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Frugivory and seed dispersal by mammals in the Amazon rainforest

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Abstract

Animal dispersers are the key in the configuration of plant communities and expanding existing populations. Knowledge about how frugivory and seed deposition are spatially distributed is valuable to understand the role of dispersers on the structure and dynamics of plant populations. Seed dispersal by animals provides a fundamental service for the ecosystems, and mammals are one of the most important vertebrate groups responsible for seed dispersal in tropical regions.

Key words : frugivory, mammals, Amazon rainforest

INTRODUCTION

The composition of the fauna is the product of an evolutionary process. Each animal species is dependent on certain characteristics of the vegetation and the biological interactions that determine where it will be able to exist [1].The structure of the forest, the distance between trees, the different types of vegetation, as well as the special arrangement of the forest elements that constitute the landscape determine the patterns of movement of these animals and explain a large part of the spatial variation in the number and categories of tree visits.

Many animals eat fruits and seeds and they are the major seed dispersers in tropical forests. Besides of that, the seeds of certain species of trees must pass through the gut of an animal in order to germinate. In this way many tropical plants and trees depend upon animals, without them, the plants will not be able to reproduce.

The dispersion of seeds represents the last phase of the reproductive cycle of plants and, therefore, is a critical event for forest regeneration [2]. Fruit-eating animals, often related to seed dispersion, are fundamental for the maintenance of the high diversity of tropical plant species [3].

The characteristics of the environment

The diversity of the environment implies a diversity of surroundings, which makes a corresponding diversity of animal species possible [4]. Only under specific conditions can environmental equilibrium exist [5], since the more diversified the environment, the less the number of limiting factors [6].

The exchange between an organism and its environment depends first on its genetic inheritance and the adaptation of its capacities. These determine its ecological valence and, finally, its share of social participation. These diverse functions correspond to the genotype, phenotype and in the long term, geobiotics. Each one of these levels of adaptation makes more or less complex classification possible [7].

The most important characteristics of the environment change from specie to specie due to their different evolutionary backgrounds, and in virtue of this, they create their own environment [8].The ecological environment both includes biotic and no-biotic factors.The climate, saltiness, soil type, availability of water and other physical and chemical characteristics are also important.Other species, including predators, prey, pathogenic agents, competitors and mutualistsare all of extreme ecological importance for the environmental equilibrium of each species.Other members of the same species as the individual, with which it can breed, compete for resources or interact in various social contexts, are also part of its environment.In this way, population properties like density, sexual proportion or genetic composition can impose themselves decisively on the prospects of each individual to survive and reproduce[9].

Interactions between vegetation and fauna

Much interaction exists between vegetation and fauna, since the majority of tropical tree species are pollinated by animals [10].In the same way, the dispersion of tropical tree species' seeds, in many cases, can be associated with the interaction with animals.Various research projects done in the riparian forests have shown a high predominance of zoochoryamong species[11].Trees attract different species of seed-dispersing frugivorous animals according to the quantity of resources that they offer or because these animals use them as rest areas, nesting grounds or shelter.

Like the other types of dispersion, zoochorydispersion is fundamental for the regeneration of disturbed areas.Frugivores carry seeds from different populations and species in their droppings in virtue of having a diversified diet of fruit from the area.This “seed rain” can also contribute to the enrichment of the seeds banks in these areas, accelerating the natural regeneration of the environment. Theseeds banksare of great importance to establish tree and pioneershrub species, which are the principle components of the ecological groups involved in the regeneration of forests after their disturbance[12].

Seed dispersion by frugivores can reduce the predation rate if they are spread in insufficient densities to be detected by predators [13]. Still, only small birds and bats deposit isolated seeds or seeds in small quantities [14]. Large frugivores, as the majority of mammals, regurgitate or defecate seeds into larger excrement[15].

A large part of the fauna species of the tropical forests acts as seed dispersersin a great quantity of the plant species. These animals play anindispensablerole in the regeneration of forests

and the conservation of sampled ecosystems as dispersing agents [16], since their behavior can influence seed distribution patterns and consequently the structure of the plant community [17].

