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Original article

Seed germination of a myrmecochorous plant endemic to the Brazilian semiarid region: the wolf is not so bad

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ABSTRACT

Studies about seed dispersal and germination are important to understand patterns of plant distribution and abundance, and help establish strategies for environmental conservation. We evaluated the role of two different dispersers, the ant *Atta laevigata* and the maned wolf *Chrysocyon brachyurus*, in the germination of *Copaifera arenicola* seeds, a characteristically myrmecochorous plant species. Germination was evaluated for seeds subjected to four treatments: (1) seeds manipulated by the ant, (2) seeds ingested by the maned wolf, (3) seeds that had the elaiosome removed manually, and (4) seeds with elaiosome (unmanipulated seeds). Seeds manipulated by the ant and seeds that had the elaiosome removed manually required less time to germinate and had higher germination percentages (98.6% and 95.8%, respectively) than the other treatments. However, seeds ingested by the maned wolf also had a high germination percentage (87.7%), above that of unmanipulated seeds (34.7%). Probably, elaiosomes of unmanipulated seeds and small remnants of this structure that resist digestion by maned wolf can decrease to some extent seed germination. We argue that dispersal of *C. arenicola* seeds by the ant and by the maned wolf result in different patterns of seed distribution in the environment and that they have complementary roles in structuring plant populations.

Keywords: Ants, *Copaifera arenicola*, maned wolf, plant assembly, seed dispersion, Zoochory.

Introduction

Seed dispersal and germination are crucial events in the life cycle of most spermatophytes that normally affect the recruitment and organization of plant communities (Levine & Murrell 2003; Klinger & Rejmánek 2010; Grman *et al*. 2015). Germination is the process of resumption of embryo growth, which begins with the absorption of water by the quiescent seed, resulting in embryonic axis elongation and seedling formation (Bewley 1997). The dispersal or transport of seeds allows the colonization of new habitats

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distant from the mother plant, where seedlings normally achieve greater success in establishment due to lower levels of competition and herbivory (Janzen 1970; Farias *et al.* 2015). Plants have evolved different strategies to disperse their seeds through abiotic agents, such as wind, water and gravity, and/or biotic agents, including invertebrates and vertebrates (Figuerola & Green 2004; Hamalainen *et al.* 2017; Snell *et al.* 2019). Analysis of the mechanisms that affect seed dispersal and germination is important to understand patterns of plant distribution and abundance, in addition to supporting the establishment of strategies for conservation and environmental restoration (Klinger & Rejmánek 2010; Thomson *et al.* 2016).

Seed dispersal by animals, or zoochory, involves interspecific interactions with different levels of specificity between animals and plants (Giladi 2006; Barroso *et al.* 2013; Acevedo-Quintero & Zamora-Abrego 2016; Camargo *et al.* 2019). For example, some myrmecochorous plants produce seeds with an elaiosome, an appendage rich in lipids, proteins, sugars and minerals that can be used directly or indirectly by different ant species as a food resource (Giladi 2006; Fernandes *et al.* 2018). In return, many ant species transport seeds with elaiosome to their nests, thus acting as important seed dispersing vectors (Gama *et al*. 2019; Fagundes *et al.* 2021) with positive effects on the organization of plant communities in different environments (Nathan & Muller-Landau 2000; Levine & Murrell 2003; Lengyel *et al*. 2009; Snell *et al*. 2019). Myrmecochory is traditionally seen as a diffuse mutualism in which several ant species can participate in seed dispersal of the same plant species (Ness *et al.* 2004; Gama *et al.* 2019). In addition, vertebrates, such as birds and mammals, can also ingest seeds adapted for dispersal by ants and act as effective dispersers (Calviño-Cancela *et al*. 2008; Souza *et al.* 2015a; Thomson *et al.* 2016; Souza & Fagundes 2017).

