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Living in the Land of Ghosts: Fruit Traits and the Importance of Large Mammals as Seed Dispersers in the Pantanal, Brazil

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Introduction

Seed dispersers play a key role in the ecology and evolution of fleshy-fruited plants; especially in tropical forests where from 70% to 90% of all woody species are dispersed by vertebrates (Fleming *et al.*, 1987; Jordano, 2000). Local plant communities with a range of fruit types are assembled under a variety of selection pressures and historical effects. Analyses of community-level variation in fruit traits indicate that they also reflect variations in the composition of the main seed dispersers in the animal community (Mack, 1993; Fleming *et al.*, 1987; Fleming, 1991, 2005). Fruit size is one of the main traits selected by frugivorous vertebrates and has multiple potential influences on seed mass, and therefore on germination and seedling survival (Jordano, 1995). Not unexpectedly, large-scale, community-wide comparisons of fruit traits have reported variation in traits related to fruit size paralleling changes in the frugivore community (see Fleming *et al.*, 1987; Jordano, 2000; Herrera, 2002, and references therein).

At a community level, the interactions among plants and frugivores often show high diversity and low specificity (Jordano *et al.*, 2003; Silva *et al.*, Chapter 26, this volume; Forget *et al.*, Chapter 1, this volume). In this context, large-scale comparisons between areas with different faunal assemblages have been widely used to investigate local co-adaptations between plants and frugivores (Snow, 1980; Fischer and Chapman, 1993; Voigt *et al.*, 2004) and are a powerful tool in analyses of ecological convergence at the community level (Schluter, 1988; Corlett and Primack, 2006). However, comparative analyses based on extant communities implicitly ignore the fact that these mutualisms build up on highly

generalized interactions, where evolutionary change and substitution of the mutualistic partners can occur.

For example, Mack (1993) proposed that the evolution of large fruits and seeds in the Neotropics has been constrained, relative to palaeotropical communities, by a scarcity of large-bodied frugivores. In a different view, Janzen and Martin (1982) proposed that frugivory by large extinct mammals such as native horses, gomphotheres, ground sloths and other extinct megafauna offers an explanation for the dispersal-related reproductive traits of Central American lowland plants. The so-called megafauna syndrome (related to large-bodied mammals >44 kg) has been the subject of considerable debate. However, the debate suffers from a lack of specific predictions and precise definitions (Howe, 1985; Hunter, 1989; Owen-Smith, 1989; Lord *et al.*, 2002). Comparative biogeographical studies have concluded that large frugivores did not shape the fruit traits of plant communities (Fischer and Chapman, 1993), while other studies have reported a strong relationship between fruit traits and the local fauna (Herrera, 2002; Bollen *et al.*, 2004; Voigt *et al.*, 2004).

In the Palaeotropics, many large-bodied mammals are a major component of the frugivore communities, while the neotropical ecosystems characteristically lack large frugivores. The largest frugivore in the Neotropics is the 300 kg tapir, *Tapirus terrestris* (Tapiridae), while in the Palaeotropics, elephants can weigh at least ten times more (Owen-Smith, 1988). However, hypotheses of co-evolution between fruits and frugivores need to account for both extant and past mutualists. Less than 10,000 years BP, South America was a land of large-bodied mammals (>44 kg), which experienced relatively recent extinction after millions of years of persistence (Martin and Klein, 1984; Owen-Smith, 1988, 1989). Megafauna taxa include primarily large terrestrial mammals (e.g. large carnivores, xenarthrans, rodents and extinct orders of ungulates), many of them considered mixed grazer-browsers and frugivores (Fariña, 1996). Only 13 mammal genera survive in contemporary neotropical communities, out of 60 whose species had >44 kg body mass that were present in the Pleistocene fauna. The South American fauna had at least seven genera that included species with body masses $\geq 1,000$ kg, yet none are present now. African faunas, in contrast, have 40 extant genera with >44 kg body mass, including herbivorous and omnivorous species (Martin and Klein, 1984). Five genera $\geq 1,000$ kg are still living in Africa and two genera in Asia (Owen-Smith, 1988).

The recent extinction of a large component of the potential frugivore community undoubtedly has a lasting signal in extant plant–frugivore interactions (Janzen and Martin, 1982), yet we still know very little about its consequences. In fact, it is vital to understand the role of the extinct megafauna on plant–animal relationships because of the ongoing defaunation throughout tropical ecosystems (Fa *et al.*, 2002).

The Pantanal, located in central Brazil and part of Bolivia and Paraguay, is the world's largest freshwater wetland, with 140,000 km² of lowland floodplain of the upper Rio Paraguai basin (Swarts, 2000). This area is subjected to seasonal flooding, creating a diverse mosaic of habitats

resulting in an extraordinarily rich terrestrial and aquatic biota (Silva *et al.*, 2000). The Pantanal has a high biomass of large-bodied mammals, such as tapirs (*T. terrestris*) and peccaries (*Tayassu pecari* and *Pecari tajacu*; Tayassuidae), and frugivorous birds such as piping-guans, *Pipile cujubi* (Cracidae) and toucans, *Ramphastos toco* (Ramphastidae; Harris *et al.*, 2005). Other conspicuous fauna in the area are cows, *Bos taurus* (Bovidae), feral pigs, *Sus scrofa* (Suidae) and horses, *Equus caballus* (Equidae). Large frugivores are vanishing from most areas in the world, due to selective hunting or fragmentation (Peres, 2000, 2001), but are still abundant in the Pantanal (Lourival, 1997; Trolle, 2003; Harris *et al.*, 2005), mainly due to the low human population density and low hunting pressure (Alho and Lacher, 1991; but see Harris *et al.*, 2005). Therefore, the Pantanal holds the highest concentration of wildlife in South America (Swarts, 2000; Mittermeier *et al.*, 2005) and represents an excellent opportunity to study plant–animal interactions in a pristine habitat.

In this study we present the characteristics of fleshy-fruited plants in the Pantanal and describe the contributions of different animal guilds to seed dispersal. We go on to compare fruit traits in the Pantanal with those in the Atlantic rain forest (Brazil), in a mosaic of forest and savanna in Africa (Ivory Coast), and in an African wetland (Okavango, Botswana), to test similarities in fruit size, colour and shape. Given that open savannas hold a large diversity and biomass of large-bodied herbivores which can supplement their diet with fruits (Owen-Smith, 1988; Fariña, 1996; Cristoffer and Peres, 2003), we predict that plant communities in the Pantanal should exhibit a distribution of fruit traits across species that is similar to those found in savannas and savanna-like habitats where megafauna still exist, such as Ivory Coast and Okavango. We expect a different distribution of fruit traits in the Atlantic rain forest, due to the low biomass of large mammals in forest ecosystems compared with the savannas and savanna-like habitats (e.g. Prins and Reitsema, 1989). A comparative test of this hypothesis will help in understanding the historical process of co-evolution with the Pleistocene megafauna and will supplement historical approximations based solely on the study of extant interactions. We also discuss some potential ecological mechanisms that contribute to plant population persistence after the extinction of major seed dispersers, and we argue, based on numerical simulations, that for some long-lived plants there is a possibility that minimal recruitment events allow populations to persist.

Methods

Pantanal fruits and frugivores

Study site

Fazenda Rio Negro is a 7,500 ha private area in the Nhecolândia region in the Brazilian Pantanal. Average annual rainfall is 1,192.5 mm and mean monthly temperature is 26°C, ranging from 19°C to 33°C ($n = 4$ years;

D. Eaton, unpublished results). The main vegetation types of the Pantanal include gallery forests, cerrado and semideciduous forests (Prance and Schaller, 1982); all are represented at Fazenda Rio Negro (Silva *et al.*, 2000), where the study was conducted.

