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Ecological aspects of arboviroses in Amazonia, South America

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■ **ABSTRACT.** Arboviruses are considered as components of ecosystems. The ecological niche of an arbovirus is thought as a multidimensional space where viral surface receptors are interacting with host's antibodies (host specificity), bloodsucking vectors are coevolving with vertebrate hosts, and non-biotic factors are influencing host population dynamics. The RNA-nature of arboviruses, allied to very fast multiplication cycles, allow them to adapt very quickly to ecological changes. However, various genetical, historical and ecological constraints are probably the cause of their non-random distribution. In Brazilian Amazonia, where endemicity is very high, 186 different species of arboviruses have been isolated, 136 of which are autochtonous to the region and only six are encountered in continents other than Americas. Their cycles have been classified according to their complexity and/or nature of their hosts, but this data did not give much insight about the dynamics of their transmission. A statistical analysis, based on multifactorial methods, allowed to propose some hypotheses about the evolution of arboviruses. The best documented results are (i) the probable existence of serological constraints, preventing two serologically cross-reacting viruses from multiplicating in the same host at the same time; (ii) the continuous ecological distribution of each arbovirus from one type of hosts and from one level of vegetation to another. Other constraints, especially genetical (or phylogenetical) ones are not yet identified.

■ **RESUMEN. Aspectos ecológicos de las arbovirosis en Amazonia, América del Sur.** Los arbovirus son considerados como componentes de los ecosistemas. El nicho ecológico de un arbovirus se piensa como un espacio multidimensional donde los receptores de la superficie viral interactúan con los anticuerpos del huésped (especificidad del huésped), los vectores succionadores de sangre coevolucionan con huéspedes vertebrados, y factores abióticos influencian la dinámica poblacional del huésped. La naturaleza ARN de los arbovirus, sumada a ciclos de multiplicación muy rápidos, les permiten adaptarse con mucha rapidez a cambios ecológicos. Sin embargo, varios condicionamientos genéticos, históricos y ecológicos son probablemente la causa de su distribución no al azar. En la Amazonia brasileña, donde el endemismo es muy alto, han sido aisladas 186 especies diferentes de arbovirus, 136 de las cuales son autóctonas de la región y sólo seis se encuentran en continentes fuera de las Américas. Sus ciclos se han clasificado de acuerdo con su complejidad y/o naturaleza de sus huéspedes, pero estos datos no arrojan demasiada luz sobre la dinámica de su transmisión. Un análisis estadístico basado en métodos multifactoriales, permiten proponer algunas hipótesis sobre la evolución de los arbovirus. Los resultados mejor documentados son: (i) la probable existencia de condicionamientos serológicos, los cuales previenen que dos virus con reacciones serológicas cruzadas se multipliquen en el mismo huésped al mismo tiempo; (ii) la continua distribución ecológica de cada arbovirus desde un tipo de huéspedes y desde un nivel de vegetación a otro. Otros condicionamientos, especialmente genéticos (o filogenéticos), no han sido todavía identificados.

INTRODUCTION

The amazonian region is probably the world's richest reservoir of arboviruses. The 186 different types of arboviruses so far detected in the brazilian part of the region (Travassos da Rosa *et al.*, 1998) account for near one third of the world's arboviruses (533) (Karabatsos, 1985). Of these, 136 (83.4 %) are endemics in this part of the neotropical zoogeographical region and 34 (18,2%) may cause disease to human beings.

The virological and serological data, obtained between 1954 and 1995 at the Evandro Chagas Institute / National Health Foundation (Belém), have been analysed from two complementary points of view: (i) the definition of the ecological niche of each arbovirus and (ii) the ecological factors which have possibly constrained their evolution.

