

# FRUIT AND SEED DISPERSAL IN AMAZONIAN FLOODPLAIN TREES – A REVIEW

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*Abstract.* More than one thousand tree species grow in Amazonian floodplain forests, an environment which is closely linked to a periodical and predictable flood pulse. All biotic and abiotic modes of dispersal which are known for trees in surrounding ecosystems are also present in the floodplains. Additionally, the seasonal flood pulse being a dominant factor, many species employ water for dispersal, i.e. hydrochory or ichthyochory. In these species, diaspores possess adaptations which enhance the dispersal linked to water and which are not found in species of the surrounding uplands, e.g. spongy tissues and air-filled spaces. Both fruits and seeds are the object of dispersal and they cover all sizes and types, e.g. pods, capsules, drupes, berries, pyxidia, etc. An updated overview of the role of the different abiotic and biotic dispersal modes for trees in Amazonian floodplain forests is given. In light of the fine-tuned relationships between plants and animals, and the imminent threats imposed by human actions in floodplain forests of the Amazon River, the need to understand the interactions and main modes of dispersal is fundamental for the maintenance of the integrity of the forests and their sustainable use.

*Key words:* diaspores, hydrochory, ichthyochory, anemochory, barochory, zoochory, Amazonian inundation forest, várzea, igapó.

## INTRODUCTION

Dispersal of fruits and seeds is of basic importance for forest ecology in that it is one of the main factors in determining species composition and the structure of ecosystems (Gentry 1982, Howe & Westley 1997, Arbelaez & Parrado-Rosselli 2005). The spatial distribution of dispersed seeds has important consequences for plants in terms of demography and the spatial pattern of recruitment (Chapman & Russo 2007).

Amazonian floodplain forests cover an area of 400 000 km<sup>2</sup> along the Amazon River and its main tributaries (Junk & Piedade 2010). Approximately 75% of the Amazonian nutrient-rich várzeas are covered by forest (Wittmann *et al.* 2004). One thousand tree species grow in these forests (Wittmann *et al.* 2006, Wittmann *et al.* 2010) which tolerate seasonal inundations of up to 8 m in height and annual flooding periods of up to 230 days year<sup>-1</sup> in Central Amazonia (Junk *et al.* 1989, Junk 1989,

Wittmann *et al.* 2004). The regular and predictable flooding with freshwater has a strong impact on growth (Worbes 1985), phenology (Parolin 2000, Schöngart *et al.* 2002), and ecophysiology (Waldhoff & Furch 1998, Parolin *et al.* 2004, Parolin *et al.* 2010b) of the trees, and on the biotic factors linked to them. Dispersal syndromes have also evolved to adapt to flooding constraints and to make best use of the available water. Earlier studies described the importance of hydrochory and ichthyochory in this ecosystem (Gottsberger 1978, Goulding 1980, Ziburski 1991, Kubitzki & Ziburski 1994). However, a general review including the latest information on the different dispersal modes in this huge ecosystem is lacking. Especially in the light of changes in the hydrologic cycles caused by dams that are built or planned in the region (Junk 1987, Nogueira *et al.* 2010, Ferreira *et al.* 2012, Ferreira *et al.* 2013), and of ongoing deforestation and fragmentation of the remaining forest, the important phenomena linked to seed ecology must be understood. With this review We hope to contribute to this understanding.

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*Dispersal modes.* All modes of dispersal which are known for trees in other ecosystems are also represented in Amazonian floodplains, be it by abiotic or biotic factors. As in upland forests or savannas, both fruits and seeds are the object of dispersal in the tree species of Amazonian floodplain forests. Linked to their taxonomic relatedness, the diaspores cover all types, ranging from pods (e.g. *Albizia multiflora*) to capsules (e.g. *Alchornea* spp.), drupes (e.g. *Andira inermis*), berries (e.g. *Aniba affinis*, *Annona* spp., *Astrocaryum jauari*), and pyxidia (e.g. *Eschweilera* spp.) (Parolin *et al.* 2010a). All size classes are present. Fruit dry mass ranges from 0,01 g (*Salix martiana*) to 96 g (*Mora paraensis*), seed dry mass ranges from 0,008 g (*Mollia speciosa*) to 69 g (*Aldina latifolia*) (Parolin *et al.* 2010a).

However, the seasonal flood pulse being such a dominant factor for organisms inhabiting Amazonian floodplains (Junk *et al.* 1989), the advantage to use water for dispersal is evident, be it by hydrochory or by ichthyochory (Gottsberger 1978, Goulding 1980, Ziburski 1991, Kubitzki & Ziburski 1994). Many tree species and their diaspores therefore evolved adaptations which enhance the dispersal linked to water and which are not found in species of the surrounding uplands (Kubitzki & Ziburski 1994).

*1. Hydrochory.* Hydrochory, dispersal by water, occurs in ecosystems where water plays an extraordinary role. This can be in deserts, where unpredictable rain events represent a unique chance for germination, and dispersal linked to the availability of water followed by rapid germination can enhance the survival of the seedling (Gutterman 1990, Parolin 2006), or in ecosystems with periodical floodings, such as Amazonian floodplain forests. It implies that the diaspores float at least for a short period of time. If diaspores do not float on the surface, the distance dispersed may be reduced but not the probability of dispersal (Moegenburg 2002). They must also tolerate flooding without losing their viability. Both are the case in several dozen species in Amazonian floodplain forests (Kubitzki 1991, Kubitzki & Ziburski 1994). Trees produce fruits or seeds which may have pre-adaptations such as wings or hairs, which in other ecosystems enhance dispersal by wind but at the same time enhance floatation in water. Other species (e.g. *Aldina latifolia*, *Vatairea guianensis*) have clear adaptations to water dispersal, e.g. forming buoyant tissues with large air-filled spaces. In *Swartzia polyphylla*, the ability to float is correlated directly

with the volume of the air pocket between the two cotyledons (6–20 % of total seed volume) (Williamson *et al.* 1999). As a particular strategy, *S. polyphylla* shows a dimorphism of its seeds, some of which float and others sink, allowing the species to have both long- and short-distance dispersal (Williamson *et al.* 1999). This strategy was also described for *Pentaclethra macroloba*, where floatation is related to specific gravity but not to seed size; the ability of *P. macroloba* seeds to float depends on imbibition (Williamson & Costa 2000). In the palm genus *Leopoldinia*, in contrast to most other palms, mature fruits of riverine species are lighter than water and do not lose their buoyancy after the decay of the fleshy portion of the fruit – a clear adaptation to dispersal by water (Kubitzki 1991).