Traits of the Pantanal fleshy fruits

We recorded colour, smell and size for 5–40 fruits of each vertebrate-dispersed, fleshy-fruited species on a monthly basis ($n = 30$). Length was measured from the peduncle insertion to the most distal part, and width as the maximum diameter at 90° to length, using digital callipers to the nearest 0.1 mm. Mass was measured with digital scales to the nearest 0.1 g. Colour of ripe fruits was recorded according to human vision. Fruits were collected from different individuals among a sample of 620 marked trees, depending on availability, or from randomly sampled individuals in the field.

For each of the species measured, we recorded life-form, and assigned a rank value of smell intensity of the fruits that varied from 0 (without smell) to 2 (very strong, sweet smell), referring to human sensitivity. We used logistic regression to relate fruit smell to both fruit length and width. We also recorded the ability of all measured species for resprouting after disturbance (e.g. fire or logging), human use (according to Pott and Pott, 1994) and the persistence of ripe fruit.

Fruit–frugivore interactions in the Pantanal

Observations of frugivore foraging behaviour were carried out using four techniques.

- *First*, we conducted focal observations of individual fruiting shrubs and trees (Galetti *et al.*, 2002). To detect frugivore activity at selected fruiting plants, those bearing ripe fruits were observed over periods of 4 h, mainly from 06:00 to 10:00 hours. Fruit handling behaviour of animals visiting the trees (i.e. whether they eat the whole fruit, only the seeds, or spit them out) were recorded to classify species as legitimate seed dispersers, fruit-pulp consumers, and/or seed predators (Moermond and Denslow, 1985; Levey, 1987; Jordano and Schupp, 2000).
- *Second*, we monitored frugivore visits to fruiting plants using camera traps in order to record terrestrial and nocturnal consumers of fruits. Camera traps were placed beneath four individuals of each species of plant, focusing on fallen fruits (Miura *et al.*, 1997; Galetti, 2002).
- *Third*, we collected gut contents (fish only – *Piaractus mesopotamicus*, Serrasalminidae) and scats of frugivorous animals (rheas, *Rhea americana*, Rheidae; tapirs, *T. terrestris*; feral pigs, *S. scrofa*; and white-lipped peccaries, *T. pecari*) and the seeds recovered from them were identified to species based on a reference collection.
- *Finally*, we also included personal observations of some fruit–animal interactions.

We combined these data into a plant–frugivore interactions database. We then examined the pattern of interaction between Pantanal fruits and frugivores by means of a canonical correspondence analysis on the matrix of family \times frugivore type frequencies. Plant and fruit voucher specimens for this data have been deposited in the EMBRAPA Herbarium in Corumbá, MS, and at Universidade Estadual Paulista (UNESP) at Herbarium Rio Clarence, SP, Brazil.

Megafauna fruit traits and intercontinental patterns

We compared the data set of fruit morphology of the Pantanal with three other plant communities, including one site in the Atlantic rain forest of Brazil (Galetti, 1996; Campassi, 2006; M. Galetti, M.A. Pizo, L.P. Morellato and P. Jordano, unpublished results;) and two in Africa: Ivory Coast and Okavango Delta. The Atlantic rain forest does not have a recent history of occupation by large mammals, as we found in savanna and savanna-like habitats in Okavango, Ivory Coast and Pantanal.

Intervales State Park is 49,000 ha of Atlantic rain forest along the south-east coast of Brazil. The average annual rainfall is 4,000 mm and the average temperature varies from 21.1°C to 26.8°C. Tropical rain forest dominates the area, including both lowland and highland vegetation (Galetti, 1996).

Camoé National Park is located in the north-eastern part of the Ivory Coast and is 1,150,000 ha in area (Hovestadt *et al.*, 1999). Long-term mean annual rainfall varies from 800 to 1,100 mm. The annual mean temperature is 26.5–27°C (Hovestadt *et al.*, 1999). The main vegetation types include a mosaic of shrubby savanna, forest islands and gallery forests along the main rivers.

Okavango Delta in north-western Botswana is a flooded habitat similar to the Pantanal and includes a similar range of habitat types. The area of the wetland is in excess of 1,200,000 ha (McCarthy *et al.*, 1998).

In addition to the data on fruit morphology presented here for the Pantanal, extensive data sets of fruit traits and plant–frugivore interactions are available for the Atlantic rain forest (Galetti, 1996; $n = 138$) and both African sites: data on fruit morphology from Ivory Coast was based on T. Hovestadt *et al.* (unpublished data, $n = 128$) and from Okavango on fruit guides (van Wyk, 1997; Thomas and Grant, 2002; $n = 44$). We used restricted paired comparisons of fruit length, fruit width and fruit colour between confamilial taxa to contrast fruit traits in different communities. Average within-family values for these variables were obtained for each community. Trends were examined by comparing each family-level value across communities. The consistency of a given trend, for example whether fruit diameter is larger for Pantanal vs Atlantic rain forest, was tested at the within-family level. The number of within-family contrasts showing a trend (e.g. increase in fruit size) was tallied and compared with a binomial expectation. The significance of a hypothesized trend was tested by a binomial test on the proportion of paired comparisons that are

consistent with the hypothesis when compared with a random expectation of 50% of the within-family trends in each direction. Family-level contrasts control phylogenetic effects when comparing species samples and account for the different representation of genera (see Mack, 1993; Jordano, 1995; Forget *et al.*, Chapter 1, this volume).

Numerical simulations and the persistence of megafauna-dependent plants

Dispersal failure is certainly one of the main potential causes for the decline of plant populations (Cordeiro and Howe, 2001; McConkey and Drake, 2002; Traveset and Riera, 2005; Galetti *et al.*, 2006). Therefore, the long-term persistence of plant populations that produce large, high-cost fruits without efficient seed dispersal remains paradoxical. In this chapter we examine some alternative mechanisms that may allow megafauna-dependent plant populations to persist in the absence of major seed dispersers. However, a more basic question is: How efficient does seed dispersal have to be for a plant species to persist in ecological time?

Simulations were undertaken using BANGU 1.0[®] (developed by P.R. Guimarães Jr and P.R. Guimarães), an individual-based, spatially-explicit model (see Durrett and Levin, 1994) that simulates individuals of a single species of plant as points occurring over a regular lattice. At each time-step, all plants reproduce (i.e. generate new individuals) following user-defined probabilities for short-distance dispersal events leading to recruitment. Short-distance recruitment was simulated assuming Moore nearest neighbourhoods (Durrett and Levin, 1994); that is, each plant may colonize the eight nearest cells. Individual plants die after a set number of time-steps, opening the possibility for the cell to be colonized by other plants. We analysed how lifespan and short-distance recruitment affect plant population persistence, described by the time until the population becomes extinct. Simulations were performed assuming lattice size = 9.0×10^4 cells, initial plant population = 1000, default lifespan = 100 reproductive events, and default probability of short-distance recruitment = 0.1% per nearest cell.

Results

Traits of the Pantanal fleshy fruits

Approximately 74% of the 620 plants observed in the phenological study produce fleshy vertebrate-dispersed fruits (C.I. Donatti, 2005, unpublished results). We collected information on fruit morphology of 75 fleshy-fruited species found in a 4-year intensive study on fruit–frugivore interactions (Appendix 3). Growth forms included 54 species of tree (72%), nine shrubs (12%), six palms (8.0%), two lianas (2.7%), one bromeliad (1.3%), one cactus (1.3%), one herb (1.3%) and one mistletoe (1.3%).

