THE RELATIVE CONTRIBUTION OF BIRDS AND ANTS TO SEED DISPERSAL IN DIPLOCHOROUS PLANTS: A TEST IN THE BRAZILIAN CERRADO

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INTRODUCTION

Since most plants are dependent on seeds for regeneration, seed dispersal is one of the main processes influencing plant population ecology because the location where seeds land produces a template for the process occurring latter in the life cycle of a plant, including the spatial patterns of seedling distribution and plant recruitment (Wang & Smith 2002). Since most plants rely on animals for seed dispersal, an evaluation of how frugivores influence this process may enhance our understanding of plant recruitment and population dynamics.

The fruit crop size hypothesis states that plants producing large fruit crops have a higher chance to attract frugivores increasing their seed dispersal success compared to plants with smaller fruit crops (Christianini & Oliveira *in press*, and references therein). However, large fruit crops may also increased the waste of fruits that are dropped under the plant crown by bad seed dispersers, or that fall naturally if not removed from plant canopy by frugivores. Plant recruitment is unlikely in the vicinity of the parent plant due to density - dependent mortality factors (see Harms *et al.,* 2000). Thus, a non - standard vector of dispersal may markedly increase plant fitness if it "rescues" such wasted seeds away from beneath the parent plant. Nevertheless, such strategies of seed dispersal and their consequences have been largely neglected. The remarkable abundance of ants in soil makes them the most likely animals to interact with those fallen seeds, and maybe provide to the seeds another chance of successful dispersal and establishment. In this study we compared the effectiveness of seed dispersal by vectors acting in the plant crown (birds) and on the ground (ants) for the regeneration of the tree *Xylopia aromatica* (Lam.) Mart. (Annonaceae) in the Brazilian savanna known as "cerrado".

OBJECTIVES

We addressed the following questions: (i) Does the crop - size hypothesis account for among - plant variation in the quantity of fruit removed by birds away from plant crown? (ii) What is the spatial scale of seed delivery by bird and ant seed dispersal? (iii) What is the contribution of each dispersal vector for plant regeneration?

MATERIAL AND METHODS

Seed production and seed fate
Field work was carried out from February 2004 to March 2006 in the reserve of the Estação Experimental de Itirapina (22º12'S, 47º51'W), a 200 ha fragment of cerrado in Southeast Brazil. Trees of *Xylopia aromatica* (hereafter referred to by genus only) reach a density of 300 ind./ha in the study site. Fruiting season is concentrated from March to July, when multiple fruits (divided in follicles) open to expose ca. 60 arillate seeds per fruit. Each seed is coated by an aril that covers a quarter of the seed, forming the diaspore (i.e. the unit of dispersal). Each diaspore is a small, 0.6 cm arillate seed that weights 0.06 g fresh mass (n = 30). Frugivorous birds are attracted by the contrasting display of the bluish diaspores against the reddish inner portion of the opened follicle. Plant reproduction is totally dependent on seeds, which remain viable for up to 2 months after dispersal.
To examine diaspore production and fate we placed 3 - 10 fruit traps under the crown of nine trees of *Xylopia* isolated from other reproductive conspecifics. Traps consisted of 0.14 m^2 plastic trays lined with 0.2 - mm nylon mesh kept 20 cm above ground by four stakes, each coated by a sticky resin (Tanglefoot®) to constrain ant access to the fallen diaspores. Traps collected fallen follicles, as well as diaspores dropped by birds. We checked out the traps regularly throughout the fruiting season. Di-

aspores were then counted and classified as: (1) ripe, (2) unripe or aborted seeds, (3) preyed on before dispersal, or (4) diaspores dropped by primary dispersers (seeds regurgitated/dropped by birds, or embedded in faeces). By the end of the fruiting season (when all follicles fall to the ground), we estimated crop size by counting the number of follicles that reached fruit traps under trees. Unless diaspores are removed by birds, they do not detach naturally from follicles. Once removed, each diaspore leaves a scar in the inner wall of the follicle. Thus the follicles on the ground allowed us to estimate the number of diaspores produced and the amount removed by birds. We estimated the number of diaspores removed by birds from the plant crown of each tree by subtracting the sum of categories 1 to 4 sampled in traps by the estimated crop size. To investigate the relationship between crop size and diaspore removal or waste we applied linear regressions.