Colorful and fleshy fruits – the signals for animal dispersion – may also be light and buoyant and can float in water. This way, fruits that are assumed to be animal-dispersed are indeed often primarily dispersed by water (Ziburski 1991). The long period of floatation without loss of viability characteristic of most species may also result in the formation of “floating seed banks” (Marques & Joly 2000). In nutrient-rich white-water floodplains called *várzea* (Sioli 1984), soil seed banks are not formed by any species with the exception of *Cecropia* spp. (Ziburski 1991). Soil seed banks in Amazonian floodplains do not play the important role they have in temperate ecosystems, where the role of propagule banks (seeds on or in soil) in maintaining biodiversity in floodplains is very relevant (Leck 1989, Middleton 2000, Bossuyt & Hermy 2001, Crosslé & Brock 2002). Contrary to this, common floating meadows or mats consisting of macrophytes, plant fragments, woody debris etc. are frequent and may likewise increase the duration of floatation and serve as transporting vectors and floating seed banks for the diaspores.

The problem with aquatic dispersal is that it operates almost exclusively in a downstream direction. Floating seeds are deposited in elevated sites, giving advantages for germination (Williamson & Costa 2000), but upstream dispersal requires other agents, such as fish and turtles, or wind (Kubitzki 1985a). There is evidence that most water-dispersed trees are dispersed upstream by secondary dispersal through animals, mainly fish (Horn 1997, Anderson *et al.* 2011, Horn *et al.* 2011).

*2. Ichthyochory.* Dispersal by fish obviously belongs to the section of zoochory described below. However, due to its importance in Amazonian floodplains and

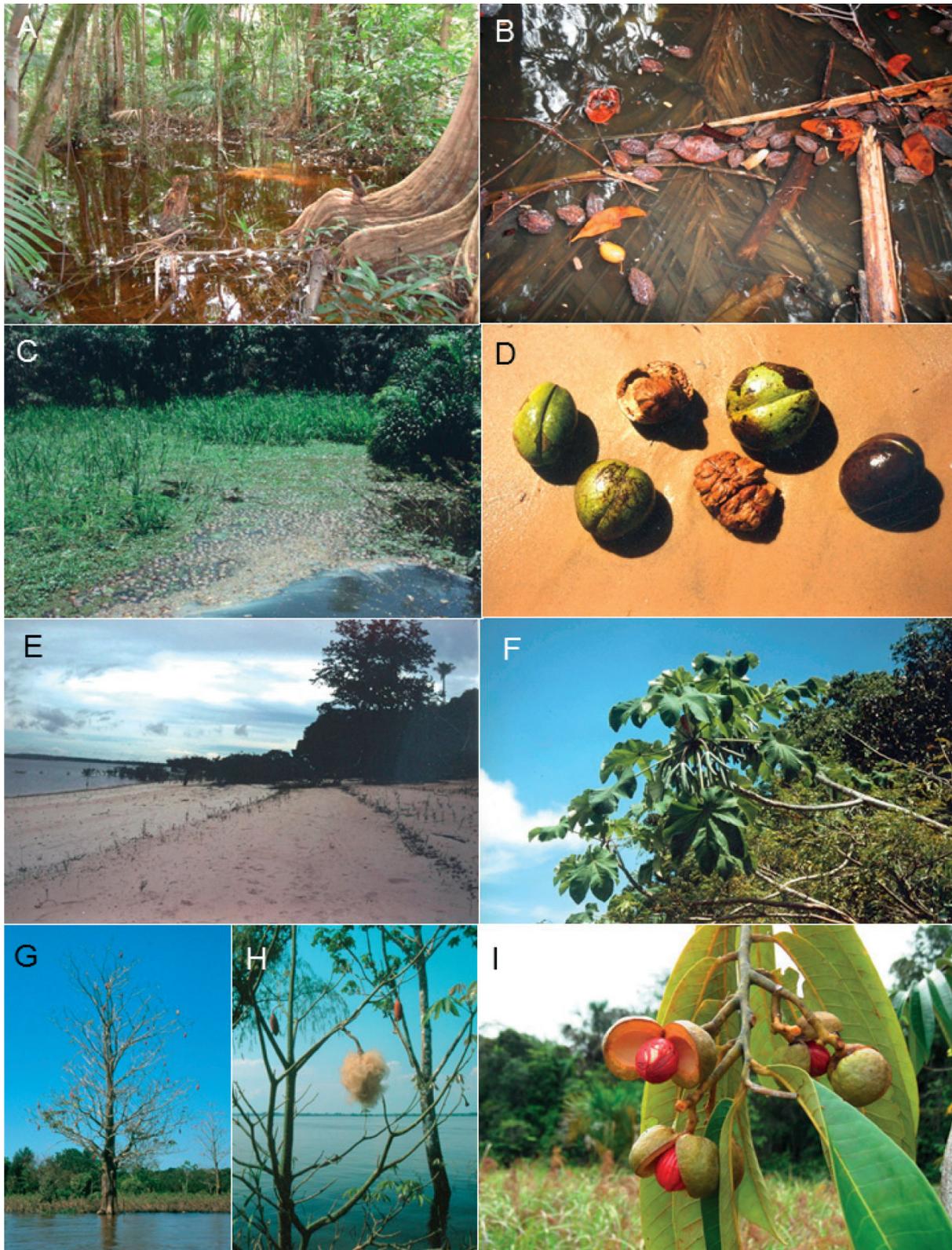


FIG. PLATE A). Water dispersal in Amazonian floodplains. A) Interior of a whitewater floodplain forest in the period of rising water. B) Floating seeds of *Erisma calcaratum* (Vochysiaceae) and *Campsiandra comosa* (Fabaceae, larger seeds). C) Floating seeds of *Vatairea guianensis* (Fabaceae). D) Water dispersed seeds of *Aldina latifolia* (Fabaceae). E) Seedlings growing on a blackwater river beach after water dispersal when the water retreats. F) Fruits of *Cecropia latiloba* (Urticaceae) which float in the water and are eaten by fish. G) Deciduous tree of *Pseudobombax munguba* (Malvaceae) at high water with mature fruits. H) Mature seeds of *P. munguba* surrounded by hairs which are carried away by the wind when the red capsules open. Seeds land in the water where some float away with the currents and others are eaten by fish. I) *Virola surinamensis* (Myristicaceae) coevolved with birds but is also water dispersed in Amazonian floodplains.

its dominant role for many tree species, it is described separately here, in direct relationship to dispersal by water, a phenomenon which in general is not associated with tree species. In the flooded forests, ichthyochory is a common phenomenon (Gottsberger 1978). Fish use the resources in the aquatic–terrestrial transition zone (Junk 1989). When the floodplain forests inundate, frugivorous fishes congregate beneath trees and consume fruits that fall into the water. Fish may also respond to the noise of fruit dropped by primates into the water (Sabino & Szazima 1999). Chemical signs released by fallen fruit to attract fish, fruit/seed buoyancy and strong multicuspitate teeth in frugivorous fishes are adaptations for efficient seed dispersal in the flooded forest community (Goulding 1980, Araújo-Lima *et al.* 1998, Mannheimer *et al.* 2003).