The fleshy fruits of the Pantanal tend to be large (length = 30.54 ± 23.75 mm and width = 23.00 ± 16.60 mm; $n = 75$; mean \pm SD; Fig. 5.1) varying from the small fruits of *Cissus erosa* (Vitaceae; length = 5.1 ± 0.5 mm, width = 5.8 ± 0.6 mm) to the huge fruits of *Attalea speciosa* (Arecaceae; length = 87.7 ± 7.8 mm, width = 50.7 ± 4.1 mm). The shape of the fruits varies with fruit size: fruits tend to be more elongated with increasing size (Log fruit width (mm) = $0.3228 + 0.8176$ Log fruit length (mm); $r^2 = 0.7623$, $n = 75$; i.e. with slope < 1.0). Most species in the Pantanal produce dull-coloured fruits, among which the colour is predominantly green (in 20% of species), yellow (16%) or brown (14.6%; see Fig. 5.2).

According to human sensitivity, 32% of the 75 species of plant have a strong sweet smell, 16% have a weak smell, and 52% are odourless. There was a significant relationship between smell and both fruit length (logistic regression, $r^2 = 0.22$, $\chi^2 = 33.23$, $P < 0.0001$) and width ($r^2 = 0.23$,

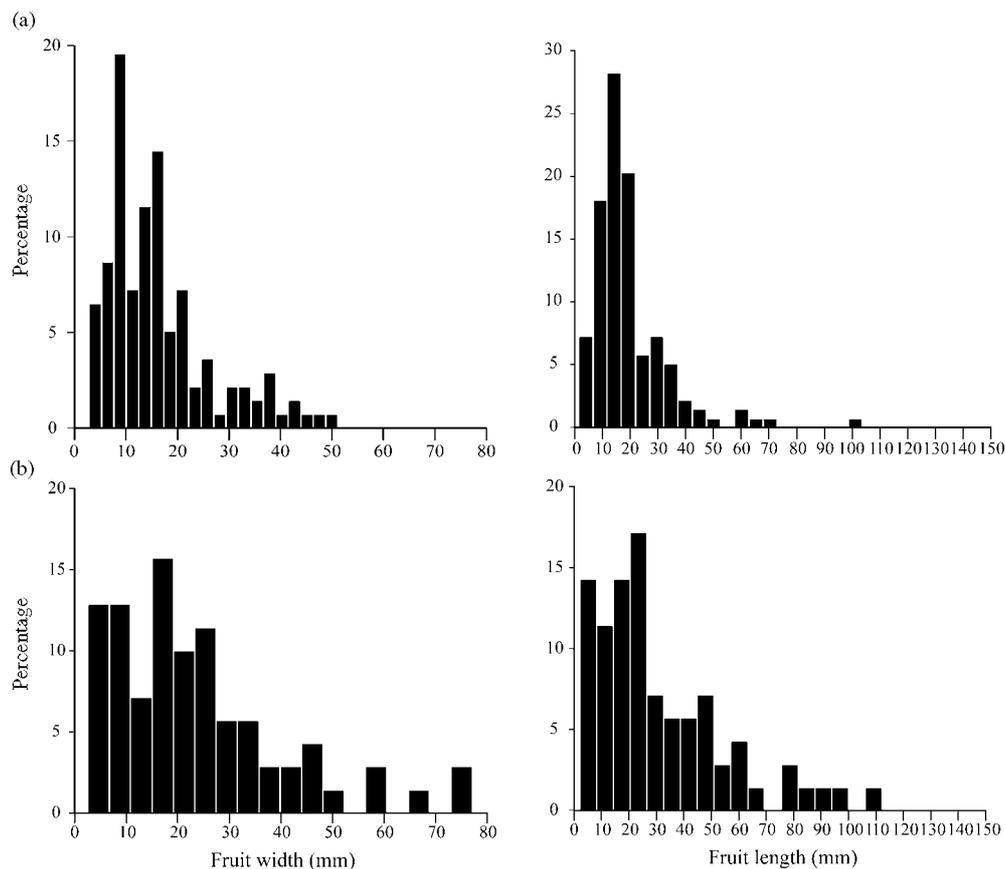


Fig. 5.1. Frequency distributions of fruit width and fruit length (mm) for species in local sites in the Pantanal (a: Fazenda Rio Negro) and the Atlantic rain forest (b: Saibadela) plant communities, Brazil.

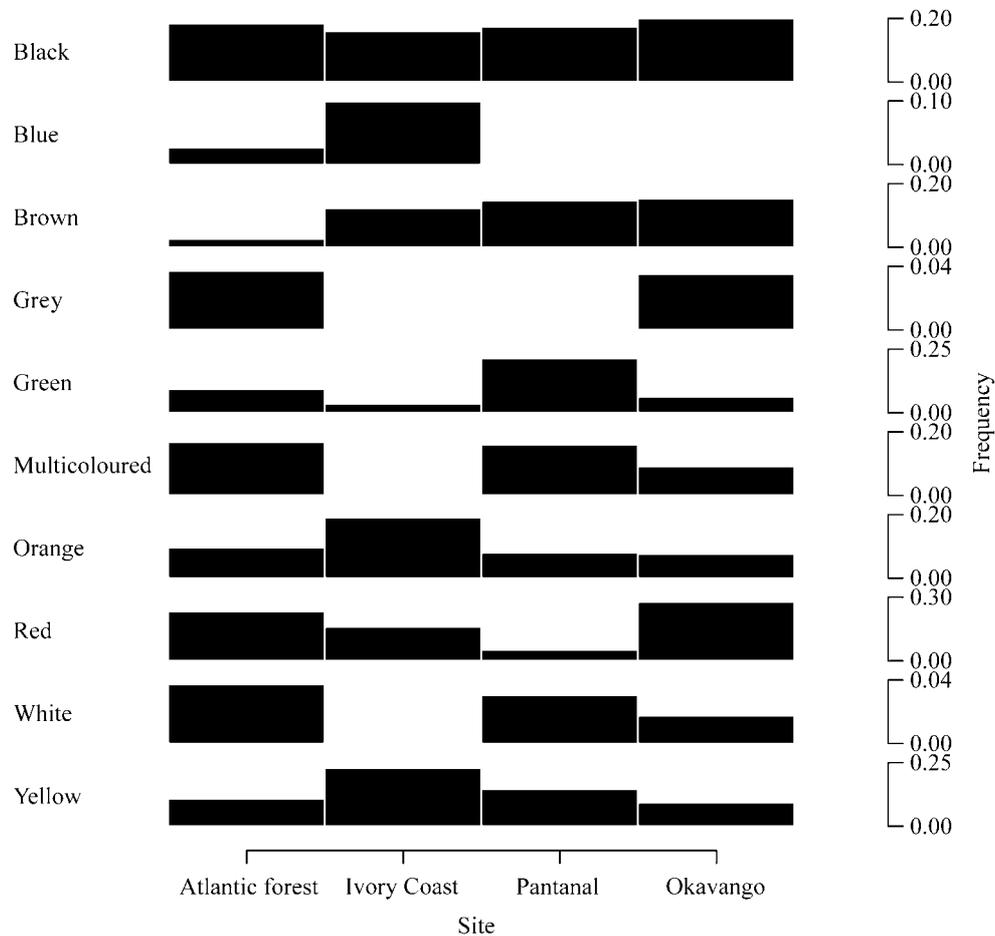


Fig. 5.2. Relative frequencies of fruit colour classes among fleshy-fruited species in the Atlantic rain forest and Pantanal (Brazil) and Ivory Coast and Okavango (Africa). Yellow includes yellow-green, and orange includes yellow-orange.