Plants' adaptations to attract consumers

Plants used as a food source possess adaptations to attract and repel their consumers [18]. Many of them possess fruits and seeds with certain characteristics aimed at attracting and stimulating the appetite of fauna. Among these attractive characteristics of fruit are color, size, form, chemical components, type of inflorescence, abundance, accessibility, type of habitat and distance between fruit-bearing plants [19]. In this context the fruit would have evolved to facilitate their use, favoring dispersion and germination of their seeds far from the mother plant, thus minimizing competition for space and protecting them from destructive consumption [20].

The distribution of zoochorous plants in the lower strata (arboreous) seems to be related to the living and activity areas of seed dispersers [21]. The development of the seed dispersion by fauna depends on phylogenetic, historical and geographical processes, as well as the availability of appropriate dispersing agents, which vary regionally and between communities in a determined region[22].

Mammals consume fruit adapted to zoochory, which can be berries, drupes or arylated ones.Compensation offered to these dispersers are soluble carbohydrates and the glucose andfructose contained in the pulp of the fruit to attract their consumption [23]. The syndrome of seed dispersion seems to be evidence of coevolution between animals and plants [24].Some authors believe that the species-specific coevolution between seed dispersers and plants seems not to occur [25], principally because there is no reason to believe that frugivorous specialists are better dispersers of seeds than generalists.

Plant species importance as fruit producers to fauna

The majority of plant species in the Amazon Forest is important as fruit producers, and is eaten by diversity of fauna species.The Annonaceae family is one of the most important in the Amazon Forest, and the main genera of it that produce fruit for fauna are *Annona, Rollinia* and *Xylopia*. The *Annona* genus contains various species that produce eatable fruit, like berries, with alarge number of seeds, slightly sweet pulp, and a pleasant smell [26].

Annonaceae fruit are among the most consumed by deer (*Mazamaamericana*, *M. nemorivaga, and M.rufina), ruminant mammals of the Cervidae family.However, deer are considered seed predators for damaging them during digestion via rumen fermentation* [27].

The tapir (*Tapirus terrestris*), an herbivore specie of the Tapiridae family, is a disperser of intact Annonaceae seeds in high percentages.It is particularly important in the ecological structure of various species of plants because it can distribute a large quantity and variety of seeds, often acting as a key species.Its absence could cause a breakdown of the key processes in the maintenance of diversity and functioning of the ecosystems [28].This mammal is very important in maintaining biodiversity in the ecosystems in which they live since they consume and defecate a wide variety of seed species, the majority of which survive intactand are dispersed in dry land areas distant from the parent plant [29].According to Fragoso[30], in many cases this maintaining dependson large frugivores, like tapirs, deer (*Mazama*spp), peccaries (*Tayassupecari* and*Pecaritajacu*), and lowland pacas (*Cuniculuspaca*).

The *Cecropia* genus (Urticaceae family) is very abundant in the Amazon Forest, and is composed of myrmecophites species, known as embaubas that offer shelter,in their internodes, to ants of the *Azteca*genus.The plants also provide food in the form of Müllerian corpuscles, compounds rich in glycogen and lipids, produced in a structure at the base of the petioles [31]. The fruit of *Cecropia* trees are much appreciated by birds, monkeys, bats and especially Three-toed sloths (*Bradypus* spp), which also feed on its young leaves.

Myrtaceaeis one of the main families used in the apiculture in South America, and is very representative of the Amazon Forest, both in number of species and density of trees and shrubs. Among the main seed dispersers of native species of Myrtaceae in the Amazon (especially the genera *Campomanesia, Eugenia, Gomidesia, Myrcia, Myrcianthes, Myrciaria*, and *Psidium*), are several species of monkeys (*e.g.Saguinus* spp, the mammals that disperse Myrtaceae seeds the most frequently), the ring-tailed coati (*Nasua Nasua*), the tapir (*Tapirus terrestris*), the deer (*Mazama*spp), thecommon opossum (*Didelphis marsupialis*), several species of rodents such as the agouti (*Dasyprocta* spp.), and the lowland paca (*Cuniculuspaca*)[32].