The ecological niche concept has been used recently by Regenmortel *et al.* (1991) in relation with the definition of the virus species: "A virus species is a polythetic class of viruses that constitutes a replicating lineage and *occupies a particular ecological niche* (emphasis by us)". A definition of the ecological niche which best suits to the arboviruses and has been used once by Dégallier *et al.* (1992a) is: "A niche is a multi-dimensional hypervolume of resource axes" (Colinvaux, 1986: 31). In the case of arboviruses, each host or alternatively, each component of the hosts' environment may represent one of these resource axes or variables, allowing for the quantification of the niche. Thus, various data analysis methods revealed themselves particularly well adapted (i) to the numerical definition of the niche of each virus species, (ii) to the study of the ecological grouping of the viruses, and (iii) of the man-made modifications of the natural environment which may cause the emergence or re-emergence of arboviruses (Pinheiro *et al.*, 1977; Dixon *et al.*, 1981).

Another question which is not yet resolved but is related to the above two points is: what are the ecological factors preventing arboviruses from multiplying randomly in all available hosts ? There are probably constraints of various origins and located at various levels, from inside the cell to the ecosystem: genetical (or physiological) (Dubois, 1991), eco- ethological and historical (or biogeographical) (Barbault, 1991).

The crude data was represented by the isolated strains and the results of haemaglutination inhibition (HI) tests (the laboratory techniques are described in detail in Shope & Sather (1979). In order to avoid the introduction of false positives in the data, even at cost of some false negatives, the HI tests have been considered positive for a particular arbovirus if it showed a titer at least four-fold above any of other tested antigen in the same serological (cross-reacting) group.

An intuitive knowledge about the intensity of the adaptive radiation of arboviruses in Amazonia is provided by both the host spectrum of each virus (Table I) and number of viruses found in each host (Table II). However, the viruses' families with greater number of species are not necessarily those which were found in the greater variety of hosts. For example, the Flaviviridae and Togaviridae with each only 8 viral species in the brazilian Amazon region, have been found associated with at least 57 and 56 different hosts, respectively, numbers above the 54 hosts known for the *Bunyavirus* which include 45 species. On the other hand, the Reoviridae, accounting for 63 different virus, are known from only 14 different species of hosts. Thus, the ecological diversification, in terms of number of hosts envolved in transmission cycles, seems to be independant from the systematic diversification of the viruses (= number of species).

Table I. Numbers of genera, serological groups and species for each family of arboviruses present in the amazonian region of Brazil; their order of enumeration follows decreasing number of species.

Family	Genera	Groups	Species
Bunyaviridae	2	11	70
Bunyavirus (a)	-	10	45
Phlebovirus	-	1(b)	25
Reoviridae	1	2(c)	63
Rhabdoviridae	1	5(d)	15
Togaviridae	1	1	8
Flaviviridae	1(e)	1	8
Coronaviridae	1	1	1
Poxviridae	-	-	1
Unclassified	-	-	12
(Arenaviridae (f)	1	1	3)
(Herpesviridae (f)	-	-	1)
(Paramyxoviridae (f)	-	-	1)

(a) with 1 *Bunyavirus*-like virus included
(b) with 4 ungrouped viruses included
(c) with 3 ungrouped viruses included
(d) with 3 ungrouped viruses included
(e) with 1 ungrouped virus included

Table II. Minimum numbers of different species of vertebrate and arthropod hosts for each family and/or genus of arboviruses present in the amazonian region of Brazil; their order of enumeration follows decreasing total number of species.

Virus Family/Genus	Min. Nr. of different species Vertebrates	 Arthropods	 Total
Flaviviridae	37	20	57
Togaviridae	39	17	56
Bunyaviridae			
Bunyavirus	15	39	54
Phlebovirus	9	3	12
Reoviridae	2	12	14
Rhabdoviridae	3	6	9
Coronaviridae	1	-	1
Poxviridae	1	-	1
Unclassified	-	2	2

Table III shows the number of different species of viruses found in each ecological type and/or systematic group of hosts. Some types of hosts seem to be more favorable to the speciation of arboviruses than others. Among the arthropods, sandflies are almost the sole hosts for the majority of Reoviridae known from our region. As these viruses do not form aglutinins in vertebrates, it is not yet possible to know if they are diversified in this respect. Due to their minuteness and the lack of identification key for fresh females, the Phlebotomine sandflies were not identified and thus, may contain many species with various habits. On average, nocturnal mosquitoes harbour more different viruses than diurnal ones do. This difference results mainly from the number of Bunyaviridae transmitted by these two types of mosquitoes. Among the vertebrates, the same may be said i. e. that the nocturnal ones harbour a larger variety of viruses, due especially to the predominance of the Bunyaviruses. The Flaviviridae seem to be as "diurnal" than "nocturnal" but the Togaviridae may be more "diurnal" if we consider their vertebrate hosts.

