phase synchronously.

A second important transition occurs when the mean depth of a lake has declined to such an extent that fine sediments on the bottom of the lake can be resuspended by wind-generated currents. The threshold for resuspension of sediments in a specific lake is determined by a combination of fetch and mean depth (Hamilton and Lewis 1990b). Because of their variation in mean depth and size, some lakes undergo resuspension very early during isolation, whereas others never do.

The great variety of conditions among floodplain lakes at any given time during the season of isolation seems to imply chaotic assortment of processes across basins. In fact, diversity among lakes can be understood and predicted to a great extent from three principles: over large spatial scales, the initial condition (setpoint, as determined by inundation) for seasonal succession in a given floodplain basin is determined by its location along the Orinoco river, which controls the quality of water entering the floodplain; the waters of any given floodplain basin pass through a trajectory of successional changes that cause even adjacent basins to become diversified as the water retracts to the floodplain lakes; and the sequence of successional changes in a given floodplain lake is controlled mainly by its morphometry and its elevation on the floodplain.

Fish communities on the floodplain

The fish communities of the Orinoco floodplain, although complex, show evidence of strong control by readily quantified physicochemical variables. Thus, the elements of determinism found in major functional attributes of the floodplain have a parallel in community composition.

The waters of the Orinoco channel flow swiftly throughout the year (1–2 m/s), and the riverbed consists primarily of sand, which shifts constantly under the influence of the river's current. There are only a few rocky outcrops in the channel, and coarse debris remains in the river only briefly. High current velocity and lack of structure make the main channel inhospitable to most fishes. Only a few highly specialized taxa are able to occupy the channel continuously (Lundberg et al. 1987). Most fishes of the Orinoco main stem use the channel primarily for migration and dispersal, and depend on the floodplain for growth and subsistence.

The fishes of the Orinoco main stem and adjacent floodplain include primarily characids (60% of species, 50% of individuals), catfishes (20% of species, 20% of individuals), new world knife fishes (10% of species, 4% of individuals), clupeiforms (5% of species, 20% of individuals), and cichlids (4% of species, 5% of individuals). Other orders and families account for less diversity but may be represented by one or a few abundant species (Rodríguez and Lewis 1990).

Adaptations of the Orinoco fishes are exceedingly diverse. Some taxa live by lurk and sprint predation; they show convergence with the elongate body form, long grasping mandibles, and well-developed vision of the
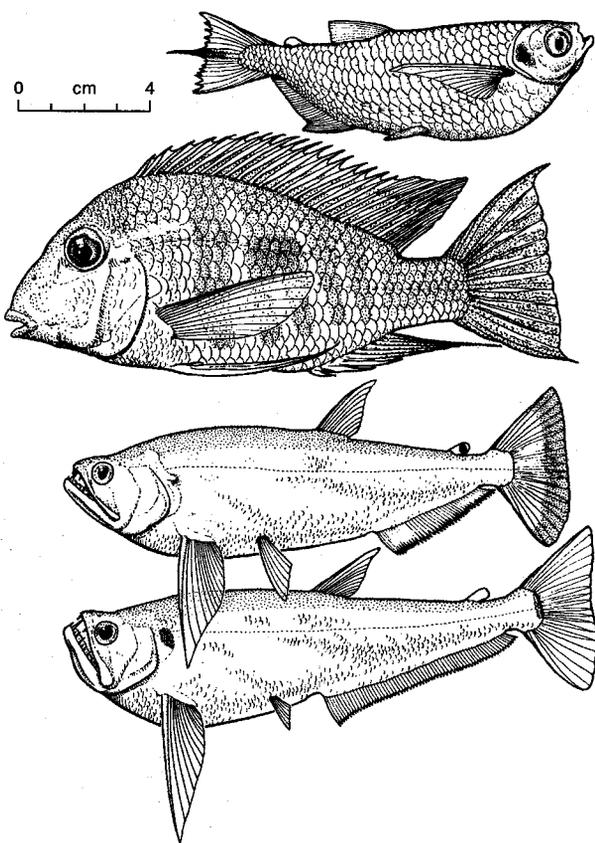
Figure 12. Illustration of adaptive diversity among the Orinoco floodplain fishes (reprinted with permission from the National Geographic Society). From top to bottom, these include **Triportheus angulatus** *(Characidae), a surface feeder;* **Geophagus surinamensis** *(Cichlidae), a bottom feeder; and two piscivores of convergent morphology (***Hydrolycus scomberoides** *and* **Raphiodon gibbus***), both of the Characidae. Scale applies to upper two taxa; the lower two are shown at approximately one-third of their actual size.*