Other very important plant families for frugivores abundant in the Amazon Forest are Arecaceae, Burseraceae, Chrysobalanaceae, Euphorbiaceae, Fabaceae, Flacourtiaceae, Lauraceae, Lecythidaceae, Moraceae, Myristicaceae, Myrsinaceae, Sapindaceae, and Sapotaceae,with species that produce large quantities of seeds dispersed by fauna[33].

Mammal seed dispersion

Mammal seed dispersion is well developed in tropical regions where certain plants produce few, large, nutritious fruits rich in proteins and lipids. That is, diaspores consumed by mammals are peel resistant that does not impede their offer, protectionforthe seeds against destruction which is aided by the presence of toxic or bitter substances, a favorable smell for attraction, and the non-essentiality of color or a large size. Mammals also have adapted characteristics to the consumption of these fruits, with a developed sense of smell and teeth, but do not possess the advantage of tree living and generally feed at night when the colors are camouflaged[34].

Animals like the tapir (*Tapirus terrestris*), the largest terrestrial mammal in South America, plays an important role in the dynamic of the environments in which it lives. Studies done [35] on the species *T. terrestris*, identify the consumption of 58 types of fruit, where the fruit from the palm tree *Syagrus romanzoffiana* the most important. Terborgh [36] find evidence of the importance of the species of palm tree in the diet of frugivores, such as the tapir. According to the author, populations of *T. terrestris*can be affected by forest fragmentation in the long run, seeing that maintenance of large frugivores depends on the high diversity of plants that have fewer scarce periods.

*Tapirus terrestris*act in a symbiotic way with many species of plants [37]. Some authors suggest that there could have been an adaptation in the characteristics of the fruit to attract the tapir and other frugivorous animals. An example is the Combretaceae family, with species that produce fruits with a sweet, fibrous, meaty mesocarp and a very stony endocarp. Also, the Annonaceae family gives very pleasant smelling fruit and sweet pulp [38].

Coatis (*Nasua nasua*) are omnivores of the Procyonidae family, with a high rate of fruit consumption and are consequently potential seed dispersers. They consume fruit of various species [39]. Armadillos (Dasypodidae family), also are seed dispersers of various plant species, eating fruit that falls to the ground below the plants, dispersing the seeds along with their feces [40].

Ungulates (deer, tapirs, and peccaries) are important seed dispersers in the Amazon region, consuming large quantities of fruit and frequently spitting out the seeds during mastication [27]. These animals normally consume the fruit that were not consumed by species that feed at the tree crown. The fruit that they eat are those that fall to the ground, and on a smaller scale, those produced in lower vegetation strata. Therefore, their diet encompasses a restricted part of the diversity of existing fruit.

Some palm trees of the *Attalea* genus are consumed principally by peccaries (*Pecari tajacu* and *Tayassu pecari*), coatis (*Nasua nasua*), and tapirs (*Tapirus terrestris*), that aid in the dispersion of the seeds of these species. Peccaries consume fruit pulp of multiple palms, such as the *Euterpe oleracea* (manicole) and *Mauritia flexuosa* (moriche palm), dispersing their seeds [27]. Moriche palms produce fruit between December and June, and are present in various flooded environments in the Amazon region. Other animals are also considered moriche palm dispersers, such as parrots, macaws, and deer.

Although birds and monkeys frequently eat the same fruits, the quality of seed dispersion produced by these animals can differ in various aspects. While monkeys defecate the seeds in groups while moving around the forest or under their sleeping areas [41], birds frequently regurgitate them one by one while moving around the environment [24]. In this way, monkeys produce a more aggregate spectrum of deposition than birds, which can lead to differences in the survival of seeds and the resulting seedlings. Seeds grouped together can suffer from greater rates of predation than isolated seeds [42], even though this not a universal pattern [43]. The seedlings produced from the seeds grouped together are subject to greater intraspecific competition than isolated seedlings [44].

Depending on many plants that are part of their diets [23], primates tend to exercise an important role in the forest ecosystem, principally as seed dispersers, *e.g*. howler monkeys - *Alouatta* spp [45, 46, 47], capuchin monkeys - *Cebus* spp [46, 48], and tamarins - *Saguinus* spp [49]. Monkeys of the Amazon open large arboreal legume *species Cassia* spp (Fabaceae family) in order to eat the pulp that surrounds the seeds. They also eat various fruit species of the Euphorbiaceae, Loganiaceae, Rubiaceae, and Sapindaceae families, among others.