The manipulation of plant propagules by ants during the removal of the elaiosome or during the transport of the seed to nests can affect seed germinability (germination speed and percentage) (Oliveira *et al.* 1995; Prior *et al.* 2014). In fact, the presence of an elaiosome can affect seed germinability because these appendages have germination-inhibiting substances, or simply because they negatively affect seed imbibition (Fernandes *et al.* 2018). Thus, the simple removal of these appendages by dispersers could break seed dormancy and accelerate germination (Souza *et al*. 2015b; Fagundes *et al.* 2021). Seed manipulation by ants can also cause grooves in the seed coat, which favors water absorption and germination (Prior *et al.* 2014). On the other hand, the removal of the elaiosome can expose the micropyle, facilitating the entry of microorganisms into the seed that degrade the embryo negatively affecting the germination (Souza *et al.* 2015b; Fernandes *et al.* 2018).

Although poorly documented, seeds of some myrmecochorous plants can also be used as food by vertebrates, especially when the elaiosome represents a great energetic reward (Calviño-Cancela *et al*. 2008; Souza & Fagundes 2017; Snell *et al.* 2019). The passage of these propagules through the vertebrate digestive tract can eliminate external seed appendages, such as the elaiosome, and/or break dormancy through chemical or mechanical scarification, thereby increasing seed germinability (Traveset *et al.* 2007; Farias *et al*. 2015; Karimi *et al.* 2020). Finally, the elimination of seeds in fecal cakes can also provide some shelter from predators and greater availability of organic matter for the initial development of seedlings (Farias *et al.* 2015). Thus, vertebrates are important and effective long-distance seed dispersers in most ecosystems (Nathan & Muller-Landau 2000; Levine & Murrel 2003), although some studies indicate that seed ingestion by vertebrates may have neutral or negative effects on seed germination for some plant species (Schupp *et al.* 2010; Karimi *et al*. 2020).

Copaifera arenicola (Fabaceae) is a shrub-tree species endemic to the Brazilian semi-arid region (Gama & Nascimento-Junior 2019). The species produces shiny black seeds partially covered by an orange elaiosome. Recent studies suggest that ants of the genus *Atta* (Formicidae) are important dispersers of *Copaifera* species (Gama *et al.* 2019). These ants collect the seeds of plants and transport them to inside their nests, where they remove the elaiosomes and use them to grow fungi, which is their main food resource. After the elaiosomes are removed, the ants discard these seeds close to the loose soil of the anthill (Gama *et al.* 2019; Fagundes *et al.* 2021). Several other animals, such as birds and mammals, also use the elaiosome of *Copaifera* seeds as a food resource (Rabello *et al*. 2010; Souza *et al*. 2015a; Gama *et al*. 2019).

Here we evaluate the role of two potential dispersers (*Atta laevigata*: Formicidae and *Chrysocyon brachyurus*: Carnivora: Canidae) on the germinability of *C. arenicola* seeds. We work with these two seed vectors of *C. arenicola* seeds as they occur naturally in our study area, have overlapping and widespread distribution in others regions of the Brazilian semi-arid as Cerrado and Caatinga, and seed vectors have distinct behavior that can impact differently seed distribution patterns in the landscape (Bueno *et al*. 2002; Melo *et al*. 2007; Gama *et al*. 2019; Fagundes *et al*. 2021). Specifically, we tested the hypothesis that seeds ant-manipulated and seeds ingested by maned wolf present greater germinability than seeds hand-manipulated and intact seeds (i.e. seeds with elaiosome) since: seeds of myrmecochorous plant, ant-manipulated, generally have high germinability (Souza *et al*. 2015b; Fernandes *et al*. 2018), and the passage of seeds through the digestive tract of vertebrates can remove external appendages and promote wear to the seeds that promote germination (Farias *et al*. 2015).

Methodology

Obtaining seeds

All *Copaifera arenicola* (Ducke) J. Costa & L. P. Queiroz seeds used in the experiment were collected in an area of cerrado in the Caminho dos Gerais State Park (15°01′55″S 43°02′46″W) during March 2021. Seeds were collected directly from plants or from a top the loose soil of *Atta laevigata* nests or within feces pellets of the maned wolf in a regenerating cerrado area with approximately 4 ha (see below). This conservation unit is located in the Serra Geral mountain range in northern Minas Gerais State, Brazil (Fig. 1). The Park encompasses approximately 56 thousand hectares with an average altitude of 1090m asl and typical vegetation of the Caatinga and Cerrado (with their different physiognomies, including campos rupestres/ rupestrian grasslands, dry forest, cerrado fields and cerrado *stricto sensu*). The climate is semi-arid with well-defined dry and rainy seasons. The average annual temperature is 24°C and the annual precipitation is 830 mm/year, which is mainly concentrated between the months of November and February (INMET, 2022).

