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SHORT COMMUNICATION

Macrophyte rafts as dispersal vectors for fishes and amphibians in the Lower Solimões River, Central Amazon

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Large rivers have played a prominent role in biogeographic theory for their potential to act as barriers for the dispersal of terrestrial organisms, and therefore be involved in the generation of species diversity (Brown & Lomolino 1998). In this paper, we document the potential role of macrophyte rafts as a mechanism by which Amazonian rivers could act as dispersal agents rather than barriers, transferring organisms across banks and possibly across very large distances. These vectors could therefore act against speciation and towards homogenization of the local biota.

These rafts originate from extensive macrophyte stands that grow along the margins and banks of the nutrient-rich, white-water rivers and lakes in the Amazonian várzea floodplains (Junk 1970, 1973; Junk & Piedade 1993, 1997; Junk *et al.* 1989). Macrophyte stands support an extremely rich community of over 380 species of herbs of floating and rooted habits, but are commonly dominated by the grasses *Paspalum repens* Berg. and *Echinochloa polystachya* (H.B.K.) Hitch. and floating vegetation such as the water hyacinth (*Eichhornia crassipes* (Mart.) Solms.) and the pteridophyte *Salvinia auriculata* Aubl. (Junk & Piedade 1993). Macrophyte stands constitute a peculiar habitat encompassing aquatic and terrestrial biotopes. The rapid growth and production of detritus, and shelter availability in the root zone of macrophyte stands provide conditions for the development of an abundant aquatic fauna of invertebrates (especially microcrustaceans, molluscs and insects; Junk & Robertson 1997) and vertebrates (mostly fish; Henderson & Hamilton 1995, Junk *et al.* 1997). The aerial portion is habitat for invertebrates (mostly insects and arachnids), anuran amphibians, which use the stands of floating macrophytes as calling and breeding sites (Hödl 1977), and for other vertebrates such as birds (Petermann 1997).

After explosive growth during the period of rising water levels, stalks of floating meadows often get weak and break, forming drifting rafts that may flush into the main river channel and be carried away by wind and water currents (Junk & Piedade 1997).

Field work was conducted on 20 and 21 August 1994 in the Ilha da Marchantaria (03°14′S, 59°57′W), near Manaus, Central Amazon, Brazil. This island is located in the lower Solimões river, 15 km above the confluence with the Rio Negro. Following the yearly peak in water level in June (Irion *et al.* 1997), around August the strongest water currents occur and many macrophyte rafts drift down the river. We approached the rafts by boat, and measured their length and width. Rafts were encircled with a 7-m × 3.5-m (mesh 0.5 cm) seine net. Rafts were not compact and therefore could be entirely encircled even if their perimeter exceeded net length (7 m). The net was subsequently brought to the boat, where every plant was carefully screened for vertebrates. All vertebrates were collected, identified whenever possible to species,

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and counted. Fish were identified as adults or juveniles according to Géry (1977), Kullander (1986), Burgess (1989) and Botero & Araújo-Lima (2001). Voucher specimens were deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

We sampled eight floating macrophyte rafts of 3.02–24.7 m^2 (mean ± SD: 9.11 ± 6.30 m^2) which were found drifting down the river. Two rafts were constituted predominantly of *Eichhornia crassipes*, and six of *Paspalum repens*. Associated vertebrates were represented by fishes and amphibians (Table 1).

Fishes were present in the root zone of all rafts. We found 286 individuals of 39 species and 19 families (Table 1). Characidae were the most abundant (32.9% of all individuals, n = 94) and species-rich (35.9% of all species, n = 14) family, followed closely by Cichlidae in abundance (29.0%, n = 83), but not species richness (10.2%, n = 4). Hypopomidae were represented by 35 individuals (12.2%) and three species (7.7%). Apteronotidae and Serrasalmidae were represented by two species each, while the 14 remaining families were represented by only one species and most commonly by less than four individuals each. The most common species were *Apistogramma agassizi* (Cichlidae), *Hyphessobrycon eques* (Characidae) and *Pyrrhulina* sp. (*brevis* species group) (Lebiasinidae), with respectively 49 (17.1%), 24 (8.4%) and 23 (8.0%) individuals. Fish species richness was significantly related to raft area (number of species = 3.87 + 0.81 × area; $r^2 = 0.70$, $P = 0.01$). No significant relationship was found between fish abundance and raft area. Nearly half (49.30%) of individual fish collected were juveniles.

