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Interactions between vegetation and avifauna in Amazon Forest

Fabio Rossano Dario*

Instituto de Pesquisas e Estudos da Vida Silvestre,Brazil

E-mail : fabiorossano@hotmail.com

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Abstract

Vegetation is one of the most important characteristics of the environment because it supports animal life. 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.

INTRODUCTION

The diversity of fauna is more directly correlated with the structure of the forest than the quantity of plant species in the natural environment [1].Tropical forests possess a large variation of internal microclimates, taking advantage of both its horizontal and vertical structure[2].The increase in structural complexity of the vegetation on various vertical levels makes new forms of occupancy of the environment possible. The increase in the number of animal species is principally due to the increase of both the new food guilds and the number of species in the existing guilds [3].

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 [4].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.

The characteristics of the environment

The most important characteristics of the environment change from species to species due to their different evolutionary backgrounds, and in virtue of this, they create their own environment [5].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[6].

In a determined geographic area, the distribution of each species is irregular, due to the special variation of physical characteristics, availability of resources and interactions with competing, predatory or parasitic species[7].

The diversity of the environment implies a diversity of surroundings, which makes a corresponding diversity of animal species possible[8].Only under specific conditions can environmental equilibrium exist [9], since the more diversified the environment, the less the number of limiting factors [10].

The dispersion of tropical tree species' seeds

Much interaction exists between vegetation and fauna, since the majority of tropical tree species are pollinated by animals [11]. 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[12].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.

The dispersion of seeds represents the last phase of the reproductive cycle of plants and, therefore, is a critical event for forest regeneration [13].Fruit-eating animals, often related to seed dispersion, are fundamental for the maintenance of the high diversity of tropical plant species [14].Some studies [15]have found that between 50 and 90% of plant species in tropical forest have seeds adapted to zoochory.

Like the other types of dispersion, zoochorydispersion is fundamental for the regeneration of disturbed areas.Frugivorous 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[16].

Theoretically, zoochorous species posses fewer chances of randomly disseminating their diaspores.In a research[17]was observed dispersion patterns for animals with an accumulation of seeds in specific spots, while a large part of the area was not reached by this dissemination, contrasted to the more uniform general patterns of anemochoric species.The seed distribution is spatially fairy heterogeneous, due to the animal component, which can cause deposits in preferred sites, like burrows and nests, or even routine pathways[18].However, for zoochorous species, the distance reached by the seeds must outweigh the possible advantages that could be achieved for spatially more uniform dispersion.

The bird group performs an important role in the equilibrium of ecosystems, not only by their abundance, but also the frequency with which they eat fruits.Some families of birds are highly dependent on fruit, *e.g.*Cotingidae and Cracidae[19], essentially forest-dwelling families. In Neotropicalforests, between 20 and 30% of birds include a significant amount of fruit in their diet and, in the process receive nutrients, the plants have their seeds taken long distances from their parents[20].

Plants' adaptations to attract and repel their consumers

Plants used as a food source possess adaptations to attract and repel their consumers [21]. 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 [22]. 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 [15].

Generally, fruits consumed by birds are small and spherical with fleshy pulp rich in lipids and protein.They are conspicuously colored, varying between red, black, blue and purple, and stay on the plant until removed[20].For having evolved in areas with little light in the understory of humid tropical forests, ornithochoric species must have fruit with conspicuous visual signals, such as contrasting colors, and must be in large quantities in order to be seen by frugivorous[23]. The understory of tropical forests presents the greatest specific richness and density of zoochorous plants, being a very important food sourcefor frugivorous species [24].

The distribution of zoochorous plants in the lower strata (arborous) seems to be related to the living and activity areas of seed dispersers [25]. 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[26].

Many plants offer fruit to birds, and some of this fruit contain hundreds of miniscule seeds. Some birds swallow the fruit whole, including the seeds, and digest the pulp.But, many of these miniscule seeds pass through the digestive system intact, and when the bird regurgitates or defecates, the seeds are long distances from the mother plant.The plants benefit from the dispersion of their seeds in new locations, where there is generally a greater chance of germination and survival. Therefore, birds as well as plants benefit from the interaction[27].