The system

Copaifera arenicola (Fabaceae) occurs in open areas in the Brazilian semi-arid region. The plants reach 2 to 5 meters in height and are semideciduous. The leaves are composite and usually have two pairs of leaflets. The plants produce pale-yellow panicle inflorescences and dry, dehiscent and monospermic legume-type fruits. Fruit dehiscence occurs from January to March, when they expose a shiny black and rigid seed coat partially covered by an orange elaiosome. The elaiosome is rich in lipids, carbohydrates and proteins and serves as a direct or indirect food resource for various animals, including mammals, birds and ants (Gama & Nascimento Junior 2019; Fagundes *et al*. 2021). Ants of the genera *Atta* and *Acromyrmex* are mainly characterized by the habit of collecting and transporting plant material through trails into their nests to cultivate fungi that constitute their basic food resource (Holldobler & Wilson, 1990). These ants can also collect propagules from different plant species and transport them to the interior of their nests, thus acting as seed dispersers (Dalling & Wirth 1998; Lopes *et al*. 2018).

The maned wolf, *Chrysocyon brachyurus* (Carnivora: Canidae), is a generalist omnivore with a broad geographic distribution (Pinto & Duarte 2013). Its diet can vary

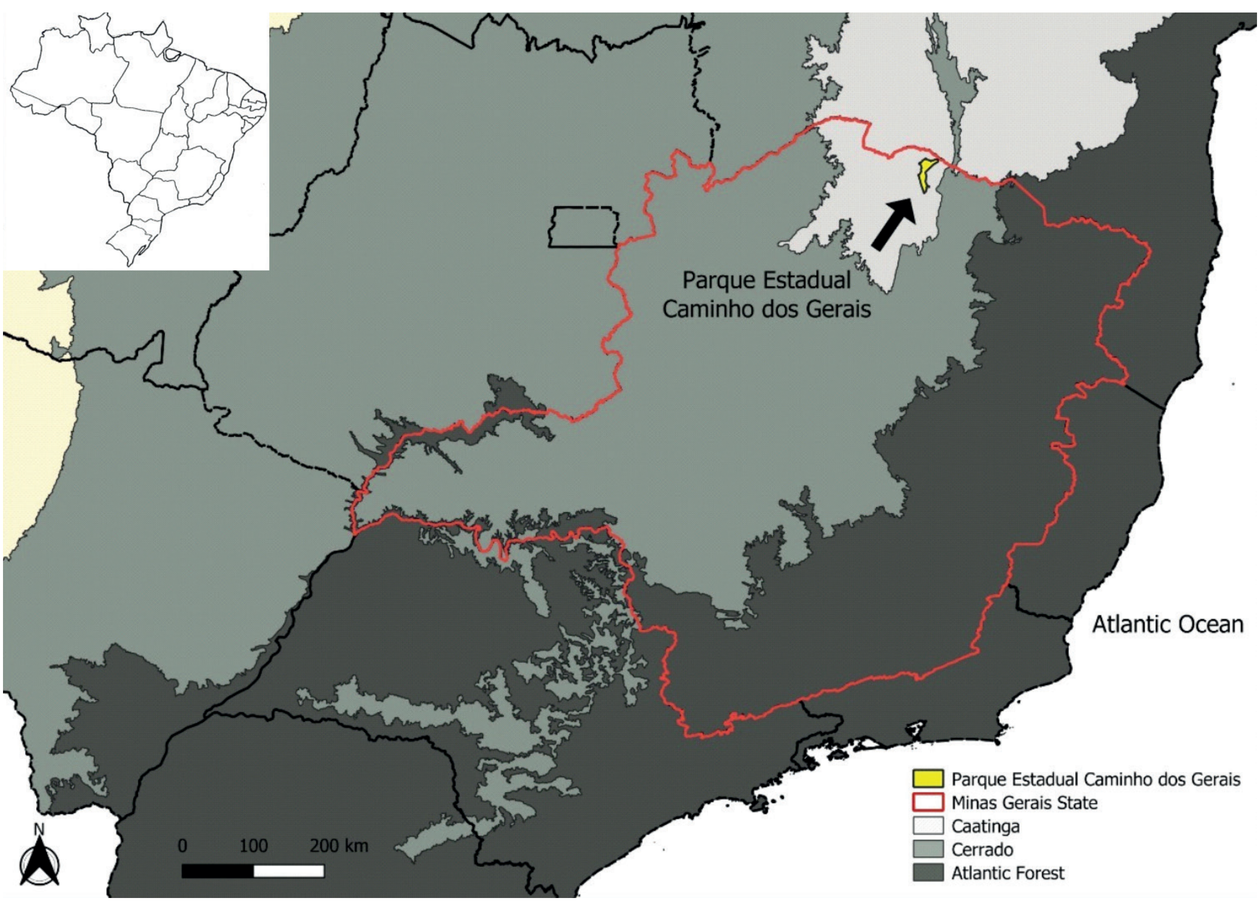

Figure 1. Map showing the location of Parque Estadual Caminho dos Gerais in a transition between Caatinga and Cerrado vegetation in the extreme north of the Minas Gerais state, Brazil.

depending on the availability of resources (Bueno & Motta-Junior 2009) and includes small mammals and fruits of different plant species, such as *Allagoptera campestris* (Arecaceae), *Solanum lycocarpum*, (Solanaceae), *Parinari obtusifolia* (Chrysobalanaceae) and *Byrsonima* sp. (Malpighiaceae). In Brazil, the species occurs from the state of Maranhão to the state of Rio Grande do Sul, especially in areas of cerrado (Rodden *et al.