Complex plant-disperser-pest interactions in NW Amazonia: beetle larvae and companions travelling inside *Attalea maripa* palm nuts

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Abstract

The dispersal and predation, by vertebrates, of bruchid beetle larvae living inside *Attalea maripa* palm nuts are described in the region of the Middle Negro river (state of Amazonas, Brazil). The complexity of the ecological relationships between palm trees, seed dispersers, beetle seed predators and parasitic or commensal organisms is discussed and their importance to the biological diversity of the Amazonian ecosystems is argued.

Key words: Arecaceae, Bruchidae, larvae dispersal, multitrophic associations, mutualistic relationships, Pachymerini, parasitic insects, plant-vertebrate-insect interactions, zoochory.

Resumen. *Interacciones complejas de tipo planta-diseminador-plaga en el noreste de la Amazonía: larvas de escarabajos y acompañantes viajando en el interior de nueces de palmera* Attalea maripa.

Se describe la dispersión y depredación por vertebrados de larvas de coleópteros de la familia Bruchidae que viven dentro de las nueces de la palmera *Attalea maripa*, en la región del Medio río Negro (estado de Amazonas, Brasil). Se discute la complejidad de las relaciones ecológicas entre palmeras, diseminadores de semillas, escarabajos depredadores de semillas y organismos parasitarios o comensales, evidenciando su importancia para la diversidad biológica de los ecosistemas amazónicos.

Palabras clave: Arecaceae, Bruchidae, dispersión de larvas, asociaciones multitróficas, relaciones mutualistas, Pachymerini, insectos parásitos, interacciones planta-vertebrado-insecto, zoocoria.

Introduction

Worldwide, fruiting plants and vertebrates maintain mutualistic relationships in which the plant provides food (the pulp or the endosperm of the fruit) to frugivorous or granivorous species that disperses its seeds to sites where germination and colonisation can occur.

The transport of seeds away from the parent plant enhances seed survival in natural conditions. Usually, seeds that are not removed from the parent plant fail to establish seedlings and to colonise new areas (Connell, 1971; Janzen, 1970, 1971).

Larvae of Curculionidae living inside palm nuts and consuming the seed endosperm (seed predation) can also be benefited by seed dispersal. In southeastern Brazil, frugivorous birds and mammals frequently ingest fruits infested by *Revena rubiginosa* larvae (Curculionidae), which resist the passage through the digestive tract, and are regurgitated or defecated alive (weevil dispersal) (Guix, 1995; Guix & Ruiz, 1995, 1997, 2000). These weevil larvae have acquired the capacity to feed on the very nutritious endosperm without being predated by a fruit-eating animal. In this way, weevils may have incorporated a new dispersal mechanism (endozoochory) by exaptation.

The transport of seeds in the mouth of animals (exozoochory) is another important mechanism of dispersal in tropical forests. Here, I examine beetle larvae dispersal through the transport by rodents of *Attalea maripa* palm nuts that have fallen to the ground. Implications of this dispersal mechanism for parasitic and commensal species associated with beetles are discussed.

Material and methods

Attalea maripa (Arecaceae), formerly called *Maximiliana maripa* (10 - 18 m height), is a monoecious palm species widely distributed throughout Amazon and southern Orinoco basins, being frequently abundant in secondary forests (Uhl & Dransfield, 1987). The fruit is an ovoid drupe (41.9 - 38.0 mm long and 30.6 - 20.4 mm wide) covered by a yellow creamy pulp and a coriaceous epicarp. The nut (41.4 - 37.6 mm long and 20.2 - 16.7 mm wide) contains one to three seeds and is composed by a thick, hard endocarp (wall: 4.8 - 1.9 mm wide).

The fleshy pulp of its fruits is widely consumed by many species of mammals and is frequently eaten mixed with manioc flour by the Amazonian people. The main seed dispersers of this palm are tapirs (mainly *Tapirus terrestris*), Cebid monkeys (e.g. *Cebus albifrons, C. apella*), seed-hoarding rodents (*Dasyprocta fuliginosa, D. leporina*, *Myoprocta pratti, Sciurus igniventris*) and man (Guix, 2005; Silvius, 2002; Silvius & Fragoso, 2002).