The multidimensional ecological niche. The data, under the form of a contingency table, was explored either by ordination (factorial analysis of correspondances) or classification (ascendent hierarchical classification) methods (ADE-4 package) (Thioulouse *et al.*, 1997). In order to study more specifically the ecological relationships existing between the arboviruses, the hosts have been grouped according to (i) their vertebrate *vs.* arthropod nature and (ii) their known ecological preferences, e.g. their terrestrial/ arboricolous and diurnal/ nocturnal habits. A more detailed study of the bird-associated arboviruses, based on data about habitat and level preferences of the hosts has been done separately by Dégallier *et al.* (1992a). Also shown by the previous authors (Dégallier *et al.*, 1998), the arboviruses may thus be grouped ecologically according to the predominance of different types of hosts:

- Nocturnal terrestrial vertebrates/ Nocturnal mosquitoes: BEN, ICO, BSB, MOJU, ACA, BSQ, CAR, CAR-like, CATU, MUC, NEP, CAP, GMA, BVS, ITQ, MUR, ORI, BIM, GJA, GAM, AURA, Trombetas;
- Diurnal terrestrial vertebrates/ Diurnal mosquitoes: UNA, MCA, ILH, TNT, KRI, MAG (+ KWA-like, ANU ?);
- Diurnal canopy vertebrates/ Diurnal mosquitoes: YF, GRO, MAY, SLE, TCM, TUR, WEE, ORO, TCM, JUR.

The viruses EEE and PAC-like seem to localize at intermediate positions, between diurnal and nocturnal and between canopy and ground-dwelling hosts. Although the above categorization may be useful, it remains unrealistic because there is a continuum (or gradient) from "diurnal" to "nocturnal" viruses and from "arboricolous" to "terrestrial" ones. Some viruses as GAM, WEE, TUR, ACA Trombetas and GRO are intermediate, being isolated also from "Nocturnal mosquitoes". It is interesting to note the contrast between the predominantly "diurnal" and "terrestrial" PIX, TNT and MAG viruses, and the almost strictly "canopy-liking" viruses MAY, ILH, YF and UNA. The ecology of some viruses like ORO, ANU, Tapara, KRI and ICO needs more informations to be gathered, especially about their vectors.

With few exceptions, each serological group has but one virus in one ecological group; however, we need finer definitions of the niches of 21 viruses pertaining to A, B, BUN, C, CAP, CGL and GMA serological groups.

In a specific approach, Dégallier *et al.* (1992a) considered a subset of the data which included 30 different bird-associated arboviruses. In this case, more precise ecological variables have been used to classify the viruses, namely five types of vegetation, two of which (igapo or inundated forest and "terra firme" forest) has been subdivided in two and five strata, respectively. A gradient has been observed between the birds' species which are preferring secundary vegetation or

Table III. The hosts of sylvatic arboviruses in brazilian Amazonia, grouped according to their ecological characteristics. For each type of host is indicated the number of virus species associated with.

	Mosquitoes		**Sandflies**	**Midges**	**Ticks**	**Vertebrates**			
Arbovirus	**Nocturnal**	**Diurnal**				**Diurnal**		**Nocturnal**	
Families						**terr.**	**can.**	**terr.**	**can.**
Flaviviridae	4	4	0	0	0	6	6	6	6
Togaviridae	6	6	0	0	1	6	7	5	5
Bunyaviridae	37	19	2	2	2	13	17	21	17
Reoviridae	8	5	51	0	0	0	1	2	0
Rhabdoviridae	3	3	3	0	0	4	2	1	1
Coronaviridae	0	0	0	0	0	1	0	0	0
Poxviridae	0	0	0	0	0	0	0	1	0
Unclassified	4	2	2	2	0	0	0	0	3
Total	62	39	58	4	3	30	33	36	32

forest (= "capoeira") and, those which are found mainly in primary forest.

