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Complementary roles of two resilient neotropical mammalian seed dispersers

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ABSTRACT

Capuchin monkeys (*Cebus* spp. and *Sapajus* spp.) and coatis (*Nasua* spp.) coexist in most neotropical forests, including small forest remnants. Both capuchins and coatis eat fruit and disperse seeds, but little is known about whether their roles in seed dispersal are redundant or complementary. We compiled 49 studies from the literature on feeding by capuchins and/or coatis, of which 19 were comprehensive enough for our analyses. We determined the relative importance of fruit eating to each species and compared their diets. Additionally, we analysed the structure of three fruit–frugivore networks built with both animal groups and the fruits they eat and evaluated whether fruit traits influenced the network topology. Fruits represented the largest part of capuchin and coati diets, even though coatis have been known for their opportunistic and generalist diets. Capuchins and coatis also exhibited similar general diet parameters (niche breadth and trophic diversity). The three networks exhibited high connectance values and variable niche overlap. A Multiple Correspondence Analysis, failed to detect any trait or trait combination related to food use. In conclusion, capuchins and coatis both have generalist diets; they feed on many different species of fruits and exhibit important complementarity as seed dispersers. Both are likely to be particularly important seed dispersers in disturbed and fragmented forests.

1. Introduction

Plant–animal interactions are among the main processes that generate and maintain biodiversity (Odum and Barrett, 2008). In the tropics, mutualisms such as pollination and seed dispersal play a central role, with up to 90% of plant species dependent on animals for their reproduction (Howe and Smallwood, 1982; Jordano, 2000). Many plant species produce fruits with edible parts which attract frugivorous animals (Howe and Smallwood, 1982). These animals benefit from the interaction because the fruits act as an energy source, while the plants have their seeds carried away from parent plants, increasing their probability of recruitment (Howe and Miriti, 2004; Janzen, 1971). Seed dispersal by frugivores is a key process in plant population dynamics (Terborgh, 1995), and in highly fragmented landscapes it can increase the chances of restoration of degraded lands (Duncan and Chapman, 2002) and gene flow among natural vegetation patches (Jordano and Godoy, 2002).

However, medium and large-sized frugivores are becoming extinct or have extremely reduced populations in many tropical ecosystems (Wright et al., 2007), mainly as a result of hunting and habitat loss (Chiarello, 1999; Cullen et al., 2000; Peres and Palacios, 2007). This can impact ecosystem structure and dynamics due to the disruption of key interactions, including those related to seed dispersal (Donatti et al., 2011; Galetti et al., 2013; Galetti and Dirzo, 2013; Peres and van Roosmalen, 2002). In this scenario, some resilient seed dispersing species may become very important because they can provide continuity to essential processes in the forest (Alves-Costa and Eterovick, 2007).

Capuchin monkeys (Primates: Cebidae, genera *Cebus* Erxleben and *Sapajus* Kerr) and coatis (Carnivora: Procyonidae, genus *Nasua* Storr) are among the medium-bodied frugivores that can persist in small Neotropical forest fragments (Chiarello, 1999). These two mammal groups are omnivores, but fruits can comprise a major part of their diets, reaching up to 89% for capuchins (Galetti and Pedroni, 1994;

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Janson, 1985; Mikich, 2001; Moscow and Vaughan, 1987; Rocha, 2001), and 72% for coatis (Aguiar et al., 2011; Gompper, 1996; Mikich, 2001; Russell, 1983).

Capuchin monkeys are arboreal and social primates (Freese and Oppenheimer, 1981), which are widely distributed throughout the Neotropics. Species of the genus *Cebus* are found in the Amazon and Central America, while species of the genus *Sapajus* are distributed through South America, occupying a variety of habitat types, from dense rainforests and wetlands to areas of Cerrado and Caatinga (Freese and Oppenheimer, 1981; IUCN, 2013).

Coatis are scansorial (they can travel and forage on the ground but are also adapted for climbing trees, where they can forage, avoid predators, sleep and breed), social mammals, although adult males are solitary (Gompper, 1995; Gompper and Decker, 1998). The two extant species have non-overlapping distributions: *Nasua narica* (Linnaeus, 1766) in Central America and southern North America, and *Nasua nasua* (Linnaeus, 1766) in South America, from Colombia and Venezuela to Uruguay and Argentina (IUCN, 2016).

Capuchin monkeys and coatis are relatively common to abundant in Neotropical forests (Eisenberg and Thorington, 1973; Gompper and Decker, 1998), and their geographical ranges overlap. Given their potential importance as frugivores in highly disturbed habitats, where large-seeded plant species may depend on only a few frugivorous species for seed dispersal (Alves-Costa and Eterovick, 2007; Vidal et al., 2013), information on their diets and interactions is valuable to inform forest conservation and restoration programmes. Due to their diets, habits and behaviour, it is expected that these two mammal groups will exhibit both similarities and dissimilarities regarding their ecological functions and interactions, even in shared habitats, which may affect the wider ecological community.

