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Plant-disperser-pest evolutionary triads: how widespread are they?

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Fleshy fruiting plants and frugivorous vertebrates frequently establish mutualistic relationships. The plant provides packages of food (the pulp of the fruit) to frugivorous species and, in exchange, the legitimate frugivore disperses its seeds to sites where germination and colonization can occur. These ecological relationships are not species-specific but have coevolved diffusely by means of multiple selective pressures on several interacting species. In other words some characteristics of the fleshy fruiting species evolved with some characteristics of the frugivorous species, making the relationships sufficiently widespread to survive the extinctions of some of their components (Herrera, 1985).

In 1984, Carlos Herrera proposed a more complex type of coevolved relationship, «the plant-disperser-pest evolutionary triad», which is constituted by three groups that interact with each other inducing evolutionary changes between them (Herrera, 1984). One of the first evolutionary triads described was composed of the palm tree *Syagrus romanzoffiana*, frugivorous birds and a curculionid beetle (*Revena rubiginosa*), all of them living in Atlantic rainforest and the subtropical forests of Southeastern Brazil (Guix & Ruiz, 1995, 1997). The weevil larvae live inside the palm nut, consuming the seed endosperm (seed predation) in hypoxic or anoxic conditions, and do not preclude fruit development or maturation. Frugivorous birds such as guans, toucans or thrushes ingest whole ripe fruits of *S. romanzoffiana*, not infested by weevils, and disperse their seeds (seed dispersal). The triad is closed when the frugivorous birds ingest fruits infested by *Revena* weevils, which resist the passage through their digestive tract, and are regurgitated or defecated alive (weevil dispersal). There is evidence that adults of *Revena* and other weevils do not disperse over long distances by their own means (Guix & Ruiz, 1997; Leather et al., 1999). Weevil larvae acquired the capacity

to feed on the very nutritious endosperm without being predated by a fruit-eating animal, and may thus have incorporated the new dispersal mechanism by exaptation.

Between 1996 and 1999, there were found another 21 species of vertebrates belonging to 11 families that transport *S. romanzoffiana* seeds and potentially disperse weevils of *R. rubiginosa* in SE and SW Brazilian forests (mainly coastal Atlantic rainforests and inland subtropical forests). These species together with other five previously found (Guix & Ruiz, 1995, 1997) make up a total of 26 species belonging to 12 families which can disperse weevils. Some, like the Greater Rhea (*Rhea americana*), the howler monkeys (*Alouatta* spp.), and the Crab-eating fox (*Cerdocyon thous*) can transport live larvae in their digestive tract. Others, are seed-hoardings (e.g. squirells, *Sciurus ingrami* and agoutis, *Dasyprocta* spp.) or frugivorous bats (e.g. *Artibeus* spp.; Phyllostomidae) which transport weevil-infested seeds without ingesting them (table 1) .

Considering the characteristics of the fruits consumed (including the size of the fruits and the seeds swallowed) and the characteristics of the digestive tract of other frugivorous species, possible bird dispersers of *S. romanzoffiana* seeds and *Revena* larvae by endozoochory are: *Daptrius americanus* and *Polyborus plancus* (Falsonidae), *Cariama cristata* (Cariamidae), *Trogon* spp. (Trogonidae); *Bailloncus bailloni* and *Selenidera maculirostris* (Ramphastidae); *Pyroderus scutatus* (Cotingidae); other *Turdus* spp. (Muscicapidae); *Mimus saturninus* (Mimidae), *Tityra* spp. and *Pitangus sulphuratus* (Tyrannidae). Other possible mammalian dispersers by endozoochory are: *Chrysocyon brachyurus*, *Lycalopex vetulus* (Canidae), *Eira barbara* (Mustelidae), *Tapirus terrestris* (Tapiridae) and domestic horses (*Equus caballus*). Possible mammalian dispersers by exozoochory are: *Dasyprocta leporina* (Dasyproctidae), and several large species of Phyllostomidae bats belonging to genus *Artibeus, Phyllostomus, Platyrrhinus* and *Sturnira*.

Possible seed and larvae predators of *S. romanzoffiana* are among mammals: *Pecari tajacu, Tayassu pecari* (Tayassuidae), *Echimys* spp. (Echimyidae), *Coendou prehensilis, C. villosus* (Erethizontidae), and among birds, *Odontophorus capueira* (Phasianidae). Although *Tinamus solitarius* (Tinamidae) and *Crax fasciolata* (Cracidae) are predators of several hard seeds by digestive action, they may also disperse *Syagrus* seeds.

Kuhlmann & Kühn (1947) cite *Nasua nasua* (Procyonidae) as a common consumer of fruits of *S. romanzoffiana*, and previous studies reported the presence of entire seeds of this palm in scats of *Cerdocyon thous* (Kuhlmann, 1947; Kuhlmann & Kühn, 1947; Motta-Junior et al., 1994, Facure & Monteiro-Filho 1996).