The second most important food category for fish in this ecosystem is plant material, including fruits and seeds: it accounted for 27% (after fish with 35%) of diet volume in fish species studied in the floodplains of the Rio Caura in Venezuela (Gonzalez & Vispo 2003), an ecosystem which is comparable to many respects to the Amazonian floodplain ecosystems. In the annual cycle, there are clear changes in the diets of the fish, the percentage of ingested fruits and seeds being highest at high water (Gonzalez & Vispo 2003, Knab-Vispo *et al.* 2003). In the Peruvian Amazon, 700 000 intact seeds from 22 tree and liana species were found in the guts of 230 *Colossoma* individuals, representing up to 21% of the flora fruiting during the flood season (Anderson *et al.* 2011).

Many of the over 2000 species of freshwater fish are dispersers of many rain forest fruits and depend on flooded forests for food. Fruits and seeds of the floodplains of Central Amazonia that are eaten by fish or other animals have a high nutritional value (Waldhoff & Furch 1999, Waldhoff & Maia 2000, Parolin *et al.* 2010a). The question remains as to what extent the forest regeneration depends on seed dispersal by fruit-eating fishes. Many fishes destroy the seeds, the most notorious seed-eaters belonging to the genera *Brycon* and *Colossoma*. Studies on *Colossoma macropomum* showed that juveniles under 4 kg are omnivorous and prefer a diet of fruits, seeds, and zooplankton, whereas adults are exclusively frugivorous (Roubach & Saint-Paul 1994). They have evolved an extraordinarily strong dentition which enables them to masticate even the hardest diaspores (Kubitzki 1985b). Gottsberger (1978) found that of

33 plant species studied, 16 had seeds that were not regularly broken by fish and 17 had seeds that were. The former seeds belong mainly to very primitive groups whereas the latter belonged mainly to more recent plant groups.

Many fish, especially of the large order of the Characinoidea, have specialized teeth for certain kinds of fruit (Horn 1997, Lucas 2008). *Colossoma macropomum* is a specialist eater of the fruits of *Hevea spruceana* (Roubach & Saint-Paul 1994). Fishes of the genera *Mylossoma*, *Myleus*, and *Broco* are also important eaters of the fruit of palm trees, *Cecropia* spp. and others. The “piranheira” (*Piranhea trifoliata*) is a plant preferred by some piranha species. In *Astrocaryum jauari*, a common palm, the fruits are eaten by at least 16 species of fish that either gnaw the pulp, fragment the seed, or ingest the entire fruit thus acting as dispersal agents (Piedade *et al.* 2003, 2006). Gut passage plays a major role for the breaking of dormancy, possibly by enzyme action (Ziburski 1991, Maia *et al.* 2007). Some species have a significantly higher germination percentage (e.g. *Psychotria* sp.; Mannheimer *et al.* 2003) in seeds removed from the intestine of fishes than in those from stomachs, but in other species (e.g. *Cecropia* sp.) no such differences were found.

There are controversial statements regarding the importance of ichthyochory for seed dispersal in Amazonian floodplains. Some authors claim that the dispersal of plants by floodplain fishes has an importance comparable to the classic dispersal of seeds by birds and mammals in dry land forests (Galetti *et al.* 2008). Gottsberger (1978) states that seed dispersal by fish may have played a significant part in the evolution of seed plants, and relates this form of dispersal to relatively primitive flowering plant groups. He concludes that “migrating fish might be responsible in a decisive way for dispersal of many diaspores throughout the whole of the Amazon and its tributaries.” In certain environments ichthyochory may be a very efficient and reliable seed dispersal mechanism, with a significant role in the development and maintenance of dispersal strategies of the early angiosperms in the Cretaceous and possibly even the early seed plants as far back as the Carboniferous and Devonian (Gottsberger 1978).

Other authors report that most fruits are propagated only occasionally by fish: Ziburski (1991) stated that out of 40 tree species only three really depended on fish for propagation (*Crateva benthami*, *Astrocaryum jauari*, and *Crescentia amazonica*).

Banack *et al.* (2002) describe that the riparian fig tree *Ficus insipida* – which is dispersed mainly by fish and bats – is more establishment-limited than disperser-limited, with mortality being linked mainly to low light conditions, treefalls, frequent flooding, and bank erosion, but not to limitations in dispersal.

Also Kubitzki (1985b) assumed that seed-eating by fish is highly opportunistic, since among diaspores dispersed by fish there is little uniformity in shape, texture, color, and taste. Perhaps one exception is represented by *Gnetum venosum*, a gymnosperm liana growing along the margins of the flooded forests, which may show adaptations to dispersal by fish (Kubitzki 1985b). This species has very large seeds (8 cm long) which are swallowed whole by the large catfish *Practocephalus hemiliopterus* (“piarara”). The fish strips off the outer fleshy layer and regurgitates the rest (instead of gut passage, as is common in many other fishes).

The primary role of fishes may be to remove fruit-pulp from seeds and to carry seeds against the prevailing water current (Anderson *et al.* 2011). Unfortunately, the best seed dispersers are often the largest fish, which are preferred by commercial fisheries (Goulding 1980, Galetti *et al.* 2008).

**3. Anemochory.** Wind dispersal is a very ancient form of dispersal and is possible only for lightweight fruits or seeds. Some groups of plants characteristically show a preponderance of adaptations for dispersal by wind, especially the emergent trees. Examples include many species of the Malvaceae (seeds surrounded with hairs), Bignoniaceae (with broad-winged lightweight seeds), Fabaceae (with one-seeded alate pods) and Vochysiaceae (with small winged seeds) (Kubitzki 1985a). In Amazonian floodplains wind-dispersed seeds are common, e.g. in *Salix martiana*, *Ceiba pentandra*, or *Pseudobombax munguba* (Kubitzki 1985a, Gribel & Gibbs 2002, Oliveira & Piedade 2002) which produce a large quantity of small seeds provided with cotton-like hairs. Other anemochorous species are typically adapted for dispersal via wind by wings on the seed (*Couratari oligantha*), by alate drupes (*Triplaris surinamensis*), or minute seeds (*Calycophyllum spruceanum*) (Kubitzki 1985a, Bremer & Eriksson 1992, Mori & Brown 1994).