Once birds are visually-oriented animals, one of the most important characteristics of fruits for their ornithochoric-dispersion is color; the more conspicuous the fruit is, the easier it is to be spotted and dispersed by a bird. Some studies [23, 28, 29] show that birds prefer red fruit. The small appreciation for green fruit by birds is important in understanding the co-evolution between plants and seed-dispersing frugivorous birds, since the fruit is normally fleshy and greenish when immature. If birds fed easily on fruit before the seeds' maturation, they would probably not be good dispersers.It is probable that the green coloration of immature fruit, being not very attractive to birds, is a strategy to avoid being fed upon before the seeds are ready to be dispersed.

The syndrome of seed dispersion seems to be evidence of coevolution between birds and plants [30]. On one side,there are birds that are extremely specialized in large, nutritious but not very abundant fruits. On the other extreme are more generalized and opportunistic bird species, related to plants with a great abundance of small, not very nutritious fruits.Some authors believe that the species-specific coevolution between seed dispersers and plants seems not to occur [31], 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

Of the plant species of the Amazon Forest, the majority of plant species very important as fruit producers, and are eaten by diversity of fauna species. The genus *Palicourea(*Rubiaceae family), common in the Amazon Forest,comprehends dozens of shrub and small tree species distributed in thetropical forests. Their fruit are small berries and are fairly attractive due to their dark coloration [32].This attractiveness is related to mutations for seed dispersion. Among the fructivorous birds that feed on these species were members of the Pipridae family,*e.g.Pipra Pipra, Pipra erythrocephala, Neopelma chrysocephalum, Tyranneutes virescens,Lepidothrix suavissima, Manacus manacus, Xenopipo atronitens* and *Corapipogutturalis*[20].

Others genera of the Rubiaceae family have species that produce fruit for fauna, such as *Alibertia,Bothriospora, Genipa, Psychotria* and*Randia*[33].

Some species of the *Trichilia* genus (Meliaceae*family) possess attributes evident to birds, such as coloration and accessibility of the fruit positioned closer to the extremities with long* pedicels.The physical accessibility, determined by the structure of the fruit and their position on the branch, can determine in large part the birds' choice [34].This could explain the large quantity of bird species that eat the fruit of these plants.Species of the *Miconia*genus (*Melastomataceae* family) are characteristic of secondary vegetation and have small, rounded fruit consumed by birds [35].Many small seeds are embedded in its sweet pulp, another characteristic of plants that belong to secondary formations that invest more in the number of seeds than nutritional reserves for the establishment of its descendents[36].Snow [36] studied 19 shrub and tree species of the *Miconia* genus in the Amazon Forest.Each species produced fruit during a specific season of the year, and none bore fruit all year long.Nevertheless, fruiting season of all of the 19 species did cover the whole year.The author suggested that the various *Miconia* species compete among themselves for the services of animal seed dispersers like manakins (*Pipridae* family) and, to reduce the competition between them for dispensers, they segment the market for dispersers, offering fruit in different seasons of the year.

Interactions between vegetation and birds

Manakins are fairly abundant birds in the understory of tropical forests in low elevations of South America.The abundance of these birds comes from the fact that they feed almost exclusively on an extremely abundant and easy to find food source: shrub and tree fruit, especially from the *Melastomataceae* family, abundant in these forests [37].

Krijger *et al.*[37] studied the dispersion of seeds in courtship locations of the White-throated Manakin (*Corapipo gutturalis*) in French Guiana. They collected soil samples where the males perch for courtship and compared them to soil samples taken from

a location with similar vegetation 50 meters away.The authors verified that the total density of viable seeds in the soil was twice higher around the courtship areas than adjacent forest.The authors concluded that a large density of viable seedsduring the courtship of the White-throated Manakin, especially seeds from the shrub and tree species of the Melastomataceae family, can influence the potential of the forest to regenerate in these locations, since seeds banks and their composition of species in the soil can be important factors in the initial phases of forest regeneration.

Another bird that reproduces in courtship locations is the Guianan Cock-of-the-rock (*Rupicola rupicola*).It alters the flora and vegetation in these locations by way of seed dispersion.So far, this has not been confirmed in manakin courtship locations, although few locations have been analyzed.Perhaps the explication for this is that manakin courtship locations are generally located in dense forest, while the seeds of Melastomataceae species generally germinate better under conditions where the soil receives abundant sunlight [38].Therefore, in depositing the seeds in dense forest, the manakin could indeed be harming the dispersion of these seeds, sending them off in locations where they will not be able to germinate.

