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Conclusion. The forest as a functional entity

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The subjects of the seven articles are tightly interrelated by a straight sequence of causes and effects as well as by multiple cross-links.

Leopoldo et al. analyze the water cycle as a result of large scale geography on the one hand and of evapotranspiration on the other. Their table 7 leaves no doubt that 50–75% of precipitation is recycled more-or-less on the spot by the forest itself. This water balance, by the way, does not yet include the nightly dew formation which is a regular and marked feature of the Amazonian forest, notably also during the dry season (personal observations). In fact, dew produced by the swamp (stream valleys) and inundation forests may well balance, in part, the water deficit in the terra-firme forest of the plateau, established for the months of August to November by Ribeiro and Villa Nova[10]. The results of the water budget give strong support to the ever growing conviction that large areas of arid lands on this globe are man-made. The second, important aspect of this article is nutrient cycling. A considerable fraction of the scarce, but vital elements in exchangeable form, such as Ca, P, K, Mg (Klinge 1976 and Chauvel 1981 in Luizão and Schubart) are cycled via biological activity in the canopy and via leaf drip, for example by the activities of the monkey populations and their insect prey, dealt with in Rylands' article.

Chauvel et al. explain the transformation of the tertiary barreira sediments (sandstone interlaced with clay) into today's soils as a function of vertical and horizontal pedogenetic processes which are influenced by the infratopography and by the chemistry of decomposition under the forest canopy. Vertical dissolution of quartz and neoformation of kaolinite led to the heavy clay soils that dominate the plateau today and is responsible for the high silica content of Amazonian waters, whereas lateral disintegration and loss of clay particles over the shoulders of stream valleys leads to the transition to sandy podzols. The resulting mosaic of soil types gives rise to the mosaic of different streams mentioned in Walker's article: black water from podzols and crystal clear water from heavy latosols. The horizontal processes in particular imply that stream valley formation (sagging of the shoulders!) is largely the result of internal, quasi chemical erosion which leaves the soil surface and the vegetation cover intact. This interpretation agrees with data on soil hydrology[7,8] and on variation of stream discharge in relation to the magnitude of precipitation[3], which show that runoff is minimal and that streams swell essentially by percolation of the water through the soil; there is virtually no mechanical soil erosion despite the fact that approximately 70% of precipitation falls in the form of heavy rains (Leopoldo et al. article). The water of forest streams remains essentially clear and transparent during and after heavy rains, whereas streams in deforested, urbanized areas (for instance in Manaus) carry white water, i.e. water with a heavy load of suspended sediments. This observation makes one wonder how much of the Amazonian white water carried by the large whitewater rivers (Amazonas, Rio Madeira, etc.), might be of man-made origin, perhaps in ancient times.

Guillaumet's comprehensive review shows evidence that local topography and soil types determine very different tree communities with surprisingly little species overlap: the high terra-firme (sensu stricto) forest on the latosols of the plateau, the open campina on the sandy podzols, the campinarana on the transition zone between the two and the swamp forest of the stream valley bottoms. The rich epiphyte flora with the tree orchids that Europeans know from their flower shops is characteristic of the sparse, open canopy of the campina, a forest formation which is of no immediate economic use. The campinas, therefore, need special protection. As it is not determined yet whether the campinas are the final stage of the podzolification process described by Chauvel et al., or man-made clearings of campinarana forest which will revert to campinarana through a slow series of succession stages, programs for the protection of the campinas need special attention and flexibility (Anderson 1981 in Rylands; Prance and Schubart 1977 in Chauvel et al.). The two interpretations of the origin of the campinas are, by the way, not mutually exclusive; it is quite conceivable that white sands with open vegetation are the result of different processes. Certainly desertification of podzols is a real threat should the climate get drier. Large scale deforestation leading to a reduction of evapotranspiration, and deforestation of campinaranas in particular, would precipitate this process.

The sensitivity of the Amazonian forest flora to its micro-environment is exemplified by Kahn's erudite study of palm populations. Relief, soil type and soil humidity determine forest architecture which, in turn, conditions light intensity. These combined factors determine the composition and richness of palm communities; either one of the components may turn out to be the key factor for the success of a given species. Thus, the smoother relief in the Tucurui region with a denser canopy and well-drained soils reduces the palm community as compared to the Central Amazonian region[4].