* 2004). The large home range of the maned wolf (about 25.2 to 57.0 km^2) (Melo *et al.* 2007, Rodrigues *et al.* 2007), in association with the accelerated fragmentation of its habitat (Massara *et al.* 2012), has resulted in its categorization as Vulnerable in the Brazilian Cerrado. The maned wolf ingests *Copaifera arenicola* propagules with the elaiosome, collected directly from the plants, and eliminates the seeds in its feces (M. Fagundes, Personal Note).

Experimental design

A total of 144 mature seeds in good phytosanitary condition (well-formed and without signs of attack by herbivores or pathogens) were collected from 20 plants of *C. arenicola*. The seeds were divided into two groups of 72 seeds each: (1) intact seeds with elaiosome and (2) seeds that had their elaiosome manually removed using a scalpel. In addition, another 144 seeds were collected, of which 72 were found without elaiosomes on the loose land of six *Atta laevigata* nests (6 to 12 seeds collected from loose land per ant hill) and 72 found in 18 maned wolf feces pellets (3 to 8 seeds per pellet). Thus, the experiment was delimited with four treatments: t_1 = ant-manipulated seeds (seeds without elaiosome, found on loose soil of anthills); t_2 = seeds ingested and defecated by the maned wolf (seeds taken from maned wolf feces); t_3 = hand- manipulated seeds (seeds collected directly from plants that had the elaiosome removed manually), and t_4 = unmanipulated seeds collected directly from plants (seeds with elaiosome) (Fig. 2).

All seeds of the four treatments were placed to germinate in individual cells of four styrofoam trays (one tray per treatment). This experimental design assumes that each seed represents an independent experimental unit (Fagundes