north temperate true pikes (Esocidae). Others are well adapted for visual plankton feeding or for chemosensory benthic feeding (Figure 12). Adaptations that seem bizarre by comparison with those of fishes found at temperate latitudes include electrosensory capability and specialization for scale eating or fin eating. The natural histories of most of the Orinoco fishes are unknown.

As barriers between individual basins are obliterated by rising water, the fishes of the Orinoco floodplain have access to the entire floodplain; they are potentially panmictic. By the middle of the isolation season, however, the Orinoco fishes have resolved themselves into communities that show wide variation in species composition and relative abundance of taxa among lakes (Rodríguez and Lewis 1994).

Interbasin variation among fish communities on floodplains is well known (Lowe-McConnell 1975, Welcomme 1979), but its cause has been difficult to diagnose. The

causes of variance in community structure on floodplains are part of a larger debate concerning the assortment of fishes across habitats in a range of aquatic systems. One possibility is that fishes assort randomly across habitats, in which case variation among habitats could be attributed largely to the ecological equivalent of genetic founder effects (Grossman et al. 1982, 1985). Another possibility is that fishes assort in a deterministic fashion but according to factors too complex to be understood without detailed studies of the individual natural histories of the fishes (e.g., Lowe-McConnell 1987, Goulding et al. 1988). A third possibility, which seems to apply well to at least certain fish communities of temperate lakes, is that the assortment of fishes is dictated deterministically by a small suite of key factors that can be quantified and used in the prediction of species composition (e.g., Robinson and Tonn 1989, Tonn et al. 1990). For the Orinoco floodplain, it appears that the third of these three possibilities applies, and that the key factors are among the same ones that explain diversity among basins with respect to water quality and plankton growth. Two major causes of variation are identifiable: biogeographic and morphometric.

Biogeographic variation of fish communities is explained by differing proportions of black-water and white-water tributaries along the main stem that generate variety in fish communities over scales of hundreds of kilometers (Rodríguez and Lewis 1990, 1997). Nested within the biogeographic component of variation is the morphometric component, which is even larger. A 2-year study of fish communities comprising 170 species and spanning 22 physical, chemical, and biotic factors produced an unexpectedly simple result: Water transparency explains the bulk of variability in species composition of fishes; it predicts with a high degree of accuracy the numerical density of the most abundant taxa (Rodríguez and Lewis 1997). All other environmental factors have either small or undetectable associations with community composition.

The association of community composition with water transparency suggests a mechanism sustaining diversity among fish communities of the floodplain (Rodríguez and Lewis 1997). Fish communities vary most markedly in the proportions of fishes having strong and weak dependence on vision. Any index of community composition that is based on the proportions of visually and nonvisually oriented fish is strongly related to transparency (Figure 13). Furthermore, as transparency declines, there is a smooth progression in community composition from nonvisual predators to visual predators.

The fish communities of individual floodplain lakes appear to be molded by a winnowing process that is determined by the optical environment, which in turn is strongly related to basin morphometry. With the exception of a few species (small planktivores), the initial assortment of fishes among basins appears to be random, as indicated by high similarity among the basins during

inundation or the earliest phases of isolation (Rodríguez and Lewis 1994). The distinctive features of fish communities in individual basins develop rapidly during isolation through interactions involving predation and competition mediated by gradations of visibility in the environment and visual acuity among the organisms. Biological pressures, which are intensified by the shrinking volume of individual lakes during the isolation season, are reflected in differences among the fish communities of lakes having different morphometries. Similar processes also occur on the Amazon floodplain (Tejerina-Garro et al. 1998).

Food webs and energy flow

Food webs raise the prospect of complexity caused by the varied use of multiple carbon sources by a diverse group of consumers. Studies based on stable isotopes show, however, that the floodplain food webs are not so complex as might be supposed.