Those species that have evolved aids for wind dispersal have diaspores which are neither exceptionally large nor small (Ridley 1930). The hairs and wings have been shown to increase the efficiency of wind dispersal (Andersen 1993) by decreasing fall

velocity, either by increasing drag or by creating lift (Augspurger & Franson 1993, Matlack 1987). Often these seeds are dispersed in more than one way (Plitmann 1986). For example, *Pseudobombax munguba* (Malvaceae) has comose seeds which are carried away by the wind when the capsule opens (Van der Pijl 1982). Many of its seeds, if not most, land in the water where some float away with the currents and others are eaten by fish (Ridley 1930). This species, however, would be classified as wind-, and not water-, dispersed because wind is the mechanism by which the seed departs from the mother plant (Mori & Brown 1994).

We do not know what percentage of species is wind dispersed in Amazonian floodplains. We postulate that it is a comparatively low percentage compared with water- and animal-dispersed seeds, due to the fact that the forests are rather closed and the climate is relatively wet – i.e. the same reasons why in upland tropical rainforests wind dispersal also plays a minor role (Mori & Brown 1994). The advantage of this type of dispersal for the plant is that it is less costly than dispersal by animals (Kubitzki 1985a).

The sporadic occurrence of wind-dispersed species with non-wind-dispersed species in the same families or even genera suggests that adaptations for wind dispersal evolved within different phylogenetic lines without excluding adaptations for dispersal by other modes (Mori & Brown 1994). Bremer and Eriksson (1992) point out that the evolution of wind-dispersed diaspores in the Rubiaceae has evolved independently in several different lineages. We expect this to be the case also in Amazonian floodplain forests. Some efforts must be devoted to determining the importance of wind dispersal, as well as of other dispersal modes, for the ecosystem of Amazonian floodplain forests.

**4. Autochory.** Autochory, the process of fruit and seed self-dispersal by means of physical expulsion, is quite common in Amazonian floodplains, although it has never been quantified and it is often difficult to separate this dispersal mode from other kinds and from secondary dispersal. Autochory is intended here as both passive and active forms of dispersal. Passive ballistic or barochoric dispersal takes place when the diaspores fall from the plant or are released by passing animals, wind, or rain drops (Gottsberger & Silberbauer-Gottsberger 1983). Hard, often large, woody fruits are often dispersed by barochory, followed by secondary dispersal by rodents (Forget & Milleron

1991, Forget *et al.* 2002). Passive ballistic systems are typical for many species in the genera *Eperua* and *Mora* that grow in flooded forests (Ter Steege 1994). Barochoric dispersal takes place in the palm *Astrocaryum jauari*, one of the commonest palm species occurring in nutritionally poor Amazonian black-water floodplains, called *igapó* (Sioli 1984). The large heavy fruits fall off the palm tree and may be accumulated near the adult plant (Piedade *et al.* 2003). This dispersal mode increases the local density of the species, enhancing the occurrence of large masses of individuals, for example on the Anavilhanas islands (Piedade *et al.* 2003). *A. jauari* is also classified as fish-dispersed, as the fruits fall or roll into the water and are then transported in the stomachs of large fish.

Active autochory involves explosive liberation of dispersal units, as found for example in *Hura crepitans*, a commercially harvested species common in Amazonian floodplain forests. In this tree species, the maximum dispersal distance recorded was 45 m from the parent tree, with a marked modal dispersal distance at about 30 m (Swaine & Beer 1977). Other members of the Euphorbiaceae family found in the floodplains, e.g. *Hevea* spp. and *Maprounea guianensis*, have active explosive mechanisms, where the ballistic fruits expel their seeds significant distances (Ducke 1949).

**5. Zoochory.** In many tropical trees, fleshy-fruited plant species are the rule rather than the exception: they are produced by over 70% of the plants (Wilson *et al.* 1987) and depend on vertebrate dispersers to move their seeds (Gentry 1982, Howe & Smallwood 1982, Kubitzki 1985a). In Amazonian floodplains, the percentage of fleshy-fruited plants has never been quantified, but a considerable number produce fleshy fruits and/or seeds that are disseminated by animals. Similar to the adjacent upland forests (Kubitzki & Ziburski 1994), birds, bats, and primates are the principal potential dispersers of zoochorous species (excluding fish).

Animals are attracted to the fruits by their edible pericarps (e.g., Myrtaceae and Sapotaceae), brightly colored, fat-rich arils (e.g. species of *Virola*), sugar-rich arils, edible seeds, and even false arils (e.g., some species of *Ormosia*), although there is a species of *Ormosia* in the *várzea* that has lost its red pigment, increased its size, and floats, in contrast to the false arils of upland *Ormosia* species (Howe & Westley 1988, Mori 1992, Mori & Brown 1994).

The seeds of many tree species are not dispersed by a single group of animals only, but rather by

several. The diaspores of *Virola* are dispersed mainly by toucans and other birds, but also primates harvest them (Howe 1990). The fruits of *Trichilia* spp. (Meliaceae) are taken by ruminants, squirrels, primates, porcupines, hornbills and other birds (Howe 1990). It is often presumed that uncommon visitors are seldom effective as dispersers, but this is generally an unproven contention. From the viewpoint of dispersal, it is important to make a distinction between frugivores and seed dispersers. For the disperser the seed is only ballast which it gets rid of as quickly as it can. There is much evidence of the rapidity with which some birds can remove the edible parts of a fruit and regurgitate the seed, clearly an important part of their adaptation to such diet (Kubitzki 1985a).

Fleshy fruits have evolved to attract animals to ingest them and thus act as dispersal agents for the seed, ensuring that diaspores are dispersed away from the parent tree and providing, by way of animal feces, a microsite of moisture and extra nutrients (Grice 1996). This latter advantage may be very important in the relatively nutrient-poor *igapó*.

As opposed to endozoochorous dispersal, which is common, the role of epizoochorous dispersal has never been described or analyzed in Amazonian floodplains. It is clear that morphological structures like awns, bristles, or hooks increase the retention potential of plant diaspores to the coats of animals (Tackenberg *et al.* 2006), but not many diaspores of the Amazon floodplain have such structures so that we may assume that this dispersal mechanism plays a minor role.

**5.1 Myrmecochory.** The role of seed dispersal by ants in floodplain forests is poorly understood. Ants do not play an important role in the dispersal of diaspores, except for some forest floor herbs (Van der Pijl 1982, Kubitzki 1985a). Some species move the seeds 1 to 2.5 m.