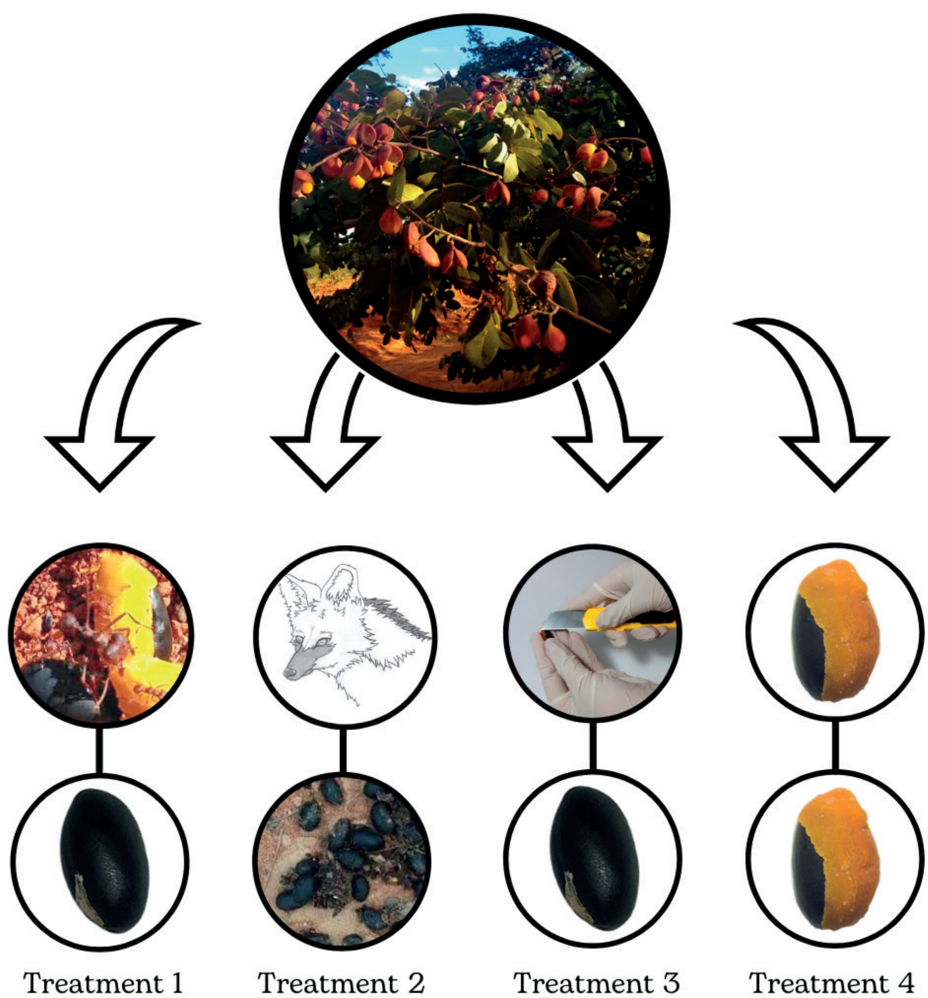

Figure 2. Images illustrating the four treatments used in the germination experiment of *Copaifera arenicola* seeds: (1) ant-manipulated seeds, (2) seeds collected in feces of the maned wolf, (3) hand-manipulated seeds, and (4) unmanipulated seeds (control).

et al. 2021). Approximately 3.0g of sterile vermiculite was placed in each cell of the trays and used as a germination substrate. After sowing, the four trays were placed in a germination chamber with controlled temperature, photoperiod and light intensity (12 h/light at 28 °C and 12 h/dark at 28 °C, 47.5 μmol.m.$^{-2}$s^{-1} irradiation). The humidity of the germination substrate was kept constant by adding 3mL of distilled water daily in each cell of the germination trays. The experiment was monitored daily and a seed was considered germinated when its primary roots protruded.

Statistical analyses

Variation in seed germination time among the four different treatments was tested by survival analysis. Thus, treatment was used as the explanatory variable and germination time as the response variable, following the Weibull distribution (Weibull & Sweden 1951; Fagundes *et al.* 2021). The model was compared with the null model through analysis of variance (ANOVA). Contrast analysis were used to group significantly similar levels and separate significantly different levels. Generalized linear models, followed by ANOVA, were used to test differences in seed germination percentage among treatments. In building the models, treatment was used as the explanatory variable and seed germination (0 or 1), based on the binomial distribution (corrected for quasibinomial), as the response variable. Contrast analyses were subsequently used to group statistically similar levels and separate statistically different levels. Residual analyses were used to check the suitability of all models. All analyses were performed using R software version 3.5.0 (R Core Team 2013).