From 15 to 24 July 2004, surveys of palm trees were performed in the region of the Middle and Lower Negro river, from the confluence with the Solimões river (near the city of Manaus) to the confluence of the Caurés river, state of Amazonas, Brazil (Fig. 1).

The Middle and Lower Negro river basin is a large blackwater drainage system (oligotrophic), composed of hundreds of islands and river margins that remain inundated for almost six months per year.

These plain lands are composed of sedimentary sandy soils that lie between 30 m and 70 m.a.m.s.l. (Rossetti et al., 2005). The climate is equatorial humid; the average annual temperature is above 26º C and the annual rainfall exceeds 2,000 mm, being more abundant between December and May.

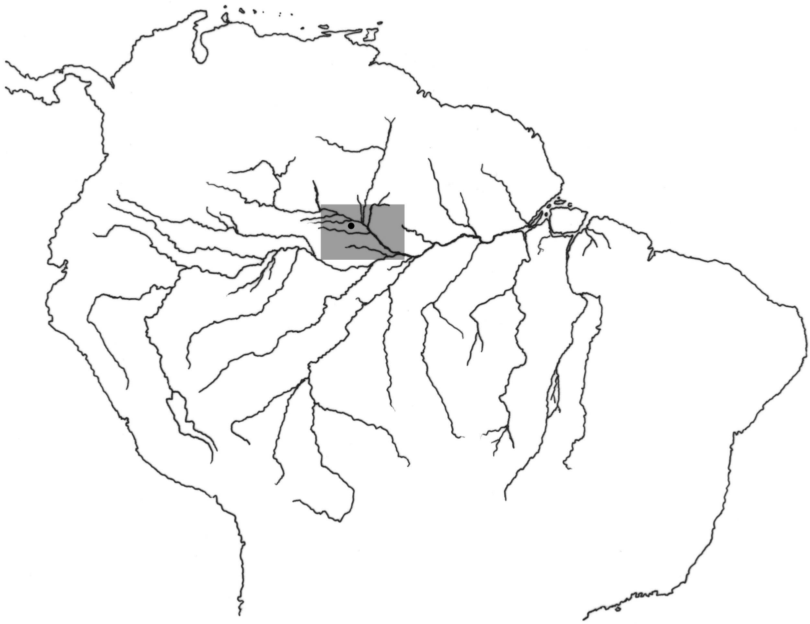

Figure 1. Map of the Amazon basin showing the Middle and Lower Negro river system (state of Amazonas, Brazil), where surveys of palm trees were performed in July 2004. The black dot indicates the area of Apoloaca, located on the right margin of the Caurés river, at the confluence with the Negro river.

The main vegetation formations are the *igapó* forests (tall floodable forests located in river margins and some islands), the *terra firme* forests (tall forests not subjected to flood periods), the *campinarana* forests (also known as Amazonian *caatinga* forest), and the *campina* (Amazonian *caatinga* shrubland).

Attalea maripa palm trees were surveyed from 17 to 20 July 2004, walking through the *terra firme* forests of Apoloaca, located on the right margin of the Caurés river, between Igarapé Peixe-Boi and Igarapé Gregório (1º 19' 45" S, 62º 13' 28" W; Altitude: 30 - 45 m; Fig. 1).

Fruits and pulpless nuts of *A. maripa* were found under isolated palms or beneath adult palm concentrations. Most of the nuts were opened and inspected for larvae. Intact nuts containing larvae were placed in separated plastic recipients and monitored under controlled conditions of temperature and humidity for 13 months.

Results and discussion

Bruchid development

Pachymerus cardo and *Speciomerus giganteus* (Bruchidae: Pachymerinae) larvae were found inside fallen *Attalea maripa* nuts in the study area. Most of the larvae (112, 95.7%, n = 117) found in fallen nuts were attributed to *P. cardo* and only 2 (1.7%) of the larvae were attributed to *S. giganteus*.

The females of *Pachymerus cardo* lay eggs on fallen fruits of this palm species, mostly when the pulp has been removed (totally or partially) by frugivorous birds and mammals (Silvius, 2002). Instar larvae perforate the endorcarp and enter the seeds of each nut and feed on the endosperm and embryos for 2 - 3 months. Each seed contains only one developed larva (Delobel et al., 1995). Two- and three-seeded nuts may contain respectively two and three developed larvae (Silvius, 2002). Pulpation occurs inside the nut and each adult beetle emerges from the nut by boring through the endocarp.