CDU virus has been found mainly in canopy birds which are dwelling mainly (50 %) above 15 and 30 m. This virus, as for some others (CPC, MAY, ILH, TCM), has an important secundary forest component (25 %). The birds which are the hosts of UTI, KWA, GAM and ICO viruses are species living exclusively in the "terra-firme" forest.

EEE virus has been "found" in all but one rare type of vegetation or strata (forest on sandy ground) and is considered as ecologically versatile. This may be linked to a great potential of this virus to colonize new niches, including in urban environment.

The viruses which may be considered the more prone to infect human people in rural places are BSQ, GMA, MUC, MUR and APEU because they have been found in birds which are living in the secundary (or degradated) environments mixed with cultivated areas as is often the case in Amazonia. Antibodies to them are actually fairly prevalent in human sera.

Impact of environmental modifications on the cycle of arboviruses. A special concern is that of the interface between wild viruses and human activities. In tropical countries, the need for energy and extraction of minerals are ever growing, in most cases without knowledge of the impact on the environment and the transmission of diseases. In Brazil, some surveys have been done to evaluate the impact of dam construction or mining exploration on the transmission of sylvatic arboviruses to man.

Among important studies were those of the dams of Tucurui (Pará) (Dégallier *et al.*, 1992b), Itaipu (Parana) (Teodoro *et al.*, 1995), São Paulo (Natal *et al.*, 1995), Combu (Pará) (Anonymous, 1996), and Samuel (Rondonia) (Luz & Lourenço-de-Oliveira, 1996). Mining areas that have been studied were Carajas (Pará) (Travassos da Rosa *et al.*, 1992), Serra Pelada and Barcarena (Pará) (Travassos da Rosa *et al.*, 1995; Anonymous, 1996). In the first case, there have not been any significant augmentation of human infections due to the construction of the dam. However, some arboviruses of bird (*i. e.* Gamboa) or other such as the *Anopheles* A group have evolved from an undetectable level to a high level of transmission, induced by a great proliferation of their vectors, *Aedeomyia squamipennis* and *Anopheles* spp., respectively. On the other hand, the transmission of arboviruses from "terra firme" forest did not seem to have been modified by the presence of the lake. Modifications of the environment, as in the case of gold extraction, may have favoured the epidemics of Oropouche virus disease in Serra Pelada (Travassos da Rosa *et al.*, 1995). In the region of Carajas, many arboviruses are circulating and thus constitutes a risk for the populations employed in the mining activities.

DISCUSSION AND CONCLUSIONS

Previous works have already described the probable sylvatic cycles of many amazonian arboviruses (Woodall, 1967; Dégallier, unpubl.; Hervé *et al.*, 1986). However, the grouping of ecologically similar viruses was made mainly after the number and nature of the hosts, i. e. the relative "complexity" of the cycles. We have reexamined the same data with quantitative methods. In a quantitative ecological study of the viruses pertaining to the group C of *Bunyavirus* Woodall (Woodall, 1979) has shown a marked niche separation between canopy- and ground level-transmitted viruses and, when two viruses appeared to share the same niche, that the vectors were distinct species. Thus, for establishing themselves in a locally stable equilibrium, related viruses cannot share the same arthropod and/or vertebrate hosts. It may even be said that the less they are serologically related, the more they can share the same ecological niche.

The complexity of tropical environments, exemplified by an extreme diversity of vertebrate and arthropod species, and consequently of niches, have favoured the diversification and therefore sympatry of many arboviruses of the same group. As our studies have shown, the presence of two or more different viruses of the same serological group in what has been characterized as one niche may be due to the coarseness of the ecological variables which have been considered. As many ecologists have shown, temporal and spatial variables may also be included in the multidimensional definition of the niches. The isolations of strains and/or serological conversions in sentinel animals should be interpreted in the future for the "temporal" characterization of the niches.