Ants frequently deposit seeds in their nests, and many of these germinate and develop into healthy seedlings (Passos & Ferreira 1996). In uplands, interactions between seed-harvesting rodents and ants are probably important. For example, temperate zone ants remove and sometimes disperse small seeds before seed-consuming rodents find the seeds, resulting in many more seeds surviving than without the ants (Heithaus 1981, Pierce & Cowling 1991, Gibson 1993). Whether ants and rodents remove the same seed species has never been observed in Amazonian floodplain forests.

5.2 *Sauvorchory*. Several reptiles are frequent diaspore dispersers in the tropics (Olesen & Valido 2003, De Castro & Galetti 2004, Godinez-Alvarez 2004). In Amazonian floodplains, potential dispersers are turtles, both terrestrial and aquatic (Moll & Jansen 1995), and iguanas, which may be important for large or unpalatable fruits not dispersed by small birds or bats (Iverson 1985). *Genipa americana*, which grows in Amazonian floodplains, is dispersed by terrestrial vertebrates such as tortoises in Northern Brazil (Strong & Fragoso 2006). No publication so far refers to any kind of dispersal by reptiles in this ecosystem.

5.3 *Ornithochory*. Fruits adapted to dispersal by birds possess optical lures in the form of a vivid coloration, often of contrasting colors in which red is the most frequent color of the exterior or aril – corresponding to the fruit type that (Amazonian) birds prefer (Kubitzki 1985a, Gorchov *et al.* 1995). Numerous birds choose their breeding sites within the zone of inundation in Amazonian floodplains (Petermann 1997), and many of these species eat fruits or seeds, digest the mesocarp or the aril, and defecate or regurgitate the seed. Toucans and toucanets (Ramphastidae) swallow whole, while parrots, macaws and parakeets (Psittacidae) split and eat fruits and seeds – they are seed predators that occasionally drop seeds. They also split and eat hard fruits that other birds are unable to consume (Loiselle 1987, Stiles & Skutch 1989). For example the Amazonian floodplain palm tree *Euterpe oleracea* and parrots have a close ecological relationship (Moegenburg 2002).

In uplands, the seeds of various tree species of the genera *Cordia*, *Virola*, *Protium*, *Tetragastris*, *Xylopia*, and others are dispersed in this way (Howe 1990, Howe & Ritcher 1982, Howe & Vande-Kerckhove 1981).

We know that birds play an important role for long distance dispersal – in contrast to local dispersal (Nathan *et al.* 2008) – in wetlands, and in Amazonia in particular (Macedo & Prance 1978, Snow 1981, Gorchov *et al.* 1995, Petermann 1997, Hayes & Sewlal 2004). In an Amazonian upland forest, ornithochory made up for 50% of seed dispersal (Skatulla 2002). Since many tree genera occur also in Central Amazonian floodplains, this dispersal mode is expected to play a role, although the extent is not known.

Kubitzki (1985a) states that “from the viewpoint of dispersal, two different classes of birds have to be distinguished: Unspecialised, or opportunistic,

frugivores, that utilise fruits primarily as a source of carbohydrate and water; otherwise they are more or less insectivorous. Birds belonging to this group are mostly smaller than those of the second group, the specialised frugivores. These cover their demand for carbohydrates, lipids and proteins from fruits that are relatively large and do not eat anything except fruit (Snow 1981). The favourite fruits of the unspecialised frugivores are berries that have a rather watery flesh – good examples are many members of the Melastomataceae, Myrtaceae and Rubiaceae. Such plants are typically understory trees or shrubs often occurring in secondary vegetation like edge habitats or recently cleared ground, also in the floodplains”.

Fruits adapted for dispersal by specialised frugivorous birds are often large, and frequently have only one seed per fruit, with ample food reserves so that the seedlings have a chance to establish themselves on the forest floor (Kubitzki 1985a). The fruits generally have a firm, dense flesh that is rich in fats and proteins (Waldhoff & Furch 1999, Waldhoff & Maia 2000, Parolin *et al.* 2010a).

The effectiveness of birds in long-distance dispersal upriver in Amazonian floodplains is not known. In fact the lower Amazon River is known to act as a barrier to migration for forest birds (Hayes & Sewlal 2004). It would be interesting to analyze over which distances dispersal occurs within the floodplain forests fringing the Amazon, long-distance dispersal along the forest edges, without crossing the river.

5.4 *Mammaliochory*. 5.4.1 *Chiropterochory*. Bats are abundant and effective seed dispersers inside the forests (Fleming 1997, Galindo-Gonzalez *et al.* 2000, Lobo *et al.* 2009). Huber (1909) stated that in Brazil fruit bats were the most important agents for seed dispersal in the Amazonian forests. In the American tropical lowland forests, bats as major consumers and dispersers are found in the Phyllostomidae (Microchiroptera). Bats are commensals and, in many cases, dispersers, e.g. of the fruits of *Calophyllum brasiliense*, *Minuartia guianensis*, *Lecythis* spp., and *Ocotea* spp., which are transported to feeding and resting roosts (Greenhall 1965, Fleming 1988, Van der Pijl 1982). Bat-dispersed seeds often hang outside the foliage because bats, with their sonar navigation system, have difficulties in flying inside the foliage (Kubitzki 1985a). However, the extent and importance of chiropterochory has never been analyzed in Amazonian floodplain forests.

**5.4.2 Dispersal by primates.** Primates comprise between 25% and 40% of the frugivore biomass in tropical forests (Chapman 1995), eat large quantities of fruit, and defecate or spit large numbers of viable seeds (Lambert 1999). Primate frugivory and seed dispersal have been quantified by studies in South America (Kubitzki 1985a, Garber 1986, Stevenson 2000, Vulinec 2002, Culot *et al.* 2010, Heymann *et al.* 2012) but little knowledge is available for the floodplains (Ayres 1993, Haugaasen & Peres 2005, 2009).