In the study area, one to seven instars of *P. cardo* were found in each nut (n = 32 nuts), but only one mature larva per seed was found. Thus, when two or more instars penetrate at the same seed, predation among larvae may occur and only one of them may survive until the mature stages.

In lab conditions, it was observed that larvae of *P. cardo* can live for up to seven months inside the nut until they leave it or die prematurely.

Due to natural pores of the nut and the small entry holes (0.4 mm in diameter; 1 to 7 holes per nut) made by *P. cardo* instars when penetrating the endocarp, larvae of this species do not develop in anoxid or hypoxid conditions inside the seed.

Seed/larva dispersal mechanisms

Attalea maripa seeds are dispersed by animals (zoochory), and bruchid larvae living inside this palm nuts can also be dispersed in the same way. Indeed, nuts of *A. maripa* infested by larvae were found far away from parent palm trees in *terra firme* forests of Apoloaca.

Neither infested nor non-infested nuts float on water. The seed chambers of infested nuts became inundated when immersed in the water. Thus, hydrochory in periodically flooded forests (igapós) and channels (igarapés) was discarded for this species.

The role of Psittaciformes and large-bodied monkeys (Atelidae and Cebidae)

Parrots (e.g. *Amazona farinosa*, *A. amazonica*, *A. autumnalis*, *Pionus menstruus*) and macaws (e.g. *Ara ararauna*, *Ara chloroptera*) can selectively extract and feed on the pulp of *Attalea maripa* ripe fruits without damaging the seeds. These species often drop large quantities of undamaged seeds under the mother tree and thus are not considered as legitimate seed dispersers.

Large-bodied primates (e.g. *Alouatta* spp., *Ateles* spp., Atelidae and *Cebus* spp., Cebidae) are critical for the dispersal of large seeds. Usually they are the few wild frugivores of a given Neotropical area that can open hard-husked fruits (Kubitzki, 1985; Guix, 1996; Van Roosmalen & Garcia, 2000; Peres & Van Roosmalen, 2002; Balcomb & Chapman, 2003).

Although *Ateles* spp. and *Cebus* spp. are considered as potential dispersal agents of several large-seeded plant species (see Van Roosmalen & Garcia, 2000), in contrast to the *Alouatta* spp., they do not swallow large seeds whole. *Ateles* spp. and *Cebus* spp. usually transport large fruits (e.g. *Theobroma cacao*), in the mouth or in one hand, over distances less than 50 m from the mother-tree. Thus, most large seeds were dropped by these monkeys beneath the mother-plant.

Pulp handling by primates, parrots and macaws, and fruit dropping under the mother-tree, increase the susceptibility of nuts to bruchid beetle infestation (Silvius, 2002; Sivius & Fragoso, 2002).

The role of seed-hoarding animals

Seed-hoarding by agoutis (*Dasyprocta* spp.; Dasyproctidae) and acouchys (*Myoprocta* spp.; Dasyproctidae) is a common dispersal mechanism for several large-seeded palm species in Amazonia (Hallwachs, 1986; Jansen et al. 2004).

Agoutis and acouchys are common seed predators that usually transport and store large seeds, scatterhoarding them via burial. In years in which food resources are abundant or when an agouti or an acouchy dies, several of the seeds previously buried by these rodents germinate and produce seedlings.

The role of tapirs

The Brazilian tapir (*Tapirus terrestris*) frequently consume *Attalea maripa* fruits fallen under the mother-tree and they can transport viable seeds in the gut over large distances. This ungulate might be also a legitimate bruchid disperser (by endozoochory), if the larva has already entered the seed when the fruit is swallowed by the tapir. But beetle larvae are unlikely to survive the gut passage of this or other species of mammals, since the instars perforate the endocarp and the gastric fluids may kill the larvae. Nevertheless, seed dispersal in the gut of tapirs cannot be discarded *a priori*, and experimental tests on infested fruit passage in the digestive tract of captive animals need to be conducted

Humans and palm trees in the Amazon basin

Man also participates in mutualistic relationships involving plant species that produce fleshy fruits or large seeds. Like seed-hording agoutis, humans can also be seed-predators and, at the same time, seed-dispersers of several Amazonian species of palms (Arecaceae).