$\chi^2 = 34.15$, $P < 0.0001$), with larger fruits showing a significant trend to have a strong odour when ripe. Fruits of typical mammal-dispersed species in the Pantanal, such as Sapotaceae and Annonaceae, usually smell stronger than bird-dispersed fruits. Resprouting after fire or clear-cutting was recorded for 32% of these species. Due to their extremely large fruit, some species in the Pantanal lack efficient long-distance seed dispersal (e.g. *Caryocar brasiliense*, Caryocaraceae; *A. speciosa*) and in 6.7% of species the ripe fruits persist on the tree (e.g. *Alibertia sessilis*, *Tocoyena formosa*, Rubiaceae; and *Simarouba versicolor*, Simaroubaceae). Usage by humans (47% of species sampled) varied from fruits used locally from wild trees in the neighbourhood of human settlements (e.g. *Annona* spp.) to regional plantation of species with economic value (e.g. *C. brasiliense*, *A. speciosa*).

Fruit–frugivore interactions in the Pantanal

We observed the fruits of 23 species during 690 h of focal observations in the Pantanal and set up camera traps in 27 fleshy-fruited species during 7040 h. We analysed 196 fish guts (*P. mesopotamicus*), 68 scats from *R. americana*, 45 from *T. pecari*, 136 from *S. scrofa* and 213 from *T. terrestris*.

Our observations of non-predatory plant–frugivore interactions indicate that mammals are responsible for the dispersal of 56% of all fleshy-fruited species, while birds disperse 48% and both share 21% of the fruits in the Pantanal. Fish and reptiles disperse 18.6% of the species, but none exclusively (see Appendix 3). This contrasts with other plant communities. In the Atlantic rain forest of Brazil, for instance, 59% of the fleshy-fruited species are dispersed by birds, 28% by mammals and 12% by both groups (Galetti, 1996). In Ivory Coast, Hovestadt *et al.* (1999) found that birds disperse 42% of the fruits and mammals disperse 41%. We do not have information on the seed dispersal syndromes for plants in Okavango.

Colour combinations differed significantly among major disperser categories ($\chi^2 = 96.64$, $df = 7$, $P = 0.02$). Bicoloured, black, and white displays were over-represented in bird- and bird+fish-dispersed species; dull colours (brown and green) were over-represented among species dispersed by mammals in combination with other groups, while yellow was over-represented in fruits consumed by mammals+tortoise (*Geochelone carbonaria*, Testudinidae). Fish, in combination with other frugivore taxa, consumed a variety of colours and showed no specific association with a colour type.

Our data indicate that feral pigs dispersed not only large-sized fruits (e.g. *A. phalerata*: fruit length = 62.7 ± 3.7 mm and fruit width = 34.9 ± 2.9 mm), but also more species than the native fauna: feral pig scats contained 15 species, compared with 11 in tapirs (the largest fruit species dispersed by both was *Dipterix alata*, Fabaceae: fruit length = 48.8 ± 3.6 mm and fruit width = 39.9 ± 2.4 mm), seven in *R. americana* and five in *T. pecari* (the largest fruit species dispersed by both was *Bactris glaucescens*, Arecaceae: fruit length = 18.8 ± 3.7 mm and fruit width = 17.7 ± 1.5 mm). Among the native animals, only the tapir dispersed *A. phalerata* and *D. alata* seeds, species that were also dispersed by feral pigs. In addition, humans used the fruits of 47% of all species of plants that we sampled in the Pantanal, mainly for consumption.

Megafauna fruit traits and intercontinental patterns

The frequency distributions of fruit length and width differed significantly among the four areas ($F_{(3, 363)} = 10.79$, $P < 0.0001$ and $F_{(3, 371)} = 7.06$, $P < 0.01$, respectively). Pantanal, Okavango and Ivory Coast had more species with fruits >20 mm than the Atlantic rain forest. Species with fruit width >55 mm were not represented in the Atlantic rain forest (Fig. 5.3). The

Pantanal showed a frequency distribution of fruit widths much closer to the African sites but still lacked some species with fruits >100 mm wide, which comprise approximately 8% of the species in the African sites (Fig. 5.3).

Controlling for the phylogenetic effects at family level, the average size of fruits in the Pantanal was bigger (length = 30.54 ± 23.75 mm and width = 23.00 ± 16.60 mm; $n = 74$) than the Atlantic rain forest (length = 19.51 ± 13.99 mm and width = 16.34 ± 10.05 mm; $n = 138$; binomial test [one-tailed] for 24 within-family contrasts, $P < 0.001$; see Fig. 5.4). Nineteen families have larger mean fruit size in the Pantanal (e.g. Annonaceae, Anacardiaceae, Clusiaceae and Ebenaceae), while only five families have larger fruits in the Atlantic rain forest than in the Pantanal (Sapotaceae, Myrtaceae, Moraceae, Meliaceae and Lauraceae). In addition, the magnitude of the differences was greater for families where the Pantanal representatives were larger. In contrast, the mean fruit width in each family for the Pantanal did not differ from either the Ivory Coast or Okavango samples. In 26 family contrasts, 15 families had bigger fruits in Ivory Coast and 11 in the Pantanal ($P = 0.577$ for the binomial test; see Fig. 5.4; Ivory Coast mean fruit length = 20.79 ± 17.33 mm and width = 32.71 ± 57.51 mm; $n = 128$). In 13 contrasts, seven families had bigger fruits in the Pantanal and six in Okavango ($P = 0.538$ for the binomial test; see Fig. 5.4; Okavango mean fruit length = 75.27 ± 154.56 mm and fruit width = 32.51 ± 45.21 mm; $n = 44$).

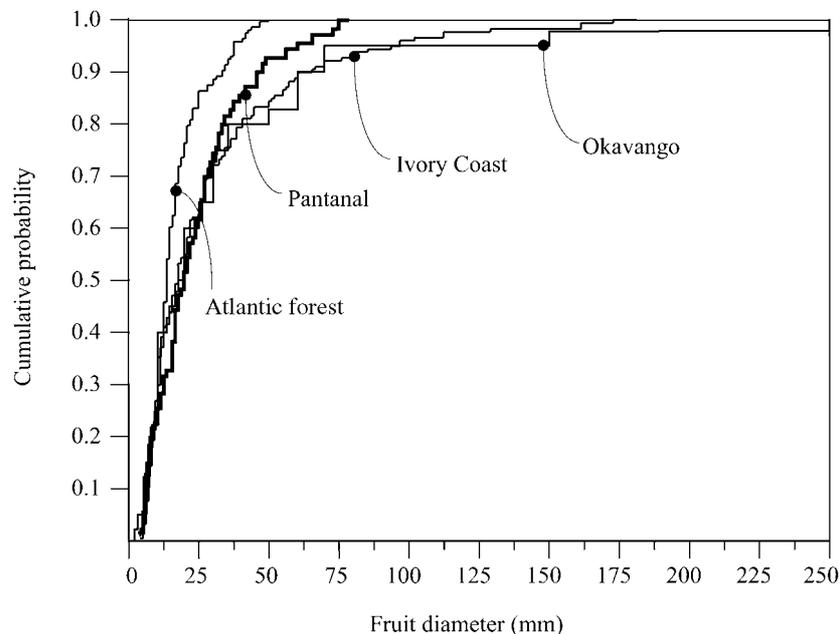


Fig. 5.3. Cumulative frequency distributions of fruit width in different study areas, two African sites (Okavango and Ivory Coast) and two Brazilian sites (Pantanal and Atlantic rain forest).