There is evidence that some seed predators cause severe losses to seed crops. Peres (1991) reports almost complete loss of seeds due to predation by *Cebus apella* for 10 individuals of *Cariniana micrantha* in one year. These primates overcome seed protection mechanisms with their manipulative skills and strong jaws. However, there is more evidence that primates enhance seed dispersal and germination (Castellanos 1997, Norconk *et al.* 1998, Culot *et al.* 2010). What is more, the role of primates in seed dispersal is increasingly understood to have significant unique effects on plant demography and forest regeneration (Koné *et al.* 2008). In Amazonia, many fruits dispersed by primates have a sweet pulp that is enclosed in a firm pericarp which can be opened only with some effort (Kubitzki 1985a). Julliot (1996) found that primates select brightly colored fruits, and reject dull ones. Red howler monkeys are highly prevalent seed dispersers at the plant community level, dispersing the seeds of 137 species in Central Amazonian *terra firme* forest (Andresen 2002). One important seed disperser is the uakari (*Cacajao calvus*, *C. melanocephalus*) (Haugaasen & Peres 2005, Heymann & Aquino 2010). Most of their diet consists of fruit, but seeds, leaves, insects and small animals are also consumed. They subsist on a diet that includes especially fruits with hard outer coverings, which they open with their distinctive tusk-like canines. Many primates swallow seeds whole (Terborgh 1990); they extract pulp from the fruit without destroying the seeds.

Seed size plays a role in the mode and distance of dispersal. Comparisons among primates have shown that mammal body size affects seed fate (Stoner *et al.* 2007). Small primates can swallow small seeds, spit medium seeds, and rarely exploit large seeds (Garber 1986, Knogge & Heymann 2003, Barnett *et al.* 2012). Large fruit-eating primates play important ecological roles as dispersal agents of large seeds (Haugaasen & Peres 2007, Nuñez-Iturri & Howe 2007).

**5.4.3 Dispersal by terrestrial mammals.** Many large mammals swallow seeds whole and hence contribute to the seed shadows of particular plant species in tropical regions (Stoner *et al.* 2007). There are some studies focused on mammal activity in Amazonian floodplains. Few genera of carnivores are frugivorous (e.g. *Potos* spp. and *Nasua* spp.). Other groups within the Carnivora (e.g. river otters *Lutra* spp., tayras *Eira barbara*, and canids *Cerdocyon thous*, *Lycalopex vetulus*, *Chrysocyon brachyurus*) also play a minor role in seed dispersal in the Neotropics (Pizo 2002). Tapirs remove seeds which may later be buried by rodents, promoting the creation of new seedling populations (Janzen 1982). White-lipped peccary and lowland tapir exploit the greater fruit production of flooded forests (Kubitzki 1985a), although collared peccary (*Tayassu tajacu*) mostly shift from a frugivorous to a woody browser diet (Bodmer 1990), as do other terrestrial ungulates like red brocket deer (*Mazama americana*), which retreat to the floodplain islands of the Amazon basin. Peccaries also bite off seedlings and are the main source of mortality in the buriti palm (*Mauritia flexuosa*) (Antonik 2005). The white-lipped peccary uses várzea forests extensively and ranges over large areas, but as they thoroughly masticate seeds only very tiny ones escape destruction and pass unharmed through their digestive systems (Bodmer 1991). Both peccary species are primarily seed predators rather than seed dispersers. They disperse larger seeds mostly when they spit them out during mastication (Bodmer 1991), although they may also eat, bury, and defecate seeds thus contributing to seed dispersal (Kiltie 1981).

Acouchies (*Myoprocta* sp.) and agoutis (*Dasyprocta* sp.) are common dispersal agents in *terra firme* forests – they are not typical floodplain inhabitants but they migrate there when the water is low. Their role for (secondary) dispersal in upland forests has been analyzed in detail in several studies, showing that seeds removed by them are likely to be scatterhoarded for later consumption (Kubitzki 1985a, Forget & Milleron 1991, Forget 1992, Galetti *et al.* 1992, Jansen *et al.* 2012). Some of these cached seeds often escape rediscovery by the rodents and germinate (Smythe 1989, Forget 1990, 1991a). They may also escape infestation by insects, a common fate for large tropical seeds (Smythe 1989, Forget & Milleron 1991). Most seeds cached by rodents, however, are rediscovered and consumed (Kubitzki 1985a, Forget 1990, 1991b, 1993). As a result, secondary removal by rodents is usually assumed detrimental for plant

fitness. New evidence, however, indicates that secondary seed dispersal by scatterhoarding rodents facilitated the persistence of large-seeded tree species when the megafauna went extinct in the late Pleistocene and small rodents acted as their mutualist dispersers instead, emphasizing the importance of this animal group for dispersal in forests (Jansen *et al.* 2012).

Overall, the contribution of mammals to the dispersal of seeds within and between the two adjacent ecosystems, Amazonian uplands and floodplain forests, has to be further analyzed. There are quite a number of tree species occurring in both ecosystems (Wittmann *et al.* 2010, 2013) and about 30% of species overlap. Terrestrial mammals – as well as other animals – apparently make a considerable contribution to seed movement and genetic exchange between tree populations of non-flooded uplands and flooded forests in Amazonia.

## DISCUSSION

*Distribution of dispersal modes in Amazonian floodplain forests.* The references of the present review list

a total of 222 tree species whose dispersal syndromes are described. One-hundred-sixty-nine of these are based on assumptions which result from observations of fruit or seed morphology or taxonomic relatedness (Figure 1A). By merely assuming a mode of dispersal there is the danger of spreading false information. However, as long as we do not have better experimental evidence, this information may provide a basis that cannot be ignored. Furthermore, 53 tree species could clearly be connected to one main mode of dispersal, with the data being based on detailed field studies and/or experimental evidence (Figure 1B). Since many data result from studies that focused on the importance of the flood pulse for the ecosystem, and on dispersal linked to water, there may be a bias in the choice of species analyzed and a higher inclusion of species with dispersal linked to water. The data thus do not necessarily reflect the true distribution of dispersal syndromes in Amazonian floodplain forests. A lot more work and detailed analyses are necessary in future to better understand the functioning of this complex ecosystem in general, and of the functioning of single species and their interactions in particular.

FIG. 1. Dispersal syndromes based on the references cited in this review. Of a total of 222 tree species, the dispersal syndromes of 169 species are based on assumptions (A), while those of 53 tree species could be clearly linked to one of the main modes of dispersal (B), with the data being based on detailed field studies and/or experimental evidence, though the studies were mostly focused on water-related dispersal and thus are biased towards this mode of dispersal.