The Orinoco floodplain sustains high rates of primary production, the bulk of which is accounted for by vascular plants. In uncanopied areas of the floodplain, macrophyte mats reach densities of approximately 4000 gC/m^2 (Hamilton and Lewis 1987). Because of herbivory and other losses during the growing season (e.g., Junk and Piedade 1993), annual net production may be as much as three times higher than maximum density. Within the canopied zones, much of the net production of the floodplain forest appears as litter on the forest floor, where it is stored in dry form until inundation, when it becomes part of the aquatic inventory of organic carbon until the water level recedes.

Algae also contribute to total primary production, but algal production per unit (approximately 300 $gC/m^2/yr$ for the uncanopied zone) is much smaller than that of vascular plants. Dense populations of phytoplankton appear only after inundation has nearly ceased, and are again suppressed when fine sediments are resuspended toward the end of the isolation season. Periphyton grows abundantly on the roots and stems of macrophytes, but occupies only the uppermost portion of the water column because the lower portions are intensely shaded.

The Orinoco floodplain gives the appearance of an ecosystem in which energetics would be dominated by organic matter from vascular plants. The influence of this source of organic matter is evident in the high rate of aquatic respiration, which proceeds so rapidly on the floodplain during the inundation season that demand for oxygen greatly outstrips supply from both physical reaeration mechanisms and underwater production by algae (Figure 9). Thus, it would seem that consumer food webs should be heavily dependent on vascular plants, either directly or through the consumption of microbes that are sustained by vascular plant detritus. However logical this conclusion, it is not the case. Instead, algal production provides the bulk of support for the food web, as shown by the study of stable isotopes.
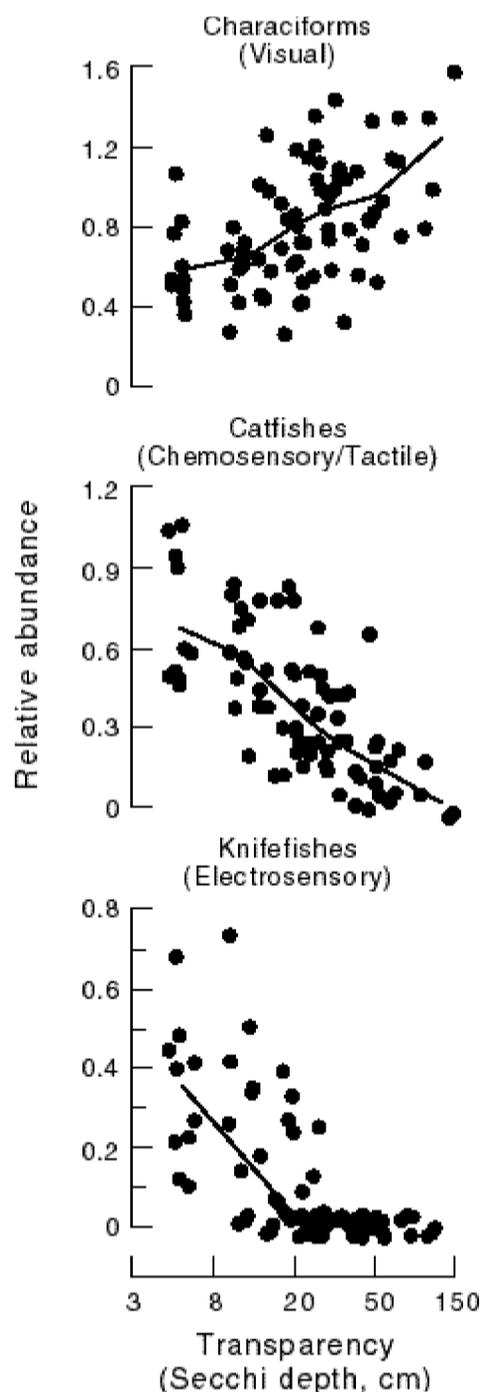

Figure 13. Relationships between transparency and the abundance of three ordinal level taxa of fishes having differing dependencies on vision. Transparency controls the ratio of visual to nonvisual feeders.