However, if one or more trees fall in the courtship locationand create a clearing in the forest and allow direct sunlight reach the soil, seeds of the shrub and tree species of the Melastomataceae family will germinate.Under these conditions, the courtship behaviors of male manakinswould increase the quantity of plants of that family botanic in the area [37].On the other hand, the Guianan Cock-of-the-rock is generally a frugivorous that eats fruit from a great diversity of forest plants.By consuming a great variety of seeds, including those from many species of plants that do not need sunlight to germinate, there is a greater probability that the male Guianan Cock-of-the-rock alters the number and diversity of plant species in poorly-lit courtship locations more than the male manakin[37].

Théry[39] studied the eating habits of six manakins in the French Guiana's Amazon (*Tyranneutes virescens*, *Pipra pipra, Pipra serena* and *Pipra erythrocephala, Manacus manacus*and *Corapipo gutturalis*) and verified that fruit from Melastomataceae species consisted of more than 50% of the diet of each of them. The author also verified that the manakins eat around 90% of all of the fruit available from Melastomataceae species.The extraction of fruit on a large scale bymanakins, as well as the fact that many seeds pass intact and rapidly throughtheir digestive system [40], suggests that manakins have an important function in the dispersion of Melastomataceae species in tropical forests.

Théry[39] also studied a seventh bird, *Schiffornis turdina* (Tityridae family) and found that fruits from Melastomataceae species averaged 25% to 28% of its diet.However, there is a controversy about this species, known as the Thrush-like Schiffornis, because many ornithologists do not believe that it is a manakin. Modern bird classifications, based on DNA mapping, classify it as a becard instead of a manakin[41].

A great diversity of bird species eat fruit from Melastomataceae species besides manakins, and in general these plants are recognized as one of the most important food sources of small frugivorous birds [42].In tropical forests, where manakins are one of the most numerous birds, they seem to be the most important dispersers of Melastomataceae species.However, the tanagers (Thraupidae family) are also important dispersers and, in medium high forests, substitute manakins as the most important dispersers of Melastomataceae species[42].

Plants of the Anacardiaceae family, like the *Tapirira guianensis*, a common species in the Amazon Forest, produce a large quantity of fruit used by birds, which distribute them commensally[43].Among the species that eat the sweet, succulent pulp of the fruit from the tree *Tapirira guianensis*there are some species likethe tyrant flycatchers *Elaenia flavogaster*, *Pitangus sulphuratus*and *Tyrannus melancholicus*, the dove *Leptotila verreauxi* and the thrushes *Turdus* spp, which swallow the fruit whole.These are in contrast to tanagers, which chew the fruit and because of that areconsidered less apt for dispersion [44].

Othersplant families and their importance for frugivores abundant

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 a large number of seeds, slightly sweet pulp, and a pleasant smell [45].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 [46]. The fruit of *Cecropia* trees are much appreciated by birds.

The 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 dozens of species of birds of the Cracidae, Pipridaeand Thraupidae families[47].

Other very important plant families for frugivorous 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[48].

The color displays of mature fruit as attractive to the attention of dispersers

Many species of lianas, a very representative group in the Amazon Forest, produce fruit that are appreciated by various bird species.*Davilla rugosa* is a woody liana from the Dilleniaceae family, whose seed dispersion system is characteristically ornithochoric, with very exposed fruit with lively coloration, bearing fruit wide and abundantly and with a meaty pulp that guarantees a high caloric return to birds [20].

The color displays of mature fruit have probably evolved to attract the attention of dispersers [49], but adaptive processes should not be discarded [50].A large portion of plants whose seeds are dispersed by birds show conspicuously colored fruit [51].Many species, such as the *Davilla rugosa*, display two or more colors, so the coloration of mature fruit can contrast with the coloration of immature fruit or with accessory structures, such as capsules, pedicels and sepals, in order to be more attractive to dispersers [49].

Davilla rugosa is a generalist species with respect to its dispersion system, producing large quantities of relatively small propagules that attract a large variety of bird species of different trophic niches [52], such as *Tangara cayana* (Thraupidae family), *Empidonomus varius* (Tyrannidae family), and *Turdus leucomelas* (Turdidae family)[13].