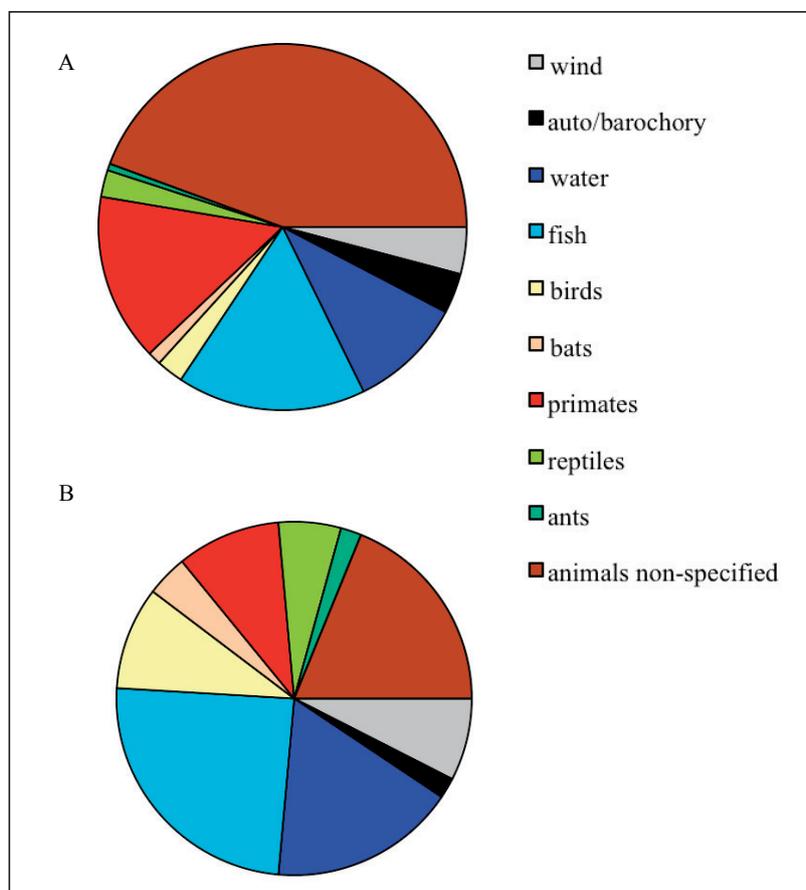


TABLE 1. Numbers of tree species whose dispersal syndromes are described in the references cited in this review.

Total number of tree species considered	Based on assumptions 169	Based on experiments 53
Dispersal by animals including fish	139 (82%)	39 (74%)
Dispersal by animals excluding fish	111 (66%)	26 (49%)
Dispersal linked to water (fish and water)	45 (27%)	22 (42%)
Dispersal abiotic	30 (18%)	14 (16%)

Using this database (Table 1), 139 (82%) of 169 tree species are dispersed by animals, 28 of them exclusively by fish; 45 tree species (27%) have their dispersal linked to water, i.e. are dispersed by ichthyochory or hydrochory, and 30 species (18%) are dispersed by abiotic factors. The data with experimental evidence focused on water-related species obviously show a higher percentage of dispersal linked to water (42%).

*Dispersal distances and gut retention times.* Proper estimates of seed dispersal distances are difficult to perform and are usually made by monitoring the behavior and movement of frugivores directly and continuously and by calculating dispersal distances accordingly (Heymann *et al.* 2012). For primates, observation of feeding and defecation/regurgitation is common, but for many dispersal agents an observational approach is not feasible. Genetic matching of seeds/seedlings and source plants is another option, as is modeling from gut retention times and animal movement patterns. This is a promising field of future research.

Generally, seeds that spend more time in the digestive tract of fishes, mammals, or other vertebrate dispersers are deposited at greater distances from the mother plant (Anderson *et al.* 2011), but there is no simple relationship between gut retention times and seed dispersal distance. A long gut retention time does not automatically result in long-distance dispersal. Howler monkeys (*Alouatta seniculus*) for example, with their partially folivorous diet, have long gut retention times, but move only over short distances. They spend many hours in the same feeding tree and range less than 600 m in a day (Bravo & Sallenave 2003). In French Guiana, 60% of *Alouatta seniculus* defecations were beneath sleeping trees, which in many cases were feeding trees; seeds that were dispersed away from the sleeping tree were moved on

average  $255 \pm 129$  m from sleeping trees (Julliot 1996). In contrast, spider monkeys (*Ateles* spp.) have relatively short retention times, but move over larger distances. They feed in several different trees in one day (Link & Di Fiore 2006) and range up to 5 km in a day (Nunes 1998). Thus, the ranging patterns of spider monkeys result in many seeds being widely dispersed throughout the forest (Russo & Augspurger 2004). Neotropical tapirs have home ranges of several thousand hectares and therefore contribute to long-distance seed dispersal (Fragoso 1997). They perform long-distance seed movement of up to 20 km (Fragoso *et al.* 2003), while small-bodied mammals such as rodents move seeds much shorter distances (5-100 m; Jansen & Forget 2001). Although peccaries are principally seed predators, they do participate in seed dispersal through endozoochory of small seeds (Beck 2004). Since they may move considerable distances (up to 10 km per day) and have a gut retention time of up to 3 days, they are important long-distance dispersers of several small-seeded fruits (Beck 2004). Communities of rodents can also provide highly effective long-distance seed dispersal (Jansen *et al.* 2012).

Ungulates have long gut retention times that enhance their ability to disperse seeds long distances. Neotropical forest deer (*Mazama* spp.) have gut retention times of between 13 and 20 h (Domingues de Oliveira & Barbanti Duarte 2006). Fishes are vectors of long-distance seed dispersal in Amazonian floodplains, e.g. the large *Colossoma macropomum* is a frugivore which disperses seeds to distant habitats (Anderson *et al.* 2011). The majority of seeds are deposited within 200 m of the maternal tree, but bigger fish have longer gut retention times owing to longer digestive tracts and disperse seeds noticeably farther than this (Anderson *et al.* 2011). Gut retention times are not solely responsible for long-distance dispersal: leaf-nosed bats (Microchiroptera: Phyllos-

tomidae) have very short gut retention times (20–45 min; Uzzurum & Heidman 1991) but their rapid travel results in long-distance dispersal. By contrast, the low retention but slow traveling times in small birds result in short-range dispersal.

*Seed fate.* Studies of “seed fate” outline the importance of multiple modes of dispersal acting together (Forget *et al.* 2004, Culot *et al.* 2009, Alvarez & Heymann 2012). Yet in Amazonian floodplains we hardly know how primary dispersal works, not to speak of multimodal dispersal (Anderson *et al.* 2011). Primary dispersers remove fruits from plants and usually regurgitate or defecate seeds elsewhere. Secondary dispersers rearrange the resulting seed shadow and sometimes place seeds in beneficial microsites (Janzen 1982, Roberts & Heithaus 1986, Forget 1990, 1991b). To complicate seed fate further, secondary dispersal agents like ants and rodents are generally seed predators as well as dispersers (Turner 2004). Thus, removal of dispersed seeds is not necessarily equivalent to seed predation (Janzen 1982, Roberts & Heithaus 1986).