Results

Germination time for *C. arenicola* seeds varied among treatments (Deviance = 171.437, $P < 0.001$). Contrast analyses showed that germination time did not differ significantly between the unmanipulated seeds (seeds with elaiosome) and seeds ingested by the maned wolf (Deviance = 2.352, P = 0.125). Germination time for seeds manipulated by ants was significantly shorter than that for control seeds and those ingested by maned wolf amalgamated (Deviance = 21.045, $P < 0.001$). Germination time for seeds with elaiosome removed manually did not differ significantly from that for seeds manipulated by ants (Deviance = 2.859, P = 0.091). Therefore, the results indicate the formation of two groups (1) seeds with elaiosome removed manually plus seeds manipulated by ants, and (2) seeds ingested by the maned wolf plus seeds with elaiosome (Fig. 3).

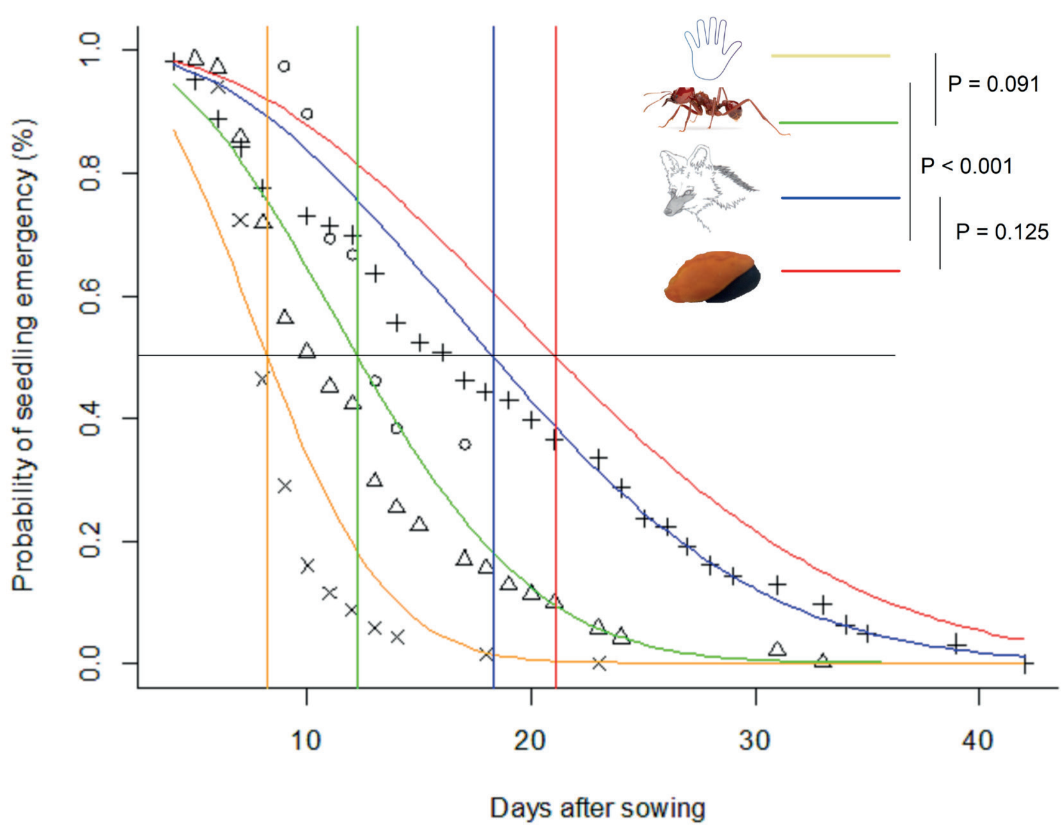

Figure 3. Variation in germination time for *Copaifera arenicola* seeds as a function of germination percentage for seeds in each treatment over time. The intersection of vertical lines with the horizontal line indicates the probability of 50% germination for seeds of each treatment (in days).