The main guilds of the birds

Omnivorous birds were an important guild in the Amazon Forest. The guild of the omnivores is composed of species which eat grains, fruit, seeds, and small arthropods, contributing considerably to the dispersion of seeds.Omnivores on the edges of the forest are the main representatives of this group, in Amazon Forest, especially for species of the following families: Tyrannidae (*e.g.* species of the genera *Tolmomyias, Elaenia*, *Myiarchus, Pitangus*, *Megarynchus*, and *Tyrannus*), Icteridae (*e.g.* species of the genera *Psarocolius, Cacicus, Icterus,* and*Molothrus*), Vireonidae (*e.g.* species of the genera *Cyclarhis, Vireo,* and *Hylophilus*), Thraupidae (*e.g.* species of the genera *Tachyphonus*, *Tangara*, *Dacnis,* and*Cyanerpes*) and Fringillidae (in special thespecies of the *Euphonia* genus)[48].

The Tinamidae family, represented in the Amazon Forest by species of birds of the *Tinamus* and *Crypturellus* genera, is endemic of the Neotropical region. The majority of Tinamidae species exhibit terrestrial forest behavior, roaming around the plant litter in the understory, eating grains, seeds, small fruits and arthropods, picking them up together with soil[44].

Some species of omnivorous birds are typical of riparian forests, streams, wetlands, swamps and adjacent open areas, and eat arthropods, aquatic plants, seeds and various fruits, and the principal representatives of the group are of the families Rallidae (*e.g. Laterallus exilis, Porzana albicollis*), Jacanidae (*Jacana jacana*) and Charadriidae (*Vanellus chilensis, Charadrius collaris*)[53].

The guild of the birds frugivorous is principally represented in the Amazon Forest, by species of the Cracidae (*e.g.* species of the genera *Ortalis, Penelope,* and*Crax),* Psittacidae (*e.g.* species of the genera *Ara, Aratinga, Pyrrhura,Brotogeris, Touit, Pionus,* and*Amazona*), Ramphastidae (*e.g.* species of the genera *Ramphastos* and *Pteroglosus*), Cotingidae (*e.g.*species of the genera *Lipaugus* and *Cotinga*), Trogonidae (*Trogon* spp) and Pipridae (*e.g.* species of the genera *Neopelma* and*Pipra*) families.These species could be considered the principle seed dispersing agents in the Amazon Forest[53, 48].

The effects of frugivorous birds on plants go beyond the removal of seeds.These birds can limit the populational growth of the plants if the quantity of seeds they disperse is insufficient or if the quality of dispersion that they provide is inadequate, i.e., when they deposit seeds in locations with a low probability of taking root[54].

Toucans and aracarisare large consumers of fruit and are excellent seed dispersers.Among the fruits consumed by these frugivorous species, species of the genera *Ficus* and *Cecropia* stand out [55].The psittacines (macaws, parrots, and parakeets) are considered more destroyers than dispersers of seeds, since they triturate and digest them[56].However, in removing a large quantity of fruits from the mother plant, these birds, which live in large flocks, could be making the fruits available to secondary dispersers,like terrestrial birds of the Tinamidae family, for example the species *Tinamus major*, *Crypturellus cinereus*, *C. soui*, *C. undulatus*, *C. erythropus* and*Cvariegatus*.

The guild of nectarivorous is composed of species of hummingbirds (Trochilidae family), which feed the nectar of flowers and complement their diet with small insects and spiders. Hummingbirds frequent the interior and the edge of the forest searching for flowers with strong coloring, feeding their nectar. In the process, hummingbirds act as polinizers of many plant species, especially bromeliads (Bromeliaceae family). Species of the genera *Thalurania, Hylocharis* and *Amazilia* are very common among the hummingbirds in the Amazon Forest[53].

The integrity and complexity of a forest are the factors that influence the composition, abundance and probably the functions of the assembly of different animal species. In that way, in forest environments, where a vertical stratification of resources occurs, these species are distributed occupying a high diversity of trophic niches. They occupy different heights of the forest and a great diversity of bird and mammal species distributed among different trophic guilds, which means ecosystems relatively balanced and of great biological value.

Understanding the interactive processes between the fauna and flora requires a complex long-term study. Furthermore, the phonological, ethological, and ecological studies of many species of fauna and flora are unknown. In that way, inferring about all of the relationships between plant and animal species with those that support the fauna is impossible. Nevertheless, more than 70% of seed dispersion in tropical forests depends on forest fauna as a dispersing agent, and the composition of wildlife will change as changes occur in vegetation.

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