Amphibians occurred on six rafts. We found 42 individuals of nine species belonging to five families, four of Anura (Hylidae, Leptodactylidae, Pseudidae and Bufonidae) and one of Gymnophiona (Typhlonectidae) (Table 1). Hylidae were the most abundant (83.3% of all individuals, n = 35) and species-rich (55.5% of all species, n = 5) family. The four remaining families were each represented by a single species and 1–3 individuals. The treefrog *Hyla walfordi* was by far the most abundant species (45.2% of all individuals, n = 19). In one single raft, with an area of 8.48 m^2, we found 11 individuals of *H. walfordi*, two of them gravid females. A gravid female of *Hyla leucophyllata* was found in another raft. Only five anurans (11.9%) collected were immatures (three tadpoles and two metamorphs). We did not find any significant relationship between raft area and amphibian species richness or abundance.

A rich and abundant invertebrate fauna was found associated to these rafts, including: a leech, pulmonate molluscs, spiders, crustaceans (shrimps and crabs), and insects such as odonates (naiads and adults), blattarians, orthopterans (ensiferans and caeliferans), homopterans, belostomatid heteropterans, hymenopterans (ants), lepidopterans (larvae and adults) and coleopterans (larvae, pupae and adults). Particularly abundant were shrimps, spiders and orthopterans.

Aquatic macrophyte rafts have been suggested to act as dispersal vectors in large lakes (Lake Mamiraua: Henderson & Hamilton 1995; Lake Malawi: Oliver & McKaye 1982) and rivers (Parana River: Achaval *et al.* 1979) for both aquatic and terrestrial faunas, although the effectiveness can vary depending on the fish group considered (Henderson & Hamilton 1995). Albeit preliminary, our sampling in the Solimões River indicates that floating macrophyte rafts can transport a remarkably diverse and abundant vertebrate assemblage. In addition to the 39 species of fishes and nine of amphibians found (Table 1), at least 13 other species of fish and seven of amphibians live in aquatic macrophyte stands (Hödl 1977, Junk 1973). Many of the fish and amphibian species that we found in the floating rafts show very wide distributional ranges in the floodplains of the Amazon basin (Burgess 1989, Frost 1985, Géry 1977, Kullander 1986). Dispersal of vertebrates through the Amazon River seems to be a common phenomenon and floating macrophyte rafts may be acting as important vectors. Moreover, transportation by floating rafts may represent an unusually predictable vector of long-distance dispersal both from spatial (unidirectional) and temporal (seasonal) standpoints (see also Henderson & Hamilton 1995).

This predictability could have favoured selection for the utilization of macrophyte stands as breeding sites and nursery grounds for several fish species. Rafts could transport juveniles and therefore return individuals to the populations of the several fish species that migrate upriver to breed. Consistent with these hypotheses, Sazima & Zamprogno (1985) observed that young piranhas sheltering among the roots of water hyacinths had no fin damage, in contrast to larger juveniles and adults. They also suggested that, apart from shelter, young piranhas might profit from water hyacinth transportation. This could explain why piranhas, which spawn during the annual floods, have a wide distribution despite the absence of known migratory movements by the adults in Amazonian rivers (Goulding 1980).

The effectiveness of the rafts as a long-distance dispersal vector is further reinforced by the observation that average current velocities in the Amazon River range from 1.0 to 1.5 m s^{-1} in the wet season (Sioli 1975). Under such conditions a raft could travel 86–130 km per day, or, in other words, travel the whole extension of the Solimões/Amazonas River system (4000 km) in as little as 31 d. The probability of establishing viable populations upon arrival could be enhanced both by the synchronization of the drift and reproductive period, and by the large observed densities of fishes (up to 10.5 m^{-2}) and amphibians (up to 1.65 m^{-2}). In summary, drifting of many rafts containing dense vertebrate populations in

Table 1. Absolute frequency of fish and amphibian families and species found in eight macrophyte rafts in the lower Solimões river, Amazonas, Brazil. Individuals classified as adults (A) or juveniles (J) ([a] = tadpoles; [b] = metamorphs).