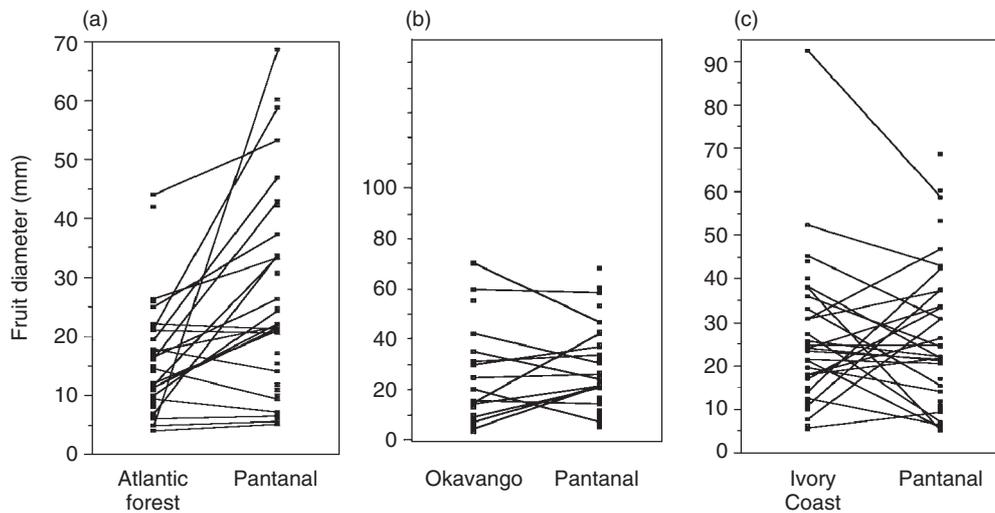


Fig. 5.4. Within-family paired contrasts for fruit width in plant communities around the world: (a) Atlantic rain forest and Pantanal, Brazil; (b) Okavango (Africa) and Pantanal; and (c) Ivory Coast (Africa) and Pantanal. Binomial tests for the comparisons among areas: (a) Atlantic rain forest \times Pantanal, $P < 0.001$; (b) Okavango \times Pantanal, NS; and (c) Ivory Coast \times Pantanal, NS.

The flora of Pantanal has a similar composition of families to both African habitats, especially when considering genera with fruits >20 mm wide and the predominance of species dispersed by mammals. Within the Pantanal, the variation in the composition of frugivore assemblages feeding on plant families was due to changes in the importance of mammals vs birds or fish (first canonical variable; Fig. 5.5) or to changes in the importance of rhesas and mammals vs other frugivores (second canonical variable, Fig. 5.5).

The distribution of fruit colours varied across locations. While all locations had a similar proportion of black fruits; the species of the Pantanal exhibit relatively high proportions of green or brown fruits; those of Atlantic rain forest exhibit high proportions of white, multicoloured or grey fruits; those of Ivory Coast produce high proportions of blue, orange or yellow fruits; and those of the Okavango produce high proportions of brown and red fruits (Fig. 5.2). There is a significant difference in the frequencies of fruit colours between the Atlantic rain forest and Pantanal ($\chi^2 = 28.99$, $P < 0.0001$), between Ivory Coast and Pantanal ($\chi^2 = 27.56$, $P < 0.0001$) but not between Okavango and Pantanal.

Numerical simulations and the persistence of megafauna-dependent plants

Preliminary simulations showed that lattice size and initial plant population do not affect the qualitative behaviour of simulations. In contrast, lifespan and recruitment probability in the vicinity of the plant had a marked affect

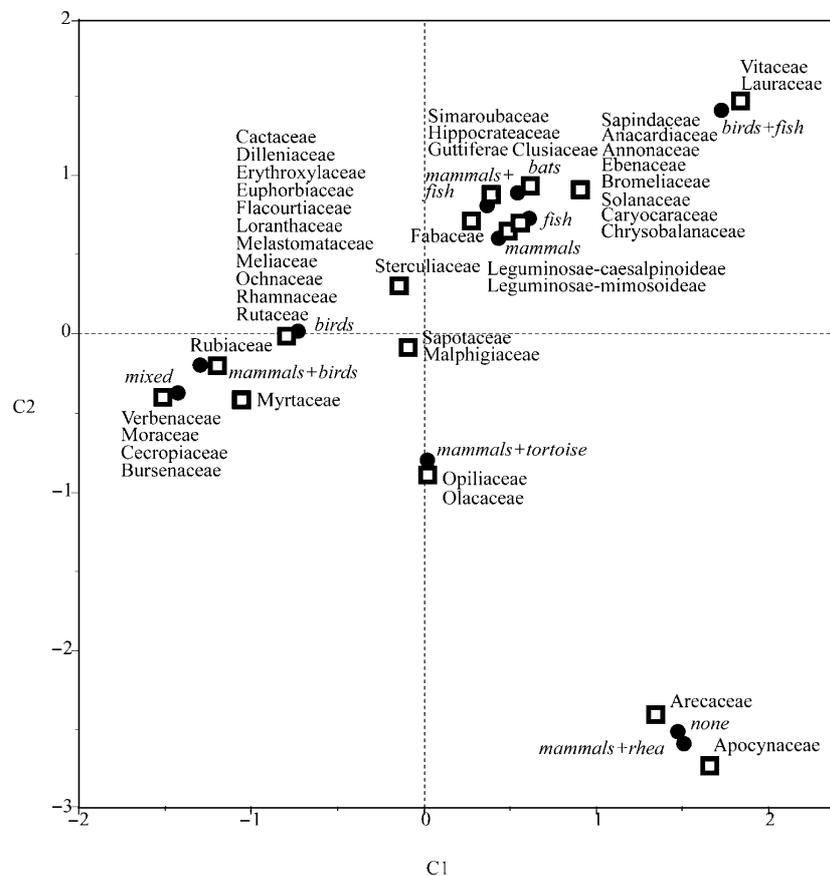


Fig. 5.5. Correspondence analysis of the interaction matrix between species of fruits and frugivores at the family level. The plot of the first two canonical variates groups different plant families (squares) with their major types of seed dispersers (dots). Overlapping family labels have been displaced for clarity.

on population persistence (Fig. 5.6). For short lifespan or small recruitment probabilities the population goes quickly to extinction. However, a very small increase in lifespan or in the probability of recruitment in vicinity of the plant generates a completely new dynamic: plant density increases and eventually stabilizes (Fig. 5.6).