Excepted for some viruses which are ecologically very distinct of all others (PAC-like, CDU), there is no clear-cut separation between one group and the next along the "ecological transects" defined either by the preferred vegetation types and strata, or by the behavior of the hosts. This may mean that, with similar historical (= biogeographical + genetical) constraints, the arboviruses' population in a defined community forms a dynamic equilibrium. Subsets of this population may share the same niche, at least at the two levels studied here, and each niche is separated from the others by ecological constraints acting on the hosts' populations. However, two very different types of perturbations can modify this equilibrium. When some fluctuations are going on in hosts' populations, as occurs seasonally for non-immune hosts, only the arbovirus transmission levels are affected. On the contrary, when the hosts' populations are permanently modified, the equilibrium of arboviruses' populations need to shift to a new state. Eventually, new niches may appear which would be filled after a short time. These may be colonized by new genotypes, obtained by recombination, reassortment or introduction from other communities (Calisher, 1994). Rapid adjustments of equilibrium have been noted in the case of the important perturbations induced by the filling of a dam reservoir, where "new" arboviruses appeared in the area, either as exogenous material or as autochtonous speciation (Dégallier *et al.*, 1992b).

The phylogenetic study of arboviruses, based on the viruses-hosts associations is yet very tentative because of the lack of phylogenetic classifications of either groups (Eldridge, 1990). This author has looked for some evidence of a host-parasite coevolution in the case of the California serogroup viruses. What we have defined as historical constraints are doubtlessly related with some effects of coevolution but it remains difficult to distinguish these from the constraints arising from viruses competition after horizontal transfers (Tabachnick, 1991). These hypothesis need to be evaluated by molecular biologists.

What happened with the viruses for which some evolutionary hypotheses are available, based on protein sequencing ? Levinson *et al.* (1990) furnished some interesting hypothesis which will be discussed from an ecological point of view. MAY (with Una, not studied by these authors), EEE/WEE, AURA and MUC (member of VEE complex) seem to have diverged in four different directions. As Hahn *et al.* (1988) have shown, WEE virus arised probably as a recombinant between EEE and another *Alphavirus* which may be AURA. EEE seems to be a very versatile virus, especially in birds whereas AURA have been found only in monkeys. The ecological link between the two may be the *Melanoconion* and *Ochlerotatus* subgenera of *Culex* and *Aedes* mosquitoes, respectively.

The available data are not detailed enough to explain why some viruses of the same serological group coexist and other do not, but it allowed us to define some main ecological groups. Each of these groups further needs to be studied separately as it has been done with the bird-borne arboviruses.

Despite the great number of tested pools between 1954 and 1995, serological and virological data are lacking either for viruses which do not form aglutinins, or about potential hosts which are difficult to collect. In fact, less than one third (28.9 % or 50/173) of the viruses known from sylvatic hosts have been found in both vertebrate and arthropod hosts, 17.7 % (29/173) are known only from vertebrate hosts and 54.3 % (94/173) only from arthropods. Among the latter, 63.8 % (60/94) are known only from phlebotomine sandflies and represent probably a very complex ecological system.

Sampling biais may account for some distortions in the quantitative delineations of the niches. For example, ground dwelling rodents, marsupials and birds are much easier to trap than canopy frequenting hosts and among them those which cannot be attracted by any type of baited trap. Thus, many species are poorly known, not only for the viruses they may harbour but also for their bioecology. An important ecological "axe" which has been yet neglected is the time or seasonal one. It is quite conceivable that some hosts may harbour different viruses of the same serological group at different times of the year. This may be especially the case with bunyaviruses whose antibodies are not lifelong lasting (Shope *et al.*, 1967). In future studies, the interpretation of serological tests ought to be fine-tuned, according to each virus-host association.

Nevertheless, quantitative multifactorial analysis seemed adequate for the study of the multidimensional niche concept of arboviruses, and it will also reveal itself a useful tool to make predictions about the natural evolution of the arboviruses in response to modifications of the natural environments.

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