The *Syagrus* species produce fruits with large differences in size and mesocarp consistency (see Uhl & Dranstield, 1987). The stemless species of *Syagrus* (e.g. *Syagrus vagans* from Brazil) produce smaller fruits and seeds, with a thinner endocarp, than those of *S. romanzoffiana*. Thus, some potential seed dispersers of *S. romanzoffiana* (e.g. *Crax* spp., *Tinamus solitarius*) may act as seed predators, by digestive destruction, when consuming fruits of *S. vagans*.

Table 1. Vertebrate species that potentially disperse weevils of *Revena rubiginosa* in SE and SW Brazil. Regurgitation (R) or Defecation (D).

Family, common name, and number of species	Type of transport		
	In the beak or mouth	In the gut	
		R	**D**
BIRDS:			
RHEIDAE (rheas): 1			
*Rhea americana**			•
CRACIDAE (guans): 2			
*Penelope obscura**			•
*P. superciliaris**			•
RAMPHASTIDAE (toucans): 5			
Pteroglossus aracari		•	
P. castanotis		•	
*Ramphastos dicolorus**		•	
R. toco		•	
*R. vitellinus**		•	
COTINGIDAE (cotingas): 1			
Procnias nudicollis		•	
CORVIDAE (jays): 4			
Cyanocorax caeruleus		•	
C. cyanomelas		•	
C. cristatellus		•	
*C. chrysops**		•	
MUSCICAPIDAE (thrushes): 4			
Turdus amaurochalinus		•	
T. leucomelas		•	
*T. rufiventris**		•	
Platycichla flavipes		•	
MAMMALS:			
CEBIDAE (monkeys): 2			
*Alouatta guariba**			•
A. caraya			•
PHYLLOSTOMIDAE (bats): 2			
Artibeus lituratus	•		
A. fimbriatus	•		
CANIDAE (wild dogs): 1			
Cerdocyon thous			•
DASYPROCTIDAE (agoutis): 1			
Dasyprocta azarae	•		
SCIURIDAE (squirrels): 1			
Sciurus ingrami	•		
BOVIDAE: 2			
domestic cow		•	•
domestic goat		•	

* Weevil survival of passage through the gut tested in captivity. Time of gut retention, terminated by: regurgitation (2-30 min) or defecation (2h 20 min to >10 h).

Distribution of *Syagrus* spp. (Arecaceae)

Thirty-two species of *Syagrus* Martius are recognized in South America, from Venezuela southwards to Argentina; one species living in the Lesser Antilles (Uhl & Dransfield, 1987). *Syagrus romanzoffiana* (Chamisso) Glassman is a morphologically variable species, widely distributed throughout South America: Brazil (from Espirito Santo, Minas Gerais, and Goiás, to Rio Grande do Sul), Paraguay and Argentina (cf. Lorenzi, 1992). It occurs in habitats as diverse as subtropical and Araucaria forests, Atlantic rainforest, cerrados, steppes and coastal restingas; mainly in scrublands and young secondary forests, but also in old secondary and mature forests (cf. Hueck, 1972; Guix, 1995).

Distribution of *Revena* spp. (Curculionidae: Baridinae)

The genus *Revena* Casey, 1922 includes nine species distributed throughout South America (Wibmer & O'Brien, 1986). Bondar (1943) pointed out the possibility that each species of *Revena* has its own species of host-palm and named some of his newly described species of Baridinae with the same name as the palm-species to which they were related (e.g. *Revena vagans* Bondar, for those found at *Syagrus vagans* (Bondar) A.D. Hawkes). Thus, the distribution of the insect parasite and its host palm would be, in great part, coincidental.

Seed/Larva dispersal mechanisms

The *Syagrus* seeds and the *Revena* larvae are dispersed by the same mechanism: zoochory. Although adults of *Revena* spp. have wings, they have not been reported to fly, only walking on the ground and on vegetation (Bondar, 1943; Guix, 1995). This behaviour suggests that larvae transport by animals may have an important role in weevil colonization and recruitment.

By analyzing the fruit characteritics of the living palm species (Arecaceae) (Uhl & Dransfield, 1987), some of their potential seed dispersers around the World (van der Pijl, 1982) and the known species of beetles that feed on palm nuts, we predict the discovery of many more of «evolutionary triads». Other plant families, such as Fagaceae (e.g. *Quercus* spp.-Curculionidae-Corvidae complexes) could also participate in these triads.

The Curculionidae are one of the largest families of Coleoptera. Only the tribe Madarini contains about 85 genera and 500 living species (Pakaluk, 1994) and little is known about their host associations and life histories.

Seed-hoarding animals, such as jays and squirels may behave both as seed predators and as seed dispersers. They feed on weevil larvae living inside acorns (weevil predators) (Johnson et al., 1993; Steele et al., 1996; Hubbard & McPherson, 1997). Nevertheless, weevil-infested acorns can also be dispersed and stored (Johnson et al., 1993; Steele et al., 1996). This is the case when several of the seeds stored by the animal are not recovered, because of food-abundance conditions or the premature death of the seed hoarder. Thus, some species of a given triad (de-

pending on the ecological condition of food abundance or predation) can participate more as a plant deparasiters and others more as a weevil disperser. These «crossings» in seed-dispersal-predation mechanisms and weevil-dispersal-predation mechanisms illustrate the complexity of mutualisms and «evolutionary triads».

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