Discussion

Many of the fruits present in the Pantanal fit the classical mammal dispersal syndrome, involving large, green or brown, often sweet-smelling fruits (Janson, 1983; Gautier-Hion *et al.*, 1985; Howe, 1986; Herrera, 1989). The high percentage of mammal-dispersed fruits was also supported by our

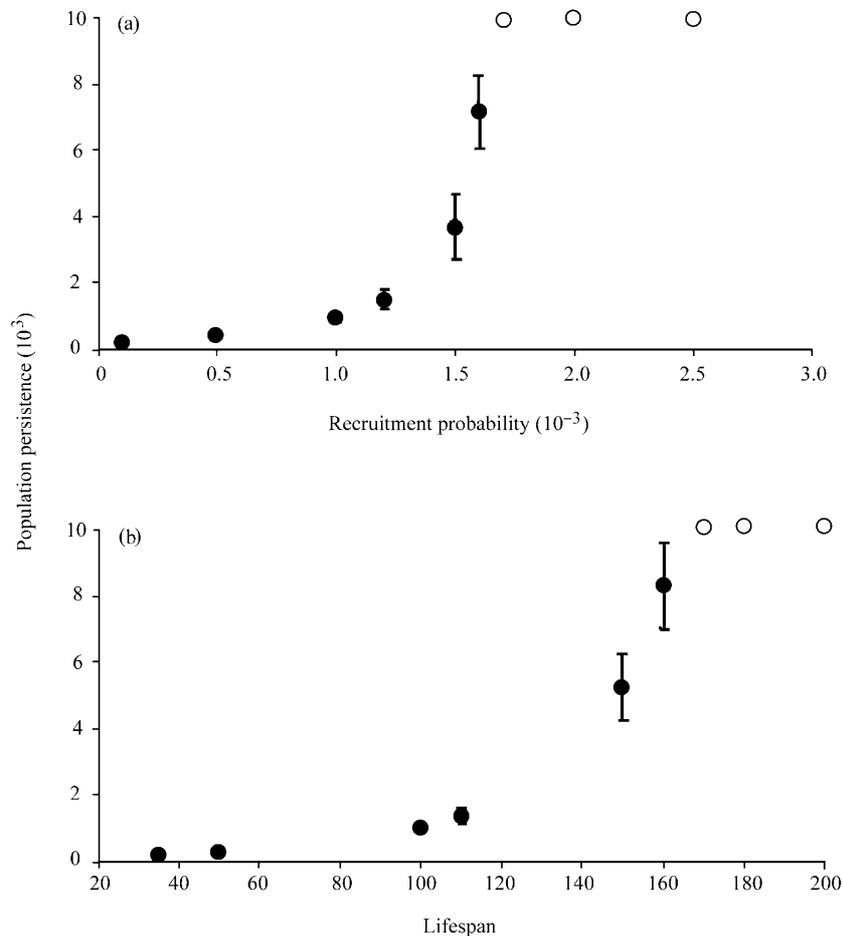


Fig. 5.6. Population persistence after seed disperser extinction under different scenarios of recruitment probability (a) and plant lifespan (b). Closed circles represent average population persistence ($n = 10$ simulation runs) and open circles represent situations in which the population survived until at least 10^4 reproductive events. Error bars indicate ± 1 SD.

observations of fruit–frugivore interactions. The similarity in fruit morphology between the Pantanal and African communities of savanna type suggests that similar evolutionary processes driven by seed dispersal have been a major force in these communities. The paired contrasts in fruit traits show consistent trends independent of family, indicating the evolutionary relevance of this pattern. Pantanal fruits were significantly more similar to African communities than to the geographically closer Atlantic rain forest assemblages, in relation to fruit size and colour. By the end of the Pleistocene, both South American and African savannas had a large biomass and diversity of large-bodied mammals (Fariña *et al.*, 1998; Cartelle, 1999) which, combined with the similarities in fruit traits (e.g. large

fruit size, dull-coloured fruits predominantly green and brown), suggests that megafauna were an important component of selective pressures on fruits. On the other hand, tropical rain forests have a lower biomass of large mammals than savanna-like ecosystems (Prins and Reitsema, 1989). Nowadays, the biomass of native mammals in the Pantanal reaches only 1,000 kg/km², while that of the exotic fauna (horses, cattle and feral pigs) reaches >5,000 kg/km² (Mourão *et al.*, 2002) and it has been estimated that the Pantanal could support about 10,000 kg/km² of large-bodied herbivores; a biomass similar to many African savannas (Galetti, 2004). In fact, anyone familiar with both ecosystems will not be surprised at such convergences (Madinah, 1982; Fariña, 1996).

A fundamental question related to megafauna-dispersed fruits in the Pantanal and other neotropical plant communities is: How have these plant species survived for about 10,000 years without the seed dispersers with which they originally co-evolved (Howe, 1985)? Several studies suggest that local extinction of large-bodied frugivores reduces seedling recruitment in vertebrate-dispersed plants. This pattern has been found on intensively studied oceanic islands where birds, bats or lizards were recently extinct (McConkey and Drake, 2002; Traveset and Riera, 2005). The idea that a population of fleshy, vertebrate-dispersed fruits can collapse under the absence of their main seed dispersers started with a study by Temple (1977), who suggested that the tambalacoque tree (*Sideroxylon grandiflorum*; Sapotaceae) relied on the extinct dodo (*Raphus cucullatus*; Raphidae) for successful establishment. Although the dodo–tambalacoque system has been an iconic case in plant–animal interaction studies in the past, it is now established that Temple’s analysis was unrealistic and it is an erroneous example of an obligate plant–animal relationship. There is no solid evidence that the dodo was absolutely required for seed germination or that the tambalacoque tree was driven to extinction due to the absence of the dodo (Witmer, 1991). Temple ignored earlier reports of Hill (1941) proving the ability of seeds to germinate without abrasion (Herhey, 2004). More recently, in-depth studies have shown that local extinction of some frugivores can drastically reduce seedling recruitment in vertebrate-dispersed plants (Cordeiro and Howe, 2001; McConkey and Drake, 2002; Traveset and Riera, 2005; Galetti *et al.*, 2006) but rarely drives populations to extinction, especially in long-lived taxa (Herhey, 2004).

The loss of the main seed dispersers, leading to severely limited dispersal and recruitment, is certainly one of the main potential causes for the demise of plant populations (see Traveset and Riera, 2005). Therefore, the survival of plants that produce large, high-cost fruits without efficient seed dispersal remains a paradox. Understanding the ecological persistence of these plants will have implications for understanding the organization of plant communities in the Neotropics after the Pleistocene mass extinctions (Janzen and Martin, 1982) and will highlight the ecological mechanisms that allow plant populations to survive after the extinction of their main seed dispersers (Chapman and Chapman, 1995).

The presence of exotic species in the Pantanal, such as feral pigs and cattle, has contributed to the seed dispersal of many plants, mainly the ones with large fruits and seeds. Fruit consumption and seed dispersal by cattle and horses are described for many species as a way to replace the extinct megafauna (Janzen, 1982; Janzen and Martin, 1982). Our data indicate that feral pigs can disperse more species than the native fauna, and also large-sized fruits (e.g. *A. phalerata*, *Acrocomia aculeate*, *Arecaceae*), because they are able to swallow and defecate their seeds, which peccaries (*T. pecari* and *P. tajacu*) cannot do. Among the native animals, only the tapir disperses fruits of *A. phalerata*, but the tapirs frequently defecate in salty lakes, a site unsuitable for successful seedling recruitment.

The ability of many species to resprout can also contribute to their survivorship, as can the ability to be dispersed by water (e.g. *Calophyllum brasiliense*, *Clusiaceae*; *B. glaucescens*; *Garcinia brasiliensis*, *Guttiferae*). In fact, in a seasonally flooded ecosystem like the Pantanal, dispersal by water may be the most common mechanism for many fleshy, vertebrate-dispersed fruits. Human use is likely to regularly contribute to the dispersal of seeds from those species used (47% – see Results). Rare events of seed dispersal, mainly done by animals with a low probability of fruit consumption (such as raptors), can also contribute to the dispersal of some species of plant (Galetti and Guimarães Jr, 2004).