When two sources of organic carbon differ in their proportions of ^{13}C, their relative contribution to the growth of a given consumer can be estimated because the tissues of the consumer reflect the proportion of ^{13}C in its diet. On the Orinoco floodplain, the ^{13}C signatures of algae
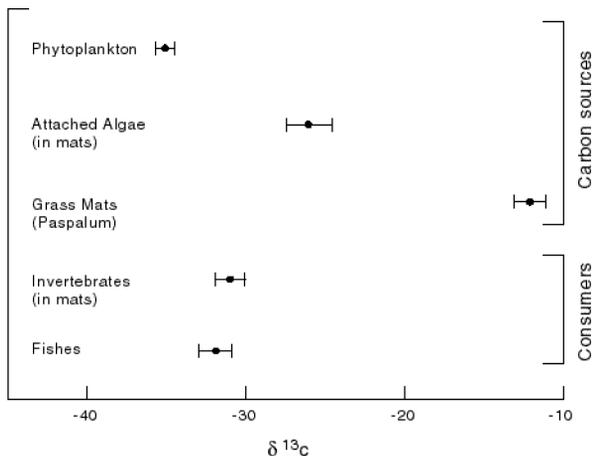
*Figure 14. Stable isotope signatures for carbon sources (autotrophs) and consumers in mats of **Paspalum**, the dominant aquatic autotroph on the Orinoco floodplain. The x-axis shows delta notation for ^{13}C; invertebrates have been corrected for trophic shift by one delta unit; fishes by two delta units. Bars show the standard error of mean.*

differ from those of vascular plants, and especially from *Paspalum*, the dominant vascular plant (Figure 14). For this reason, it is possible to estimate the relative contributions of vascular plants and algae to the support of any category of aquatic consumer on the floodplain. Analyses of this type have shown that consumers in 30 taxa spanning a broad range of trophic levels and habitats on the Orinoco floodplain depend primarily on algal carbon for growth (Hamilton and Lewis 1992).

Algae are potentially a rich food source for consumers because algal cells have much smaller proportions of structural carbohydrates than vascular plants. Even so, it would be reasonable to expect many kinds of consumers to have evolved mechanisms for the efficient use of organic matter from vascular plants, especially in view of the likelihood that vascular plant detritus is enriched nutritionally by microbes during the course of decomposition. Instead, natural selection seems to have refined and diversified mechanisms for the capture of algal carbon, which is less abundant and less concentrated than vascular plant detritus. Both phytoplankton and periphyton probably contribute to the support of consumers, but enclosure experiments and isotope data indicate that phytoplankton provide most of the algal support for the floodplain food web (Hamilton et al. 1992, Lasi 1993).

The food web studies on the Orinoco floodplain show that vascular plant carbon supports high rates of respiration by microbes but only a small proportion of production by aquatic consumers. Vascular plant carbon passes into a microbial dead end, while the food web is sustained mainly by algae. As a generalization, macrophytes provide habitat but not energy, whereas algae provide energy but not habitat.

Exchange between the floodplain and the river

A search for ecological determinism can be extended biogeochemically even to the entire floodplain–river interaction. Most important from a biogeochemical perspective is the net effect of reciprocal water exchange on budgets of carbon and nutrients. Floodplains and rivers are complementary in a biogeochemical sense because they exchange large volumes of water. It is still not clear, however, how the exchanges between rivers and floodplains operate. Given that floodplains are highly productive, whereas rivers for the most part only transport production from their watersheds, it might seem reasonable to assume that floodplains are net carbon sources for rivers. Moreover, the great demand for nutrients by autotrophs on floodplains would suggest that floodplains are sinks for nutrients carried by rivers. These generalities have been difficult to test because they can be masked by anthropogenic perturbation of floodplains and rivers. On the Orinoco, the complementary functions of river and floodplain can be observed under essentially natural circumstances.