Seed removal from plant canopy and ant attendance to fallen fruits

Information about diaspore removal by birds, diaspore waste (i.e. dropped under the parent plant) and bird behavior were obtained by focal observations of 16 fruiting trees, totaling 110 tree/observation hours. Distances of seed dispersal by birds were estimated by records of post feeding flight distances of birds departing from focal trees until the first landing perch.

To determine which ants interact with fallen diaspores of *Xylopia*, we recorded all ant - diaspore interactions observed on diaspores placed by us at 30 ground stations (10 m apart from each other), 1 - 2 m off two transects that crossed the study site. Diaspores were set at 08:00 and 18:00 h and checked through regular intervals during the fruiting seasons. We recorded the ant species attracted, and their behavior toward diaspores. We followed ants carrying diaspores until they entered their nests. The distance of displacement was then measured. Ant voucher specimens are deposited in the collection of the Universidade Federal Rural do Rio de Janeiro (CECL).

To evaluate the fate of diaspores we measured diaspore removal rates beneath the crown of 30 focal trees over two fruiting seasons (2004 and 2005). The relative contribution of ants and vertebrates to diaspore removal was assessed by means of an exclosure experiment. Vertebrates were excluded from diaspores by a wire cage (17 x 17 x 8 cm), fenced on the top and sides with mesh (1.5 cm) and staked to the ground. Diaspores used in the exclosure experiments were marked with a small dot of enamel paint (Testors, Rockford, USA) to distinguish them from other fallen diaspores. Pairs of diaspores (arillate seeds) of *Xylopia* were set out at about 08:00 h at five stations placed beneath fruiting trees. Each pair consisted of a diaspore placed on the floor under a wire cage, and an exposed diaspore (control) placed outside the cage, 15 cm away. After 24 h we recorded the number of diaspores missing. To evaluate if removal rates on the floor were driven by seed predators we performed removal trials using cleaned seeds (i.e. aril manually removed from diaspores by us) a few weeks later. Data on seed removal (square root transformed) were analyzed using factorial analysis of variance.

Seedling distribution and performance

To evaluate if ants may affect the fate and spatial distribution of seedlings we compared the number of seedlings of *Xylopia* growing on plots (0.5 x 0.5 m) established in ant nests and in paired controls established at 2 m in a random direction. Seedlings of *Xylopia* inside nest and control plots were individually marked with numbered flags and monitored for survival during one year.

RESULTS AND DISCUSSION

We observed 8 species of birds feeding on diaspores of *Xylopia*. Several birds acted as legitimate dispersers by ingesting the whole diaspore, and afterwards defecating or regurgitating intact seeds (e.g. *Elaenia flavogaster*). Nevertheless many diaspores were dropped beneath the parent plant by birds that act as aril consumers, and provide no dispersal away from parent plants (e.g. *Nemosia pileata*). We observed that birds dropped 28% of the diaspores they manipulated in the canopy, and many of which fell with the aril still attached.

The fruit crop size hypothesis was rejected for *Xylopia*. We found no relationship between fruit crop size and diaspore removal by birds beyond the plant canopy border (p=0.18), neither between seed production and the proportion of crop removed away (p=0.90). However, absolute dispersal failure (the number of diaspores that fall under parent plants) increased linearly with crop size (slope=0.95, R^2=0.88, p=0.001). The relative dispersal failure (the proportion of the diaspore crop that falls beneath parents) was independent of crop size for Xylopia. Thus, a higher number of mature diaspores reached the ground beneath rather than away from parent trees as crop size increased in *Xylopia*. Indeed, a great proportion of plant crops usually fall under parent plants, irrespective of dispersal mode (e.g. Clark *et al.,* 2005).

A high proportion of the seed crop of *Xylopia* was wasted under parent trees as ripe diaspores or as diaspores dropped by birds, comprising together 26% and 43% of the total seed crop in 2004 and 2005 fruiting seasons, respectively. More than a third of the seed crop was usually lost as immature seeds. Pre - dispersal seed predation accounted for the loss of 6% of plant crops. Birds removed up to 56% of seed crop from the plants. Thus many viable seeds were available under parent trees at each fruiting season. Ants may compensate such waste by removing away the majority of *Xylopia* diaspores found under parent plants within 24 hs. A rich ant fauna (30 species in 15 genera) was attracted to fallen diaspores. Small myrmicine ants like *Pheidole* spp. and *Wasmannia auropunctata* accounted for most records at diaspores (70%), whereas large ponerines (*Pachycondyla*, *Odontomachus* and *Dinoponera*) comprised 10% of the interactions seen. Most fallen diaspores of *Xylopia* were removed within 24 hs (82%). The exclusion treatment had no effect on removal over two fruiting seasons (ant removal=4.1 ±1.3 diaspores; vertebrate removal=4.4 ±1.1 diaspores; p=0.23), indicating that ants are the main source of diaspore removal on the ground. Aril covered seeds were much more removed than cleaned seeds (p <0.001). Plant location (block effect) influenced diaspore removal (p <0.001), but there was no effect of fruiting season (2004 -