The forest produces its own litter, the decomposition of which liberates the nutrients. These are recycled by the root system (partly via mycorrhiza, particularly on podzols[15] which penetrates directly into the litter layer on the soil. The detailed study by Luizão and Schubart shows that the intensity of this process depends on soil and forest type and on the annual pattern of precipitation. Water is not only necessary for biological decomposition, but also for transport of the nutrients into the canopy; the poorer the ion content of the substrate, the more water is needed to transport sufficient quantities for growth. Hence, Luizão and Schubart's study suggests that intensified litter fall and reduced root growth during the dry months may be coupled to drastically-reduced decomposition on the forest floor. Thus, although the solar diurnal rhythm varies little during the year, the Amazonian forest, or at least some of its tree species, may be subject to an annual cycle of growth and of flowering. These problems link up with INPA's research project on tree phenology[1].

The negative correlation between the concentration of exchangeable ions in the substrate and the quantity of water necessary for their transport implies that the presence of xerophytic tree forms in the campina forest may have the same cause as the annual periodicity of litter fall and decomposition in the high canopy forest of the latosols, namely water limitation. Even the high annual rainfall (which percolates rapidly through the nutrient-poor sandy soils) may not be sufficient to transport enough nutrients for the synthesis of adequate quantities of structural proteins (endoplasmatic reticulum, membranes, histones, etc.) in order to balance intense assimilation; whence the relative excess of celluloses and lignins. Kahn's palm populations, annual periodicity of litter fall and decomposition as shown by Luizão and Schubart, and the campina forest described by Guillaumet all point to the possibility that water may be the critical factor for Amazonian forests on the poor soils of the plateau. According to Klinge (1977b in Luizão and Schubart) the quantity of nutrients released from litter decomposition is 51 kg/ha·y; this does not include decomposition of dead wood. Leopoldo et al.'s estimate of nutrient return from leaf drip is approximately 25 kg/ha·y (both include P, K, Na, Ca, Mg). We still lack, however, data on nutrients from feces of herbivores and their predators. All told a rough estimate of the order of magnitude brings us to a value between 100 and 200 kg/ha·y of the above nutrients recycled by means of 10.000–15.000 t/ha·y of water (evapo-transpiration, Leopoldo et al.).

A specifically interesting aspect of Luizão and Schubart's article is the role of termites in soil fertilization. As Ayres and Guerra showed in 1981 (see Luizão and Schubart), the soils of the plateau are too dry during the months of August to December for earthworms which, in the temperate zone, play a considerable role in soil turnover. Thus, in the terra-firme forest of the plateau, the termites seem to fulfil this function. The same holds for the activity of *Atta*, the leaf cutter ants[5]. A comparative review of the various studies on soil arthropods in Amazonia by Walker and Franken in 1983 (cited in the review article by Walker) indicates that the density of macroarthropods is of the order of magnitude of one hundred to several hundred per square meter, and of microarthropods (Acari, Collembola[9], etc.) of 1–2/cm^3 in the top 10 cm of the soil. Apart from their function in the nutrient cycling process, their mining activity, soil transformation, and interaction with root growth allow for the immediate infiltration of rain into otherwise impermeable clay soils and for internal percolation into the streams which explains the abscence of surface erosion.

Rylands's review of Amazonian primates stresses their adaptation to, or at least their preference for, particular forest types, architectural strata (canopy, underwood, etc.) and various foods, and in so doing touches on some very challenging aspects of ecology and evolution. Contrary to the intuition of biologists working in temperate regions, that the overwhelming Amazonian species diversity should lead to a complex pattern of species-specific consumer/resource associations, one finds wide superposition of resource utilization. To repeat just one example: the insectivorous tamarins also feed on fruits and seeds, and on gums if readily available. Moreover, in any one habitat these foods are shared with birds, bats, insectivores and tree-dwelling rodents. On second thought, this is a logical state of affairs. The greater the diversity of potential resource species, the smaller the potential local abundance of individuals of each species. In a forest with 179 species of large trees per hectare (Guillaumet's review), no animal with a relatively large resource requirement can specialize on a single diet. Hence, the consumers turn out to be habitat specialists, that is, they are limited by three-dimensional, albeit flexible, spaces with specific sets of qualitative attributes, food availability being one of them[19,20]. Vast overlap in resource utilization has also been shown for parrots[11], crocodiles[16], fish (see for example dos Santos[12]) and fresh water shrimps (Kensley and Walker 1982, in Walker).