However, the survival of some plants, such as *Attalea speciosa*, is surprising when considering the few ecological mechanisms known to explain plant population persistence. They do not display vegetative reproduction, are not known to be dispersed by water, secondary dispersal, humans and/or by rare events. This palm produces large, heavy, well-protected fruits and occurs in areas away from water (*terra firme* or *cordilheira*; Silva *et al.*, 2000), so seed dispersal by water is unlikely. Moreover, we did not find any evidence of scatter-hoarding rodents or large mammals (even the exotic species) dispersing the fruits. In this context, the simple numerical simulations reported here may provide a useful insight: some plant populations may persist simply by a combination of long lifespan and some likelihood of recruitment close to the parental trees (Hubbell, 1980). Indeed, this is apparently the case for *A. speciosa*, where seeds below the mother plant have no bruchid or vertebrate predation. Fallen fruits can germinate and establish below the mother plant, creating large monodominant forests known locally as *babaquais*.

Conclusions

In this chapter we have shown that fruit traits of the Pantanal species are more similar to those from savannas in Africa than to those from the neighbouring Atlantic rain forest. Our data indicate that the high diversity of large, fleshy, vertebrate-dispersed fruits in the Pantanal is associated with a prevalence of dispersal by mammals, which is supplemented by other taxa such as birds, fish and reptiles. Among potentially mammal-dispersed fruits,

several species demonstrate anachronistic dispersal in the Pantanal and include taxa that probably interacted with the extinct, highly diverse, Pleistocene megafauna. Some of these fruits lack efficient contemporary long-distance seed dispersal and others have extremely low seed removal. A combination of life-history traits has probably allowed these plants to persist after the extinction of their major megafauna dispersers: resprouting, being dispersed by water, extensive secondary seed dispersal by vertebrates (e.g. scatter-hoarding rodents), replacing seed dispersers with exotic fauna or humans, or rare events of seed dispersal (e.g. raptors). Moreover, numerical simulations suggest that, for some species in scenarios of impoverished dispersal, no alternative mechanisms need to be invoked to explain population persistence, other than a combination of long lifespan and an ability to recruit close to parental trees.

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Appendix 3

Families, species, habitats, fruit size, fruit colour and type of seed disperser of fleshy-fruited species studied at Fazenda Rio Negro, Nhecolândia region, MS, Brazil.

Family	Genus	Species	Habitat	Fruit length (mm)	Fruit width (mm)	Fruit weight (g)	Seed disperser*	Fruit colour
Anacardiaceae	<i>Spondias</i>	<i>lutea</i>	Semideciduous forest	25.1 ± 1.7	21.7±1.4	6.45 ± 1.4	mammals	yellow
Annonaceae	<i>Annona</i>	<i>dioica</i>	Cerrado	92.7 ± 4.4	75.1±5.2	250.0±22.7	mammals	green
Annonaceae	<i>Annona</i>	<i>cornifolia</i>	Cerrado	39.0 ± 7.5	38.0±9.2	23.6±12.7	mammals	orange
Annonaceae	<i>Unonopsis</i>	<i>lindmanii</i>	Cerrado	9.3 ± 0.2	9.2±0.2	0.6 ± 0.02	birds	orange
Apocynaceae	<i>Hancornia</i>	<i>speciosa</i>	Semideciduous forest	30.7 ± 3.3	29.8±3.7	15.4±5.3	mammals+rhea	green
Arecaceae	<i>Acrocomia</i>	<i>aculeata</i>	Semideciduous forest	31.9±2.1	32.1±2.8	19.2±2.7	mammals+rhea	brown
Arecaceae	<i>Attalea</i>	<i>speciosa</i>	Cerrado	87.7±7.8	50.7±4.1		none	brown
Arecaceae	<i>Attalea</i>	<i>phalerata</i>	Semideciduous forest	62.7±3.7	34.9±2.9	39.6±6.8	mammals+rhea	orange
Arecaceae	<i>Bactris</i>	<i>glaucescens</i>	Gallery forest	18.8±3.7	17.7±1.5	2.9±0.8	mammals+rhea	black
Arecaceae	<i>Copernicia</i>	<i>alba</i>	Semideciduous forest	19.1±1.7	16.4±1.0	2.7±0.5	mammals+rhea	black
Arecaceae	<i>Syagrus</i>	<i>flexuosa</i>	Semideciduous forest	37.3±2.0	15.9±1.5	6.1±1.7	mammals+tortoise	yellow
Bromeliaceae	<i>Bromelia</i>	<i>balansae</i>	Cerrado	33.8±2.4	29.2±2.9	16.9±4.4	mammals	yellow
Bursenaceae	<i>Protium</i>	<i>heptaphyllum</i>	Semideciduous forest	21.0±1.4	15.4±1.1	2.0±0.5	mixed	red/white
Cactaceae	<i>Cereus</i>	<i>peruvianus</i>	Semideciduous forest	68.6±17.3	47.8±5.3	103.3±40.3	birds	red/white
Caryocaraceae	<i>Caryocar</i>	<i>brasiliense</i>	Semideciduous forest	60.2±1.3	65.7±3.0	137.2±12.2	mammals	green
Cecropiaceae	<i>Cecropia</i>	<i>pachystachya</i>	Gallery forest	80.1±8.5	8.0±0.6	1.9±0.3	mixed	green
Chrysobalanaceae	<i>Couepia</i>	<i>uiti</i>	Gallery forest	44.9±6.2	26.8±3.8	29.2±2.9	mammals	brown
Chrysobalanaceae	<i>Licania</i>	<i>parvifolia</i>	Cerrado	29.7±3.8	12.5±1.8	2.5±0.7	fish	green
Clusiaceae	<i>Calophyllum</i>	<i>brasiliense</i>	Gallery forest	25.1±1.8	24.4±1.9	8.0±1.7	bats	green
Connaraceae	<i>Connarus</i>	<i>suberosus</i>	Cerrado	15.4±1.6	8.9±0.6	0.8±0.09	ants	red/black
Dilleniaceae	<i>Curatella</i>	<i>americana</i>	Semideciduous forest	11.5±0.9	8.6±0.6	0.9±0.07	birds	red/white
Dilleniaceae	<i>Dollocarpus</i>	<i>dentatus</i>	Gallery forest	6.7±0.8	5.5±0.6	0.1±0.03	birds	red/white
Ebenaceae	<i>Diospyros</i>	<i>hispidia</i>	Cerrado	42.3±3.5	47.2±2.6	57.3±10.3	mammals	green
Erythroxylaceae	<i>Erythroxylum</i>	<i>anguiugum</i>	Semideciduous forest	10.0±1.1	6.0±0.7	0.2±0.06	birds	red
Euphorbiaceae	<i>Sapium</i>	<i>haematospermum</i>	Cerrado	6.4±1.3	4.7±0.6	0.1±0.02	birds	red/green
Fabaceae	<i>Andira</i>	<i>cuyabensis</i>	Semideciduous forest	40.4±2.3	31.2±0.8	21.8±2.5	bats	green
Fabaceae	<i>Andira</i>	<i>inermis</i>	Cerrado	46.4±4.9	28.8±2.5		bats	green
Fabaceae	<i>Dipteryx</i>	<i>alata</i>	Semideciduous forest	48.8±3.6	39.9±2.4	27.4±6.9	mammals	brown
Fabaceae	<i>Inga</i>	<i>uruguensis</i>	Gallery forest	59.2±14.5	19.0±1.8	9.5±4.3	mammals+fish	brown
Fabaceae	<i>Inga</i>	<i>laurina</i>	Cerrado	53.1±14.3	21.9±1.6	12.3±5.3	mammals+fish	green
Fabaceae	<i>Copaifera</i>	<i>martii</i>	Semideciduous forest	18.1±3.3	14.0±1.0	1.4±0.7	birds	white