2005) (p=0.86). Based on these data we suggest that ants can be quantitatively as important as birds for seed dispersal in *Xylopia*. For instance, take the 2004 fruiting season. If removal rates by ants of diaspores fallen under parents (mean of 4.1 diaspores/exclusion treatment, or 83%) are balanced against the amount of mature diaspores that fall under parents (mean of 26% of total plant crop size), it is possible to realize that ants may affect the fate of 22% of total plant crop. For comparison, birds affected the fate of 32% of total plant crop of *Xylopia* in the same year. Using the same approach for the 2005 fruiting season, we find that ants switched the main role of seed dispersal with birds, influencing the fate of 34% of total crop size against 15% of birds. Thus, the trend found for *Xylopia* suggests that, at least for some years and/or trees, ants can have a relevant contribution to the quantitative component of disperser effectiveness as birds. Ants may have a relevant role as seed rescuers in other plant - frugivore systems as well, especially for plants producing small - and lipid - rich fleshy diaspores that are frequently harvested by ants (Passos & Oliveira 2002, Christianini *et al.,* 2007).

The first landing perch of birds after consumption of *Xylopia* diaspores was 16 ± 12 m (N=16). Ants, on the other hand, displaced fallen diaspores to much shorter distances (0.8 ± 0.9 m, N=40, mean $\pm$ SD). The dispersal kernel of *Xylopia* suggests that the action of two vectors of dispersal may increase the chance of seed transport farther away from the parent plant, and also produce a larger variance in seed rain across distances compared to plants that rely only on birds as seed dispersers. Because birds frequently carry seeds to distances over 40 m they are more effective in removing seeds from the predation - prone zone near the parent tree and in delivering seeds to new sites for plant colonization and recruitment, with possible consequences for plant metapopulation dynamics (Jordano *et al.,* 2007). On the other hand, seed rescuing by ants decrease seed density beneath parent plants and bring seeds close to ant nests. This would produce a distribution of recruits likely to match the spatial distribution of adult plants due to relatively short distances of seed dispersal by ants. Thus birds and ants switch roles as a function of spatial scale and provide complementary seed dispersal to *Xylopia* and possibly to other fleshy - fruited trees in the cerrado.

Seedlings of *Xylopia* were found in small numbers, but only close to the refuse piles of ant nests. Sampled ant nests (N = 81) had a mean of 0.1 ± 0.3 (range 0 - 2) seedlings against zero seedlings recorded in paired control plots (Wilcoxon paired - sample sign rank tests: Z=2.2; p=0.028). Seedling survival after one year was nearly 60%. The fact that *Xylopia* seedlings were only found in refuse piles of ant nests suggests that seed - rescuing ants may act as fine - tuned directed dispersers following long distance dispersal by birds (see Passos & Oliveira 2002). Although a fraction of the seed crop is probably lost to granivorous ants such as *Pheidole*, our data show that ants do have a relevant contribution

to plant regeneration. Ant nests in poor soils are usually nutrient enriched sites that increase seedling growth and survival (reviewed by Rico - Gray & Oliveira 2007). Thus, the action of two vectors of dispersal should increase the chance of a seed hitting a safe site in patchy environments such as savannas.

CONCLUSION

We rejected the fruit crop size hypothesis for *Xylopia*. On the contrary, we found a positive relationship between crop size and seed waste under parent plants. Such large amount of fallen seeds under parent plants is quickly harvested by ants that rearrange the seed shadow to short distances. Birds, on the other hand, removed seeds from plant canopy and deliver them to much longer distances. Thus, birds and ants provide spatially complementary seed dispersal in the cerrado. Furthermore, we found that ants may be as important as birds for seed dispersal in *Xylopia*, at least for some individual plants and/or years.

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