Collection of plant products was an important part of Indian economy in the Middle Negro River and it is still an important practice among Caboclo settlers. The transport and manipulation of plant resources, first by Indians and now by the Caboclos, produced a concentration of useful plants around the settling areas (Guix, 2005). Thus, fruiting trees that were formerly dispersed throughout the forests in relatively low densities, in some cases became clustered near human settlements, thus increasing the resource availability for the group.

Potential advantages of larvae dispersal by vertebrates

Although adult bruchid beetles disperse well by flying, their larvae are enclosed in seeds that cannot move without the action of seed dispersers. Bruchid larvae living inside *Attalea maripa* seeds are a source of nutrition for several insect and mammal species (Silvius, 2002; Silvius & Fragoso, 2002). Thus, applying seed dispersal-predation theories (cf. Janzen, 1970, 1971; Connell, 1971; Van der Pijl, 1982; Herrera, 1985) to large nutritious bruchid larvae, it can be inferred that the larvae that are dispersed and burrowed by rodents would have greater chance of survival than those that stay under the mother palm for months. Several larvae predators, such as peccaries (Tayassuidae), porcupines (Erethizontidae), and wasp hyperparasitoids (e.g.: Hymenoptera: Braconidae, Chalcididae and Ichneumonidae) may more easily detect and kill larvae living in nuts clustered under the mother-palm than those dispersed on the forest floor.

The same may be true when bruchid beetles infest nuts that were previously dispersed by tapirs and other animals.

Complex interactions around palm trees

Palm nuts that contain large amounts of endosperm are frequently consumed by granivorous animals, such as rodents and beetle larvae. Seed-hoarding mammals, such as agoutis (*Dasyprocta* spp.; Dasyproctidae), acouchys (*Myoprocta* spp.; Dasyproctidae) and squirrels (*Sciurus* spp.; Sciuridae) may behave both as seed predators and as seed dispersers of *A. maripa* in the Amazon basin. These mammals species can also feed on larvae living inside the palm nut (larvae predators)(Silvius, 2002; Silvius & Fragoso, 2002).

Agoutis, acouchys and squirrels can feed on or disperse nuts collected under the mother-tree that were recently infested by bruchid larvae. Thus, larvae-infested palm nuts can also be dispersed and stored by these animals. This is the case when several of the seeds stored by the rodent are not recovered, because of food-abundance conditions or the premature death of a seed-hoarding animal.

Depending on the ecological conditions, the seed-eating vertebrate involved in the interaction can participate both as a plant deparasiter and as a larvae disperser.

Furthermore other components may be involved in these plant-disperser-pest relationships. Larvae and adults of Coleoptera that feed on palm trees frequently contain nematodes (Phylum Nematoda), which establish commensal and parasitic associations with the insect. Some nematodes infesting beetle species may be pathogenic to the larvae or adults (e.g. several species belonging to the families Steinernematidae and Heterorhabditidae). Other nematodes, such as some species belonging to the family Allantonematidae or to the superfamily Aphelenchoidea, do not prevent the larvae metamorphosis.

Also, it is known that some species of nematodes belonging to the orders Aphelenchida and Tylenchida, can parasite both the plant and it associated phytophagous insect (Giblin-Davis et al., 2003).

Beetle larvae can also be infested by protozoans, bacteria and viruses that could also be benefited by seed dispersal mechanisms involving frugivores. Such components could interact with each other to different degrees, thus forming complex ecological webs.

Fruits of several other species of palm trees that grow in the study area (e.g. *Astrocaryum aculeatum*, *A. jauari*, *A. tucuma*, *Bactris gasipaes*, *Mauritia flexuosa*, *Oenocarpus bataua*, *O. bacaba*, *O. minor* and *Orbignya speciosa*) can be infested by beetle larvae (e.g.: Bruchidae, Curculionidae, Scolytidae; Delobel et al., 1995), and in turn, may contain other parasitic or commensal species.

Taking these examples into account, diversity concepts related to ecology and conservation biology should consider not only the isolated components of a given ecosystem, but all the potential interactions and evolved relationships (e.g. mutualistic, parasitic, commensal, multitrophic) among these components.