A further evolutionary topic that emerges from Rylands' article as well as from Guillaumet's review is the following: Rylands lists 30 species of monkeys in 14 genera, and only 5 cases of sympatry of two species within the same genus; Guillaumet's table 6 presents 55 genera in 29 plant families for the campina and campinarana, and in 3 instances only do we find more than one species per genus. This pattern agrees with the theory of repeated pleistocene and holocene forest refugia, which states that isolated forest regions survived during recurrent arid periods, from which the floras and faunas spread again during intermittent humid periods (Prance in Guillaumet[17,18]). Such periodic interruptions might explain the high diversity on the generic level and low sympatric species diversity within genera; this at least for the more conservative and less mobile taxa, which were sensitive to the barriers of water courses, topography, soil and vegetation type. The sandy podzols must have been almost devoid of vegetation during arid phases, and they have the characteristics of isolated islands during humid spells. Today's systematic patterns of the campinas and campinaranas may reflect these more severe interruptions (Anderson 1981, in Rylands). The swamp forests along streams and rivers and the more continuous forests on latosols are much richer in sympatric, congeneric species (tables 2 and 5 in Guillaumet's article).

The continuous river systems, however, facilitate the movement of aquatic organisms between ecologically different water bodies. Sympatric, congeneric species are common from protozoa to fishes; the three prevalent genera *Macrobrachium, Pseudopalaemon* and *Euryrhynchus*, for instance, which make up Walker's shrimp populations, have two or more species in the same river, in the same general habitat and with essentially the same stomach contents (Walker and Ferreira 1985, in Walker). Whatever isolation there may be is of a fine-grained, ecological and behavioral nature.

Walker's article integrates stream ecology with general forest ecology. Streams, it appears, are part and parcel of the forest's nutrient recycling system rather than its excretion; loss of nutrients is minimal as shown by Leopoldo et al. The systemic aspect of the food web agrees with resource utilization by monkeys (Rylands's review); there is enormous overlap between resource types and trophic levels. The coexistence of innumerable consumers that feed opportunistically on the same pool of resources indicates that *direct* food limitation is an unlikely proposition for the Amazonian ecosystems. This state of affairs calls for a careful consideration of stability concepts. A stable ecosystem is one with a smooth, relatively stable energy transfer. This is particularly true for recycling systems where the input is a function of the output, i.e. where food chains depend on decomposition. Whether a particular channel segment has simple or compound leaves, long or short antennae, blue or yellow feathers may be of little importance, provided only that the energy is passed on. In other words, species composition may vary considerably in time and from place to place. If accidents to transfer channels are species-specific (parasites, epidemics, temperature sensitivity, etc.), then the multiplicity of species provides channel redundancy and is an element of stability. The backbone of the system's stability is, however, the non-specificity of the channels that recycle nutrients and water. If a constant number of species is an attribute of the system's definition, then overall species loss must be balanced by the arrival and/or emergence of new species on the scene.

Integrating the aspects emerging from this review into a simplified, physical concept, we may regard the Amazonian forest as a reservoir of water and nutrients that accumulated (and may continue to increase) over the millenia on poor and fragile soils, but which is relatively stable if regarded over decades or perhaps even over centuries. It is a reservoir with minimal input and output flows, which maintains itself by a massive, internal recycling flow, and which is stabilized by regenerative channel redundancy (opportunistic, alternative food chains composed of large numbers of ecologically equivalent species). Limits to renewable, economic exploitation by man are set by the magnitude of the meagre input and output flows, and the system is highly sensitive to tampering with the magnitude of the recycling flows. This message is neither new to, nor is it unheard by, the Brazilian government agencies for the development of natural resources in the Amazonian region (INPA, after all, being one of them). Discussion of concrete dangers and of errors committed reaches back for years[2,6,13,14]. The question is whether insight and foresight coupled to governmental control can counteract devastation caused by ignorance and by the desire for short-term gain, or whether a destroyed ecosystem will no longer support human populations. And this is, so it would seem, not a specifically Amazonian problem.