*Evolution of dispersal modes in Amazonian floodplains.* Today, many of the tree species of the *várzea* forests are widely distributed in Amazonia, partly because of the persistence of gallery forests in dry times and partly because of the ease of diaspore dispersal by water and fish (Prance 1973). In a recent study, Wittmann *et al.* (2013) report that approximately 90% of *várzea* tree species are not restricted to Amazonian *várzea*, but are partially or widely distributed among other Neotropical biomes and ecosystems, especially western Amazonian *terra firme* and the Orinoco floodplains. Kubitzki (1985a) gave examples of an adaptive radiation with respect to dispersal in major Amazonian plant groups. An especially wide array of relevant adaptations has evolved in the Lecythidaceae, a family of tropical trees well represented in Amazonia (Prance & Mori 1983). The large, indehiscent fruits of the cannonball tree *Couroupita* are mammal-dispersed, while the similar fruits of the riverine *Gustavia augusta* are not only rafted by water but their seeds have also been found to be dispersed by fish. In addition to indehiscent fruits, the Lecythidaceae have several genera with dehiscent fruits in which the capsules open by a circular lid or operculum. The capsules of *Lecythis* contain seeds dispersed by bats. *Swartzia* spp. are dispersed by chiropterochory and their seeds hang on a long aril which enhances bat dispersal, while *Swartzia polyphylla* has

larger seeds which float and have a reduced aril. In the Brazil nut, the need for protection of the seeds has led to a secondarily indehiscent fruit. *Eschweilera tenuifolia* and *Allantoma lineata* produce seeds dispersed by water; they have been observed to remain afloat for months.

In other families a restricted number of dispersal methods or fixation on only one type is found. In order to understand the evolutionary switch-overs that must have occurred, it is important to recognize that coevolved plant-animal relationships are frequently not exclusive but allow for considerable flexibility. *Virola surinamensis*, although coevolved with birds, is water-dispersed. All this shows that in the whole process of dispersal a high degree of opportunism occurs (Kubitzki 1985a).

*The role of seed dispersal for the ecosystem.* Intricate and fine-tuned relationships between plants and animals need to be maintained if the integrity of plants and forests is to be ensured (Smith 1995). Habitat fragmentation and pollution do not contribute to this integrity. Lin & Caramaschi (2005) describe the example of a fish community in Lake Batata, a typical Amazonian clearwater lake. From 1979 to 1989, tailings composed of water and clay, extracted from bauxite by water jets, were discharged into Lake Batata. The tailings spread into the lake, where the level of the bottom rose and turbidity increased. Sediment resuspension, which reduced water clarity, was the main factor regulating differences in the community structure between the natural and the silted areas. Reduction of clarity in the silted area was a selective factor for fish species, and thus the whole ecosystem was completely changed.

Gold mining and mercury pollution are another cause of serious environmental problems in Amazonia. Mercury contamination in fish varies according to species. Herbivorous species are likely to accumulate mercury less rapidly than predatory fish (such as *Arapaima gigas*, *Osteoglossum bicirrhosum*, etc.) (<http://archive.unu.edu/unupress/unupbooks/809006e/809006E04.htm>). What influence high mercury contents in fish have on their survival, and on their role as dispersal agents, is still not known, but these human activities definitely do not enhance long-distance ichthyochoric dispersal.

Seed dispersal is also reduced following habitat fragmentation and the changes to connectivity and hydrology caused by the building of dams (Junk 1987, Nogueira *et al.* 2010, Ferreira *et al.* 2012, Ferreira *et al.* 2013).

Besides habitat loss, hunting represents an increasingly common anthropogenic impact with far-reaching consequences for plant populations and communities (Redford 1992, Peres & Roosmalen 2002, Dirzo *et al.* 2007). Hunting can change abundances of vertebrate seed predators and seed dispersers, causing species-specific changes in seed dispersal and seed predation and altering seedling communities (Muller-Landau 2007). Hunting locally exterminates populations of large primates, and reduces primates of intermediate body size by 80% (Nuñez-Iturri & Howe 2007). Given the importance of dispersal by primates, with 15% of trees primarily dispersed by primates as shown in Figure 1A, overhunting threatens to disrupt the ecological interactions between primates and the plants that rely on them for seed dispersal and recruitment, also in the floodplains.

The specializations of fleshy-fruited plants and their vertebrate frugivores that we see in tropical forests today are the result of millions of years of evolutionary interplay. Because of these specializations, tropical plants will suffer reduced dispersal success and survival whenever their particular frugivores, be they fish, bats, birds or primates, are persecuted by man. Although much of the Amazon basin and the floodplains are still heavily forested, their mammal populations have been hunted nearly to extinction (de Thoisy *et al.* 2009, Levi *et al.* 2011), leaving an “empty forest” (Redford 1992, Wilkie *et al.* 2011). Large-seeded fruits are generally dispersed only by large vertebrates, which are often the taxa most vulnerable to hunting pressure in tropical regions (Levi *et al.* 2011). Moreover, frugivorous species showed more marked declines in abundance in heavily hunted sites than browsers (Peres & Palacios 2007). Dirzo *et al.* (2007) observed contrasts in germination and suggest that under heavy defaunation, small-seeded species are likely to be penalized by the overabundance of small rodents, while large-seeded species escape predation. As mentioned above, the largest fish are often the best seed dispersers but are also heavily overfished (Goulding 1980, Galetti *et al.* 2008).

The relative importance of the disappearance of both seed dispersers and seed predators for particular plant species is at present not clearly understood for most species. Wright *et al.* (2007) hypothesize that the harvesting of large birds and mammals that disperse many seeds favors other species whose seeds are dispersed by bats, small birds, and mechanical means.

This process also favors lianas, because the seeds of disproportionate numbers of liana species are dispersed by wind. Stoner *et al.* (2007) make three main statements concerning the impact of hunting for tropical forest plant communities: (1) Hunting tends to reduce seed movement for animal-dispersed species with very large diaspores; (2) Hunting reduces seed predation by granivorous vertebrates for species with large seeds; and (3) Hunting alters the species composition of the seedling and sapling layers.

Thus human settlers in the floodplains cause reductions or even extinctions of potential dispersers by hunting and overfishing, which has strong consequences for the composition and regeneration of the forests.

Seed dispersal interacts decisively with the major drivers of biodiversity change in the 21st century: habitat fragmentation, overharvesting, biological invasions, and climate change (McConkey *et al.* 2012). Since serious quantifications of the dispersal syndromes in Amazonian floodplain forests are currently lacking, an important basic parameter for the understanding of forest ecology and for regeneration, reforestation, and management plans is missing. It is important that future studies focus on this important aspect of forest ecology.

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