Information on the biogeochemical relationship between the Orinoco River and its floodplain comes from studies of the mass balance of carbon, nitrogen, and phosphorus over long reaches of the Orinoco main stem. When the main stem is divided into reaches of approximately
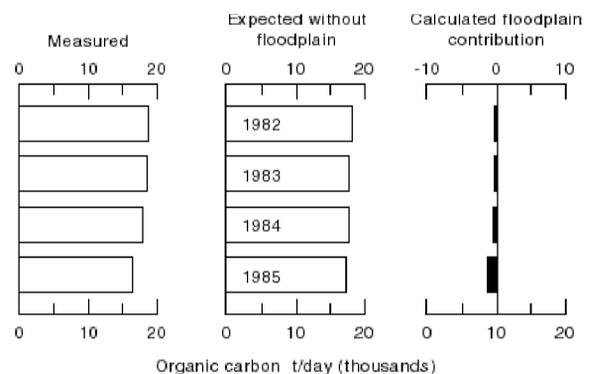

Figure 15. Mass balance for organic carbon on the Orinoco main stem showing the influence of the floodplain on carbon transport by the river (Lewis et al. 1990). The floodplain, despite its productivity, makes no net export of organic carbon to the river.

100 km, the influence of the floodplain can be isolated as the residual of a mass balance equation that takes into account transport into the top of the reach; transport from the bottom of the reach; additions by tributaries; and, for organic carbon, transformations by respiration and production in transit. Mass balances of this type were obtained on the Orinoco main stem over a 4-year period (Lewis et al. 1990). The results indicate that the 600-km reach of floodplain along the Orinoco River is not a net

source of carbon for the river. The fringing floodplain is, in fact, a sink for carbon, but the sink is of such small magnitude that the floodplain has little net influence (less than 5%) on the carbon transport of the main stem (Figure 15).

The fringing floodplain of the Orinoco River is a hydrologically open system that, contrary to expectation, behaves much like a closed system with respect to organic carbon. The explanation for the seemingly contradictory behavior of water and organic carbon lies in the structure of the floodplain. Because of the natural levee, water is routed for long distances within the floodplain. Organic carbon that might potentially exit the floodplain is in transit for long periods of time, during which it is subject to loss through physical retention (gravity sedimentation in calm waters or physical removal in dense macrophyte mats) or biological processes (consumption by invertebrates or decomposition by microbes). Thus, the physical characteristics of the floodplain greatly suppress its tendency to export organic carbon. Similar principles probably apply to exchanges of phosphorus and nitrogen as well (Hamilton and Lewis 1987). Because the mechanisms are general ones, other natural floodplains may show similar characteristics.

Conclusion

Despite its formidable size and spatial heterogeneity, the Orinoco floodplain shows clear causal connections of hydrology and geomorphology with biogeochemical cycles and with the composition and functioning of living communities. The strong deterministic nature of many of these associations facilitates understanding of the floodplain as an ecological system and creates a basis for prediction of change as the floodplain and river are altered under human influence.

As prime moderators of ecosystem structure and function, hydrology and geomorphology are the beginning points for understanding the system-level features of the Orinoco floodplain. The temporal organizer for the system is the annual hydrologic sequence featuring the flood pulse (cf. Junk 1997), but also including a sequence of hydrologic changes leading from the end of inundation to the last days of floodplain isolation. Annual repetition of the main hydrologic events forces a strong degree of repetition in biotic and biogeochemical events on the floodplain. The spatial organization of the floodplain centers on individual floodplain basins as primary functional units within a larger framework that includes hydrologically separate floodplain segments. The stability of these physical features from one year to the next reinforces the tendency for annual repetition of events at a given location on the floodplain.

Ecological processes vary spatially on the floodplain, but variation can be understood and predicted on the basis of morphometric and hydrologic factors. The depth, shape, and size of open water zones (lakes) and their

retention time for flowing water explain variation in the onset of successional events, in the rate at which these events progress, and in the final ecological status of an individual basin just before the onset of a new annual cycle. Turbidity, which controls the optical environment, is the main vector through which physical heterogeneity of the floodplain is translated into variations in communities and biological processes. At the subbasin scale, categories of autotrophs play sharply different roles: Aquatic vascular plants provide shelter but little nourishment for consumers, and algae provide no shelter but account for the bulk of energy flowing through the consumer components of aquatic food web.

Large floodplains have seemed resistant to system-level analysis, but studies of the Orinoco floodplain, whose physical characteristics are largely free from anthropogenic influences, suggest a strong degree of determinism and a simple framework of major controls on biotic and biogeochemical processes. The difficulties of analyzing large floodplains at temperate latitudes may derive largely from the diversity of strong human influences, which magnify the complexity of floodplains as ecological systems.

Acknowledgments

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