Germination percentage varied among treatments (Deviance = 28.525, F = 44.267, P < 0.001). Contrast analyses showed that: (i) germination percentage for seeds ingested by the maned wolf was significantly higher than that unmanipulated seeds (F = 43.008, P < 0.001); (ii) germination percentage for seeds manipulated by ants was significantly higher than that for seeds ingested by the maned wolf (F = 20.769, P = 0.031); and (iii) germination percentage did not differ statistically between seeds that had their elaiosome removed manually and seeds manipulated by ants (F = 0.204, P = 0.651) (Fig. 4).

Discussion

The results of the present study show that *C. arenicola* seeds manipulated by ants and those that had their elaiosome removed manually had higher germination percentages and required less time to germinate than did seeds ingested by the maned wolf and those unmanipulated seeds (with intact elaiosome). These results reaffirm the myrmecochorous character of *Copaifera* species (see also Souza *et al.* 2015b; Gama *et al*. 2019) and suggest that the elaiosome acts as a germination inhibitor that can be mediated by chemical and physical factors (Souza *et al*. 2015b; Fernandes *et al*. 2018).

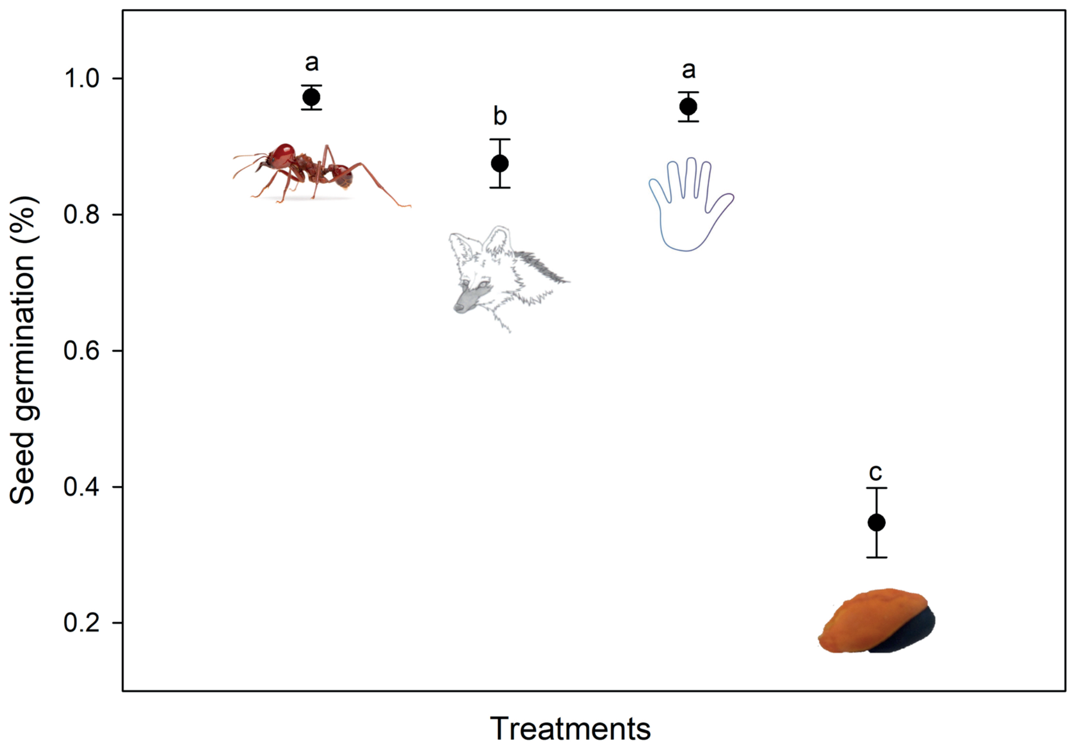

Figure 4. Variation in the percentage of seed germination (mean ± standard error) for *Copaifera arenicola* seeds (N = 72 seeds by treatment) in relation to different treatments. Different letters on the treatments indicate statistically significant differences between treatments according contrast analysis.