As with some species of howler monkey (*Alouatta* spp), some Neotropical primates are able to consume more than 100 species of fruit in their diet [46]. The genus *Alouatta* is considered the most folivorous of the Neotropical region [50], but these primates consume large quantities of fruit in the Amazon, exercising an important role as a seed disperser in the biome[46].

Studies show that the diet of howler monkeys (*Alouatta* spp) is composed of leaves (75.2%), flowers (10.2%), fruit (8.2%), and diversified material (6.4%) divided among plant parts, such as petioles and buds, and animal material obtained by ingestion of insects [11]. The authors studied groups of howler monkeys that efficiently disperse five species of fruit by way of endozoochory: figs (*Ficus* spp), genip trees (*Genipaamericana*), ice-cream-bean(*Inga* spp), snake root (*Vitexpolygama*) and jatobá (*Hymenaeacourbaril*), with mean dispersion estimates around 200 meters from the mother tree, considered relatively less than the dispersion mean of other Neotropical primates, whose mean are above 1,000 meters (*Lagothrixlagotricha*[51]; *Atelesbelzebuth*[52]; *Cebuspaella*[53]).

Figs (*Ficus* spp - Moraceae family), with more than 250 seeds per fruit and genip-trees (*Genipa* spp - Rubiaceae family), with more than 200 seeds per fruit, are examples of plant species better represented in the dispersion process with primates [11], since the species of the *Ficus* genus are considered the principal source of food for howler monkeys (*Alouatta* spp) in periods of fruit scarcity. Howler monkeys are considered folivorous, since they show adaptations in the digestive track to consume large quantities of leaves, principally species of the Moraceae family.Primates are known as good seed disseminators in tropical forests [54], directly influencing plant reproduction and consequently forest regeneration [46].

Among the small mammals, there are important opossum species in the Amazon Forest, as*Didelphis marsupialis*, considered omnivorous, predominately consuming invertebrates but complementing their diet with fruit. Others important opossum species, as*Marmosopsparvidens* and *Micoureusdemerarae* are considered frugivorous species, being able to contribute more efficiently to seed dispersion[55].

Some rat species of the Amazon Forest (*e.g*. species of the genera *Neusticomys*and *Oecomys*) are potential fruit consumers and seed dispersers. Rodents are the most abundant mammals in the Amazon forests, most of which have frugivorous habits or omnivorous / frugivorous, meaning that they eat fruits and seeds [56]. Due to their diet and abundance in the Amazon forests, these animals affect the location and survival of seeds, affecting the distribution of plant species and structure of communities [57].

Another very important group for pollination and the dispersion of fruit are bats (Chiroptera order). They are a group of mammals with the greatest richness of species in Amazon region, with the Phyllostomidae family that eat a large variety of forest fruits. Data were obtained by way of a bibliographic compilation [58], and plants of at least 189 species distributed in 44 families were used as food for 32 species of phyllostomid bats. Among the families of plans with the highest representation as food sources for bats were Anacardiaceae, Annonaceae, Arecaceae, Bromeliaceae, Chrysobalanaceae, Clusiaceae, Fabaceae, Moraceae, Myrtaceae, Piperaceae, Sapotaceae, Solanaceae, and Urticaceae. The large variety of plant species used as food sources for bats is indicative of the importance of these animals as seed dispersers and pollinizers [59].

A research done in the Amazon [60] identifies twelve genera and 32 species of bats consuming fifteen species of the genus *Cecropia* (Urticaceae family) as food. Nine of these chiropteran species belong to the *Artibeus* genus.

Solanaceae are known for their morphological characteristics that facilitate pollination by bats, especially the genus *Solanum*[61]. The large number of Solanaceae species in the Amazon is probably due to the fact that South America is considered the center of diversification of this family [62], as well as the Phyllostomidae family [63]. Thus, it could be suggested that there has possibly been a process of coevolution between species of Solanaceae and the Neotropical fruit bats.