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References

Balcomb, S. R.; Chapman, C.A . 2003. Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecol. Monogr. 73: 625-642.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In*: P. J. den Boer; G. R. Gradwell (ed.) Dynamics of populations. Centre for Agricultural Publishing and Documentation. Wageningen. p. 298-312.

Delobel, A.; Couturier, G.; Kahn, F.; Nilsson, J. A. 1995. Trophic relationships between palms and bruchids (Coleoptera: Bruchidae: Pachymerini) in Peruvian Amazonia. Amazoniana 13: 209-219.

Giblin-Davis, R. M.; Davies, K. A.; Morris, K.; Thomas, W. K. 2003. Evolution of parasitism in insect-transmited plant nemadodes. J. Nematol. 35: 133-141.

Guix, J. C. 1995. Aspectos da frugivoria, disseminação e predação de sementes por vertebrados nas florestas nativas do Estado de São Paulo, sudeste do Brasil. PhD Thesis. Facultat de Biologia. Universitat de Barcelona. Barcelona.

Guix, J. C. 1996. Aspectos da frugivoria, disseminação e predação de sementes por vertebrados nas florestas nativas do Estado de São Paulo, sudeste do Brasil. Col·lecció de Tesis Doctorals Microfitxades núm. 2798. Universitat de Barcelona. Barcelona.

Guix, J. C. 2005. Evidence of old anthropic effects in forests at the confluence of the Caurés and Negro rivers – NW Amazonia: the role of Indians and Caboclos. Grupo Estud. Ecol., Sér. Doc. 8: 1-27.

Guix, J. C.; Ruiz, X. 1995. Toucans and thrushes as potential dispersers of seed-predatory weevil larvae in southeastern Brazil. Can. J. Zool. 73: 745-748.

Guix, J. C.; Ruiz, X. 1997. Weevil larvae dispersal by guans in Southeastern Brazil. Biotropica 29: 522-525.

Guix, J. C.; Ruiz, X. 2000. Plant-disperser-pest evolutionary triads: how widespread are they? Orsis 15: 121-126.

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): The inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). *In*: A. Estrada; T. H. Fleming (eds.) Frugivores and seed dispersal. W. Junk Publishers. Dordrecht. p. 285-308.

Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132-141.

Jansen, P. A.; Bongers, F.; Hemerik, L. 2004. Seed mass and mast seedling enhance dispersal by a neotropical scatter-hoarding rodent. Ecol. Monogr. 74: 569-589.

Janzen, D. H. 1970. Herbivory and the number of tree species in tropical forests. Am. Nat. 104: 501-528.

Janzen, D. H. 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. 2: 465-492.

Kubitzki, K. 1985. The dispersal of forest plants. *In*: G. T. Prance; T. E. Lovejoy (eds.) Key environments: Amazonia. Pergamon. New York. p. 192-206.

Peres, C. A.; Van Roosmalen, M. G. M. 2002. Patterns of primate frugivory in Amazonia and the Guianan shield: implications to the demography of large-seeded plants in overhunted forests. *In*: D. Levey; W. Silva; M. Galetti (eds.) Frugivory and seed dispersion: ecological, evolutionary and conservation issues. Online publication; date 1.3.2002. CABI Publishing. Oxford. p. 407-423.

Rossetti, D. F.; Toledo, P. M. de; Góes, A. M. 2005. New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. Quaternary Res. 63: 78-89.

Silvius, K. M. 2002. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or "grubivory"? J. Trop. Ecol. 18: 707-723.

Silvius, K. M.; Fragoso, J. M. V. 2002. Pulp handling by vertebrate seed dispersers increases palm seed predation by bruchid beetles in the northern Amazon. J. Ecol. 90: 1024-1032.

Uhl, N. W.; Dransfield, J. 1987. Genera Palmarum; A classification of Palms. The L. H. Bailey Hortorium & The International Palm Society. Allen Press. Lawrence.

Van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer Verlag. Berlin.

Van Roosmalen, M. G. M.; Garcia, O. M. C. G. 2000. Fruits of the Amazonian forest. Part II: Sapotaceae. Acta Amazonica 30: 187-290.