Family	Species	Number of individuals			Number of rafts in which the species was found	Individuals per family
		J	A	Total		
FISHES						
Ageneiosidae	*Ageneiosus* sp.	1	–	1	1	1
Anostomidae	*Leporinus fasciatus* (Bloch, 1794)	1	–	1	1	1
Apteronotidae	*Apteronotus albifrons* (Linnaeus, 1766)	–	1	1	1	2
	Apteronotus hasemani (Ellis, 1913)	–	1	1	1	
Auchenipteridae	*Parauchenipterus galeatus* (Linnaeus, 1766)	3	1	4	4	4
Callichthyidae	*Megalechis thoracata* (Valenciennes, 1840)	1	–	1	1	1
Characidae	*Aphyocharax* sp.	8	5	13	3	94
	Charax sp.	13	–	13	1	
	Ctenobrycon spilurus (Valenciennes, 1850)	3	–	3	3	
	Hemigrammus sp. 1	3	5	8	2	
	Hemigrammus sp. 2	–	1	1	1	
	Hemigrammus sp. 3	7	1	8	3	
	Hemigrammus sp. 4	1	–	1	1	
	Hyphessobrycon eques (Steindachner, 1882)	10	14	24	3	
	Hyphessobrycon sp. 1	5	5	10	5	
	Hyphessobrycon sp. 2	–	1	1	1	
	Hyphessobrycon sp. 3	–	2	2	1	
	Moenkhausia sp. (*intermedia* group)	–	7	7	2	
	Prionobrama filigera (Cope, 1870)	–	1	1	1	
	Roeboides sp.	2	–	2	2	
Crenuchidae	*Crenuchus spilurus* Günther, 1863	–	1	1	1	2
	Klausewitzia sp.	–	1	1	1	
Cichlidae	*Apistogramma agassizi* (Steindachner, 1875)	27	22	49	3	83
	Apistogramma sp.	6	12	18	3	
	Cichlasoma amazonarum (Kullander, 1883)	6	6	12	6	
	Crenicichla inpa (Ploeg, 1991)	3	1	4	4	
Erythrinidae	*Hoplias* cf. *malabaricus*	3	–	3	3	3
Gymnotidae	*Gymnotus* aff. *stenoleucus*	2	–	2	1	2
Hypopomidae	*Brachyhypopomus brevirostris* (Steindachner, 1868)	6	12	18	3	35
	Brachyhypopomus pinnicaudatus (Hopkins, 1991)	3	13	16	3	
	Brachyhypopomus sp. n.	1	–	1	1	
Lebiasinidae	*Pyrrhulina* sp. (*brevis* group)	2	21	23	5	23
Lepidosirenidae	*Lepidosiren paradoxa* (Fitzinger, 1837)	–	1	1	1	1
Pimelodidae	*Paulicea luetkeni* (Steindachner, 1875)	1	–	1	1	1
Rivulidae	*Rivulus* aff. *ornatus*	1	1	2	2	2
Serrasalmidae	*Metynnis* sp.	2	–	2	2	13
	Serrasalmus sp.	11	–	11	4	
Sternopygidae	*Eigenmannia* sp.	5	5	10	3	10
Synbranchidae	*Synbranchus* sp.	4	4	8	5	8
Total 19	39	141	145	286	–	–
AMPHIBIANS						
Bufonidae	*Bufo marinus* (Linnaeus, 1758)	2[b]	–	2	1	2
Leptodactylidae	*Leptodactylus* aff. *leptodactyloides*	–	1	1	1	1
Hylidae	*Hyla walfordi* Bokermann, 1962	–	19	19	3	35
	Hyla leucophyllata (Beireis, 1783)	–	4	4	2	
	Hyla raniceps (Cope, 1862)	–	2	2	2	
	Hyla punctata (Schneider, 1799)	2[a]	2	4	3	
	Sphaenorhynchus carneus (Cope, 1868)	–	5	5	1	
	Unidentified species	1[a]	–	1	1	
Pseudidae	*Lysapsus laevis* Parker, 1935	–	3	3	3	3
Typhlonectidae	*Typhlonectes compressicauda* (Duméril and Bibron, 1841)	–	1	1	1	1
Total 5	9–10	5	37	42	–	–

breeding condition provides a scenario consistent with the hypothesis of an effective long-distance dispersal vector. This reported dispersal system could be in part responsible for the wide distribution of many of the amphibian and fish species found associated to Amazonian whitewater riverine systems.

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