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Flacourtiaceae	<i>Casearia</i>	Semideciduous forest	24.3±4.1	25.9±3.5	9.1±4.4	birds	orange
Guttiferae	<i>Garcinia</i>	Gallery forest	27.5±5.9	22.6±2.6	7.9±3.7	mammals+fish	yellow
Hippocrateaceae	<i>Salacia</i>	Gallery forest	53.2±7.3	46.0±5	66.1±21.2	mammals+fish	orange
Lauraceae	<i>Ocotea</i>	Semideciduous forest	9.4±0.8	5.9±0.4	0.2±0.04	birds+fish	red/black
Leguminosae	<i>Hymenaea</i>	Cerrado	97.0±12.5	41.7±4.3	48.5±20.2	mammals	brown
Leguminosae	<i>Hymenaea</i>	Semideciduous forest	108.9±7.9	48.3±3.1	30.8±3.9	mammals	brown
Leguminosae	<i>Enterolobium</i>	Semideciduous forest	39.1±1.6	78.8±1.6	1.8±0.2	mammals	brown
Loranthaceae	<i>Psittacanthus</i>	Cerrado	26.3±31.9	11.8±1.0	1.8±0.2	birds	green
Malpigiaceae	<i>Bunchosia</i>	Cerrado	5.8±0.07	4.8±0.4	0.1±1.5	birds	orange
Malpigiaceae	<i>Byrsonima</i>	Cerrado	12.6±1.4	12.1±1.6	1.4±1.5	mammals+tortoise	yellow
Malpigiaceae	<i>Byrsonima</i>	Cerrado	17.1±1.5	18.1±1.0	4.1±0.6	mammals	yellow
Melastomataceae	<i>Miconia</i>	Cerrado	5.7±0.7	7.0±0.4	0.2±0.04	birds	black
Meliaceae	<i>Trichilia</i>	Semideciduous forest	7.1±1.1	4.8±0.7	0.2±0.02	birds	black/red
Moraceae	<i>Ficus</i>	Semideciduous forest	7.1±0.4	7.4±0.5	0.2±0.02	mixed	purple
Moraceae	<i>Ficus</i>	Semideciduous forest	21.3±1.4	18.9±2.1	2.3±0.4	mixed	green
Myrtaceae	<i>Eugenia</i>	Semideciduous forest	23.3±7.2	25.8±8.1	9.1±7.8	mammals+tortoise	yellow
Myrtaceae	<i>Syzigium</i>	Semideciduous forest	21.3±2.2	17.1±2.4	4.2±1.2	mixed	purple
Myrtaceae	<i>Psidium</i>	Semideciduous forest	30.1±5.2	26.4±4.4	13.0±4.6	mixed	yellow
Myrtaceae	Indeterminate 1	Gallery forest	19.6±2.4	17.2±1.2	3.4±0.7	birds	orange
Myrtaceae	Indeterminate 2	Cerrado	8.8±1.0	10.8±1.3	0.7±0.2	mixed	red
Ochnaceae	<i>Ouratea</i>	Semideciduous forest	9.4±0.8	5.9±0.4	0.2±0.04	birds	black/red
Oleaceae	<i>Ximena</i>	Semideciduous forest	21.7±2.3	20.9±2.0	6.6±1.4	mammals+tortoise	yellow
Opiliaceae	<i>Agonandra</i>	Semideciduous forest	24.8±1.7	24.2±1.9	9.4±2.0	mammals+tortoise	yellow
Rhamnaceae	<i>Rhamnidium</i>	Semideciduous forest	10.9±1.5	7.5±1.0	0.4±0.07	birds	black
Rubiaceae	<i>Alibertia</i>	Cordiliera	26.2±2.5	26.1±2.0	11.4±3.2	mixed	black
Rubiaceae	<i>Genipa</i>	Gallery forest	75.7±5.0	60.0±4.6	130.2±26.7	mixed	brown
Rubiaceae	<i>Psychotria</i>	Gallery forest	12.0±0.81	10.8±1.7	0.8±0.1	birds	white
Rubiaceae	<i>Psychotria</i>	Gallery forest	5.9±0.5	5.8±0.5	0.1±0.03	birds	red
Rubiaceae	<i>Tocoyena</i>	Gallery forest	48.1±6.9	33.7±5.1	26.9±10.4	mammals+birds	yellow
Rutaceae	<i>Zanthoxylum</i>	Semideciduous forest	5.1±0.3	3.7±0.15	0.04±0.0	birds	black
Sapindaceae	<i>Melicococcus</i>	Gallery forest	26.5±3.6	20.6±1.6	6.8±1.4	mammals	yellow
Sapindaceae	<i>Paullinia</i>	Cerrado	17.4±1.7	11.2±2.1	1.0±0.4	birds+fish	red/black

Continued

Family	Genus	Species	Habitat	Fruit length (mm)	Fruit width (mm)	Fruit weight (g)	Seed disperser*	Fruit colour
Sapindaceae	<i>Sapindus</i>	<i>saponaria</i>	Semideciduous forest	18.0±3.0	18.6±3.1	2.8±0.7	bats	brown
Sapindaceae	<i>Talisia</i>	<i>esculenta</i>	Semideciduous forest	23.8±1.6	21.4±1.3	5.8±1.5	mammals	brown
Sapotaceae	<i>Chrysophyllum</i>	<i>marginatum</i>	Semideciduous forest	6.7±0.7	6.8±0.5	0.2±0.03	birds	black
Sapotaceae	<i>Pouteria</i>	<i>ramiflora</i>	Semideciduous forest	41.3±2.1	31.9±2.0	28.1±0.5	mammals	green
Sapotaceae	<i>Pouteria</i>	<i>gardneri</i>	Semideciduous forest	15.7±3.1	11.9±2.3	1.4±0.4	mammals+tortoise	purple
Simaroubaceae	<i>Simarouba</i>	<i>versicolor</i>	Cerrado	30.9±0.9	26.1±1.3	12.8±1.1	bats	green
Solanaceae	<i>Solanum</i>	<i>viarum</i>	Pasture	33.3±1.5	34.5±4.8	15.3±4.8	mammals	green
Sterculiaceae	<i>Guazuma</i>	<i>ulmifolia</i>	Semideciduous forest	18.0±1.0	19.9±1.1	3.3±0.6	mammals	black
Sterculiaceae	<i>Sterculia</i>	<i>apelata</i>	Semideciduous forest	25.5±1.3	23.6±0.8	4.9±0.5	birds	red/black
Verbenaceae	<i>Vitex</i>	<i>cymosa</i>	Semideciduous forest	22.1±3.8	16.4±4.5	4.0±2.9	mixed	black
Vitaceae	<i>Cissus</i>	<i>erosa</i>	Semideciduous forest	5.1±0.5	5.8±0.6	0.1±0.03	birds+fish	black
Vitaceae	<i>Cissus</i>	<i>spinosa</i>	Gallery forest	6.8±0.4	8.2±0.6	0.3±0.06	birds+fish	black

*Seed disperser 'mixed' includes mammals, birds and other seed dispersers.