The mutualisms between animals and plants form a complex network of interactions (Bascompte and Jordano, 2007) affecting the structure and stability of a community (Maruyama et al., 2014; Vázquez et al., 2009). Plant ecological traits can shape the interactions between plants and animal visitors, constraining the number and identity of interacting species (Jordano et al., 2003), and therefore affecting the patterns of interactions or the network structures, both for plant–pollinator (Junker et al., 2013; Maglianesi et al., 2014; Maruyama et al., 2014; Schleuning et al., 2015; Vizentin-Bugoni et al., 2014) and frugivory and seed dispersal networks (Dehling et al., 2014; Gonzalez-Castro et al., 2015). Trait-based analyses have proven the importance of traits of interacting species for the dynamics of interactions, for example morphological matches between plants and their pollinators in pollination networks (Junker et al., 2013; Maglianesi et al., 2014). Morphological matches have also been shown to be important in determining community structure, as well as species abundances, for plant and avian–seed dispersal interactions (Gonzalez-Castro et al., 2015). However, studies incorporating the influence of species' traits in structuring ecological networks are still scarce (Kissling and Schleuning, 2015), particularly for plant–seed dispersal systems. Furthermore, little is known about the role of species' traits in structuring networks involving frugivore groups other than birds.

Thus, in this paper, our objectives were: (1) to determine the importance of fruits in the diets of capuchins and coatis, and the consistency of the diets of both groups across their geographical distribution; (2) to compare diet parameters between these two mammalian groups, and to investigate the possible causes of any differences; and (3) to identify key plant traits linked to these groups' fruit preferences. We predicted that fruits should represent a lower fraction of coatis' diets compared to capuchins', considering their different life histories, foraging habits and general behaviour. Due to morphological and behavioural differences between the two groups, we expected diet breadth and diversity to differ, with capuchins favouring fruit consumption over other items, and as a result exploiting a higher fruit species diversity than coatis. We also expected plant, fruit and/or seed traits to explain the trophic interaction structure for these two taxa. It is known that morphological traits of fruits, such as colour, fruit and seed sizes, and type of fruit, can be associated with character syndromes associated with different taxa (Gautier-Hion et al., 1985). Primates tend to favour bright or multicoloured and arillate fruit species while other mammals are particularly more attracted to dull-coloured, large, and fibrous fruit species (Gautier-Hion et al., 1985).

To test our predictions, we gathered data from a systematic literature review to evaluate frugivory by capuchin monkeys and coatis and their interactions with fruit plants over the Neotropical region. Additionally, for three case studies where detailed data were available on capuchin and coati feeding associations, we investigated fruit-frugivore network structure in order to evaluate the influence of fruit/plant traits on the use of these resources by capuchin monkeys and coatis.

2. Methods

2.1. Data compilation

We performed a broad review, using the *Web of Science* database (http://apps.webofknowledge.com), our own knowledge of the literature, dissertations, theses, and our own unpublished data about the diets of wild populations of capuchin monkeys and coatis. For capuchins, the search in the database was performed using the keywords [("*Cebus*" OR "*Sapajus*") AND "diet"], and all studies listed until August 2016 were analysed. For coatis, the investigation included all studies published until August 2016 that resulted from the search of the term "*Nasua*". We did not use the "diet" filter in this last search because there were already few results and we did not want to miss any relevant studies. In order to compare the diet parameters (trophic diversity and niche breadth) between the two mammalian groups, we selected diet studies that described all recognisable food items, and not just the dominant foods, conducted during ≥12 months, and where the relative frequencies of occurrence of the different items in their diet (e.g. fruit + seeds, non-fruit plant parts and animal matter) were reported or could be calculated. We used studies where the method could quantify the frequency of occurrence of different items as this tends to include even rare and important food sources (Robinson, 1986). We used original datasets whenever available, and secondary data when the original data were not accessible.

The taxonomy of both capuchins and plants can be controversial. For the capuchins, we followed the proposal of Alfaro et al. (2012a, 2012b). For plants, scientific names and classifications were verified according to The Plant List database (http://www.theplantlist.org).

2.2. Case studies

Despite a reasonable number of studies published on the diets and/or seed dispersal of both groups (35 studies for capuchin monkeys and 16 studies for coatis) and the considerable overlap in their geographical ranges, only two study sites had the diets of both groups investigated at the same time and with the same methodology (Mikich, 2001; Rocha, 2001). Additionally, one study site (Barro Colorado Island, Panama) had a number of independent, detailed and consistent observational studies on the diets of capuchins and coatis (Oppenheimer, 1968 *apud* Freese and Oppenheimer, 1981; Hladik and Hladik, 1969; Kaufmann, 1962; Russell, 1983), making it possible to combine data from different sources for some analyses.

Our network analyses therefore focused on these three case studies, where each study had the same sampling effort for capuchins and coatis within the study—although sampling effort was not consistent across studies—which we now describe in detail.

The first study system included data on *Sapajus nigritus* (Goldfuss, 1809) and *N. nasua* interacting with 101 plant species (S. B. Mikich, in prep.). This author collected the data in a protected area called Vila Rica do Espírito Santo State Park, which is located in the interior