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Short Communications

Prey localization by surface wave ray-tracing: Fish track bugs like oceanographers track storms

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Summary. Surface-feeding fish accurately determine direction and distance to the center of a concentric wave stimulus, even if only a single, short lasting wave train is presented[1,2]. It has been suggested that one cue used by these fish to localize the wave center is the distance dependent frequency modulation of the initial part of a wave stimulus[3,4]. Here we show how the distance information contained in the fractional frequency change of a capillary wave group can be decoded. We suggest that wave source localization in surface-feeding fish in part is based on a principal similar to that used by oceanographers to track storms by the frequency change of forerunners of swell.

Key words. Surface-feeding fish; water surface waves; lateral line; distance determination; ray-tracing.

Surface-feeding fish prey on terrestrial insects trapped at the water surface. These fish detect and localize their insect prey with aid of water surface waves generated by the preys struggling[1,2]. The receptors involved are mechanosensitive lateral line organs located at the fish's head and back[5]. Visually deprived surface-feeding fish can be conditioned to respond to wave stimuli (called clicks) generated by a single air blow or by dipping a small rod once into the water. Even if a single click is presented these fish determine the direction and distance to the wave source up to 10–15 cm precisely[1,2]. Because a click lasts shorter than the time needed for the fish to reach the wave source, surface-feeding fish are able to localize the center of a concentric wave stimulus under open loop conditions, i.e. these fish can localize a remembered wave target.

Water surface waves as caused by prey objects of surface-dwelling predators are in the mm to cm (5–140 Hz) wavelength range[6]. An isolated strongly localized initial disturbance of the water surface can be thought of as the combination of large number of sinusoidal oscillations (Fourier-components[7]) with different wave lengths (λ) and frequencies (ω, where ω is 2 π f). In low-frequency ($\ll$ 13 Hz) waves gravity is the most important restoring agent. Gravity waves in deep water have normal dispersion characteristics, i.e. the longer waves travel faster than the shorter waves. In capillary waves ($\gg$ 13 Hz) the most important restoring force is surface tension. Capillary waves are abnormally dispersive, i.e. the shorter waves are faster than the longer waves. In deep water (water depth $\gg \lambda$) the following equation describes the dispersion relationship of surface waves[7]

$$c_{ph}{}^2 \equiv \frac{\omega^2}{K^2} = \left(g + \frac{T \cdot K^2}{\varrho}\right) K^{-1} \qquad (1)$$

where g is the gravitational acceleration, K is the wave number ($2\pi/\lambda$), ϱ is the density of the water, T is the coefficient of surface tension, and c_{ph} is the phase velocity. For typical parameters ($g = 981$ cm/s^2 and $T/\varrho = 72$ cm^3/s^2) the minimal phase velocity of water surface waves is 23.1 cm/s at a wavelength of about 1.7 cm (corresponding to a frequency of 13 Hz) (fig. 1). Consequently in the frequency range 5–140 Hz, waves of 1.7 cm length form the rear portion of a wave packet.

Wave energy propagates with group velocity (c_g) which is defined as the rate of change of frequency with wave number[7]

$$c_g \equiv d\omega/dK = c_{ph} - \lambda\,(dc_{ph}/d\lambda) \qquad (2)$$

Group velocity is slower than phase velocity in normal dispersion ($dc_{ph}/d\lambda > 0$) and faster than phase velocity in abnormal dispersion ($dc_{ph}/d\lambda < 0$)[7]). After traveling a certain distance, a dispersive wave group consists of a band of different wavelengths and frequencies. Locally a wavelength can be defined by the crest to crest distance, but due to dispersion the distance of successive crests differs by a small amount. These differences reflect both the distance dependent frequency modulation of the wave group and the speed with which the wave packet spreads in space.

When surface-feeding fish are confronted with a computer controlled wave stimulus which is generated at 7 cm but simulates the frequency modulation of a click at 15 cm, they swim on average 4–6 cm beyond the wave source (fig. 2). Therefore it has been suggested that these fish use the frequency modulation of the first few wave cycles of a capillary wave train to determine prey distance D[3,4]. There is, however, a variation in frequency modulation at a given source distance, if different types of wave generators are used[3]. Because the observed variations in frequency modulation were small, it was assumed that they may cause some uncertainty or variability in the orientation response of surface-feeding fish[3]. Also, to date, it has not been shown how the information contained in the frequency modulation of a wave stimulus can be decoded. Here we demonstrate that the wave source distance D unequivocally can be calculated if both the local frequency of the initial part of a wave stimulus and the fractional frequency change around this local frequency are