Myrmecochory is a seed dispersal syndrome present in about 11,000 plant species distributed among various ecosystems worldwide (Lengyel *et al.* 2009). The genus *Copaifera* comprises 37 species of plants with propagules characterized by the presence of a lipid-rich elaiosome that represents up to 35% of seed weight. Thus far, we are aware of seeds of species of the genus *Copaifera* being dispersed by some species of ants of the genera *Atta* and *Acromyrmex* (Leal & Oliveira 1998; Lopes *et al.* 2018; Fagundes *et al.* 2021). These ants are mainly characterized by the habit of collecting and transporting plant material through trails inside their nests to cultivate fungi that constitute their basic food resource (Holldobler & Wilson 1990). After the elaiosome is removed, the seeds are discarded into the loose soil of the anthill. Despite the possibility of some seeds being lost during transport by ants (Leal & Oliveira 1998; Souza *et al*. 2015b; Fagundes *et al*. 2021), this dispersal mechanism usually results in a clustered distribution of seeds close to anthills, which would explain the occurrence of dense patches of adult plants, especially where the action of other dispersers is low (see Veloso *et al*. 2017; Anjos *et al*. 2020).

The present results also show that the seeds of *C. arenicola* found in the feces of the maned wolf had a higher germination percentage than did intact seeds (unmanipulated seeds). However, germination speed did not differ between these two treatments. Several studies have shown that the passage of seeds through the digestive tract of vertebrates causes physical and/or chemical wear on the tegument that facilitates hydration, thereby increasing seed germinability (Hamalainen *et al*. 2017; Karimi *et al*. 2020). In the present case, it is likely that the great rigidity of *C. arenicola* seeds may limit such physical and/or chemical wear on the tegument during its passage through the digestive tract of the maned wolf. Here it is important to point out that the level of coat scarification of seeds depends upon the retention times in the gut of the frugivore, and the intrinsic traits of the seeds, such as seed size (see Traveset *et al*. 2007). In addition, it is also likely that the entire elaiosome is not digested during the passage of propagules through the digestive tract of the maned wolf and, therefore, small fragments of these appendages that remain on the seeds (M. Fagundes, personal observation) may be partially inhibiting germination.

Although the seeds ingested by the maned wolf showed lower germinability than those without elaiosome (i.e., seeds ant-manipulated and those with elaiosome removed manually), it is important to note that these seeds found in feces of the maned wolf also reached a high germination percentage (about 87%). In addition, the maned wolf is a large animal with a large home range (Bueno *et al*. 2002; Melo *et al*. 2007; Rodrigues *et al*. 2007). These characteristics allow this animal to disperse seeds across long distances from the mother plant, thereby decreasing mortality associated with density-dependent factors and promoting colonization of new habitats and connectivity between plant populations (see also Rehm *et al*. 2019; Karimi *et al*. 2020). Thus, the maned wolf can be considered an important disperser of *C. arenicola* seeds. Finally, it should be noted that *C. arenicola* plants generally occur grouped and produce a large number of seeds per plant during the end of the dry season, when food resource availability for maned wolves is low. Although the availability of food resources was not assessed in this study, other authors (e.g. Bueno *et al*. 2002; Massara *et al*. 2012) suggest that maned wolf´s diet varied seasonally and is dependent on the food resources availability along the whole year. Furthermore, the high nutritional quality of the elaiosome of *C. arenicola* seeds suggests that these propagules may constitute a complementary food resource for the maned wolf especially during periods of food resource scarcity.

In summary, this work reports, for the first time, the transport of *C. arenicola* seeds by the ant *Atta laevigata*. Furthermore, it is the first record of the maned wolf using *C. arenicola* propagules as food. This work also shows that seeds manipulated by the ants and seeds ingested by the maned wolf have high germination percentages, suggesting that these animals are good dispersers of *C. arenicola*. However, seed dispersal by ants results in a clustered distribution pattern, while dispersal by the maned wolf would result in a more irregular dispersal pattern of seeds in the landscape. Therefore, the presence of these vectors occurring in sympatry provides complementary seed dispersal services that are important for the conservation of diversity in areas of the Cerrado (see also Calviño-Cancela *et al*. 2008).

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