For many bird and bat species, as the Amazon fruit

bats*Lonchophyllathomasi*and*Lionycterisspurrelli,* that attraction mechanism used by the plant is nectar [64].Some studies with bat pollination systems show that these mammals are not just important in the pollination of the plants, but can also influence the evolution of their reproductive systems, due to their degree of food specialization [65]. Among the vertebrate pollinators in the Neotropical region, bats are the second biggest group in number of plant species pollinated, only behind hummingbirds [66].

Plants pollinated by bats possess characteristic attributes which, as a group, are designated chiropterophily syndrome [67]: nocturnal anthesis, exposed flower locations, usually light-colored petals, and a strong unpleasant smell. Also, flowers are generally bigger and more robust than those with other syndromes and show a large quantity of pollen and nectar but with a low concentration of sugars. These attributes are intimately associated with characteristics of pollinators that feed nocturnally, have achromatic vision, a developed sense of smell, and forage either hovering or sitting above the flower or blossom.

The preferences of a few representatives of Amazon bats of the Phyllostomidae family, as *Carollia perspicillata, Chrotopterusauritus, Lophostomasilvicolum, Artibeus obscurus, Sturnira tildae* and *Sturnira lilium* to consume certain taxa of plants, the majority of which pioneers fundamental for the initiation of the process of the forest succession, is well known [68]. This is a plant/animal relationship of fundamental importance for the reproductive success of the plants consumed, the maintenance of forests and the recuperation of degraded areas, by way of seeds dispersed in their feces [65]. The maintenance of diversity of these frugivorous species that compose the community of bats present in the ecosystems depend in large part on the maintenance of plant diversity that make fruit available during the whole year.

Carollia perspicillata, a species of bat present in the Amazon Forest, stands out for showing a strong preference for plants of the Piperaceae family [69], especially of the *Piper* genusthat generally occurs in open areas with clearings, edges of forests and *capoeira* vegetation. Its dispersion is anemocoric (via the wind) but the presence of *C. perspicillata in considerable densities in the study areas indicates the possible contribution of* zoochory as an *important seed dispersion process of plant species of the genus. C. perspicillata still consume fruit from species from the genera Cecropia, Eugenia*, *Ficus, Passiflora, Solanum,* and *Vismia, which depend to some extent on zoochorous dispersion.*

Another species of bats commonly associated with seed dispersion in the Amazon Forest is *Rhinoplylla pumilio, which is considered a bioindicator of degraded areas. The presence of this species is associated with secondary forests, seeing that R. pumiliopreferably ingests fruit from pioneer plant species, such as Vismia* spp (Clusiaceae), *Piper* spp (Piperaceae), *Solanum*spp (Solanaceae), *Miconia*spp (Melastomataceae) and *Cecropia*spp (Urticaceae)[69].

Large cats like the cougar (*Puma concolor*), the jaguarundi (*Pumayagouaroundi*), and the jaguar (*Pantheraonca*) encounter the challenge of establishing territory over hundreds of square kilometers with adequate populations of prey species. Along with the tapir (*Tapirus terrestris*) and the peccaries (Tayassuidae family), these felines appear to be the most vulnerable species [70]. The tapir (*Tapirus terrestris*), the lowland paca (*Cuniculuspaca*), the Brazilian agouti (*Dasyproctaleporina*), the capybara (*Hydrochoerus hydrochaeris*), and peccaries (*Pecari tajacu* and *Tayassu pecari*) are species sought out by hunters and were part of the diet of the big cats. The presence of these animals is related to the good quality of the environment.

CONCLUSION

Vegetation is one of the most important characteristics of the environment. The integrity and complexity of a forest are the factors that influence the composition and abundance of different animal species. In the Amazon rainforest these species are distributed occupying a high diversity of trophic niches. They occupy different niches of the forest and a great diversity of mammal species distributed among different trophic guilds, which means ecosystems relatively balanced and of great biological value.

Any interfering with the vegetation produces direct effects on the fauna through the increase, decrease, or alternation of two key attributes: food and shelter. So, the composition of life in the forest is altered as changes occur in vegetation that directly interferes with the population structure of the fauna, be those changes natural or anthropic. This fact can be realized by the alterations in the diversity and density of animal species, principally among specialist species.

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