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Disentangling plant establishment in sandy coastal systems: biotic and abiotic factors that determine *Allagoptera arenaria* (Arecaceae) germination

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ABSTRACT

Germination rate and establishment success of plants in harsh environments depend on the ability of seeds to withstand unfavorable environmental conditions and avoid predators. Brazilian coastal plains, known as *restinga*, are subject to environmental factors that seriously limit plant establishment and survival (e.g. salinity, desiccation, oligotrophy, flooding, high temperature and radiation levels). We tested, both in field and laboratory experiments, conditions for germination and establishment of *Allagoptera arenaria*, a palm tree often found in *restinga* ecosystems of southeastern Brazil, and which have a principal role in plant community dynamics. Our results showed that the absence of mesocarp, high radiation exposure, and temperature were the main drivers of seed germination. In the field, the highest germination rate was linked to nude seeds buried in open areas. High temperatures and/or predation damaged seeds that remained on the soil surface, especially if they were close to the mother plant and alongside dung piles made by dispersers. Under controlled conditions, seeds exhibited optimum germination at 35 ºC. Therefore, the germination and establishment of *A. arenaria* depend as much on environmental conditions as on a network of interactions including vertebrates and invertebrates, which allow this species to colonize harsh, open areas in *restinga* ecosystems.

Keywords: Arecaceae, facilitation, resting, secondary dispersion, seedling

Introduction

The structure of plant populations is intimately linked to recruitment, and seed germination and seedling establishment are periods of high risk in the plant life cycle, which must occur at the right time and under appropriate conditions (Silvertown & Charlesworth 2001; Tobe *et al.* 2005). Many post-dispersal factors can have profound influence on recruitment (Roberts & Heithaus 1986; Schupp 1990; Howe 1993; Shepherd & Chapman 1998) including environmental conditions such as temperature, radiation, and water availability that greatly influence the development of the embryonic axis during germination (Carvalho & Nakagawa 2000; Vandelook *et al.* 2008; Baskin & Baskin 2014), and seed predation (Janzen 1971; Howe & Smallwood 1982; Schupp 1990). Dealing with unfavorable environmental conditions (Hölzel & Otte 2004) and escaping

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predation often involve mutualistic interactions, such as long seed dispersal away from the mother plant (Janzen 1970; Wicklow *et al*. 1984; Estrada & Coates-Estrada 1991; Comita *et al* 2014). This is the case in *restinga* communities, which occur in sandy plains along the Brazilian coast and show great spatial and temporal fluctuations in water availability (Martin *et al*. 1993). Even during the rainy season, periods of water shortage can occur due to dry spells and the low water retention capacity of sandy soil (Cavalin & de Mattos 2007; Braz & Mattos 2010).

The ability to germinate under environmental constraints gives a species the chance to become established in a community (Bolfrey-Arku *et al.* 2011). In contrast to species unable to stand high temperatures and low water availability (Fialho & Furtado 1993; Pinheiro & Borghetti 2003; Mantovani & Iglesias 2008), some *restinga* species establish in open, sandy sites (Zaluar & Scarano 2000; Scarano 2002) and often act as facilitators of other plant species (Scarano 2002; Scarano *et al*. 2004).

The palm tree, *Allagoptera arenaria* grows in *restinga* areas in southeastern Brazil (Menezes & Araujo 2000), showing high recruitment rates on bare soil, and acting as nucleus of vegetation patches (Zaluar & Scarano 2000). Mature palms modify the environment under their canopy through litter accumulation, increased soil nutrient content, shade, and decreased wind velocity (Menezes & Araujo 1999). Although we have a good understanding of *A. arenaria* life history and dynamics in *restinga* environments, there is a lack of knowledge regarding recruitment conditions in exposed *restinga* soils.

Assuming that seed desiccation and predation are the main post-dispersal causes limiting plant establishment, and that long-distance dispersion from mother plants reduce predation rates (Janzen-Connell effect), we explored mechanisms by which *A. arenaria* thrives in *restinga* habitats. Our hypotheses were that establishment does occur through processes that include mitigation of adverse conditions, especially by burial, and protection against predators through a network of positive interactions involving several species of vertebrates and invertebrates.

Materials and methods

Field site and species

Our field site was at the *Restinga* de Marambaia (23°02'S 43°35'W, sea level), Rio de Janeiro State, where vegetation patches are scattered over a sand matrix with a sparse herbaceous layer (Menezes & Araujo 2005). Climate is tropical rainy (Aw in Köeppen classification) with a mean annual temperature of 23.7 °C, being February the warmest month (mean of 26.8 °C) and August the coldest (20.9 °C). Mean annual precipitation is 1,240 mm, 37 % of which falls in summer. Winter months are significantly drier, with only about 15 % of the annual precipitation falling in approximately 21 days (Mattos 2005). *Restinga* sites show significant spatial variation in environmental conditions, which are buffered in vegetation patches; surface temperature of bare sand can reach 70 °C on a typical summer day (Dias *et al*. 2005), while maximum soil temperatures beneath vegetation patches remain near 25 °C (Mantovani & Iglesias 2008).

Allagoptera arenaria is a palm species about 2 m high which forms dense populations in certain *restinga* sites (Menezes & Araujo 1999) and has a small distribution range between southern Bahia State and the northern coast of São Paulo State (Lorenzi *et al.* 2004). Infructescences contain five to 130 orange to yellowish one-seeded fruits, 12-20 mm long and 10-13 mm in diameter with a sweet fibrous mesocarp and a stony endocarp. The corolla is persistent, covering the fruit. The micropile is lateral and the three germ pores are located slightly basal or lateral. The endosperm is homogeneous and highly rich in lipids (Henderson *et al*. 1995; Moraes 1996; Henderson 2006; Grenha *et al.* 2010). Fruits are mainly dispersed by the crab-eating fox, *Cerdocyon thous*, and the raccoon, *Procyon cancrivorus* (Gatti *et al*. 2006; Andreazzi *et al.* 2009). As other palm species, *A. arenaria* fruits are highly predated by Bruchinae beetles (Grenha *et al.* 2008) and exit holes of Bruchinae species evidencing fruit predation, are easy to recognize at naked eye. The type of germination in *A. arenaria* seeds is the remote tubular. After germination, the seedling develops a plagiotropous form and becomes upright after a short or long period of growth (Moraes 1996).

The *A. arenaria* seeds used in the experiments were collected at the Marambaia restinga in November 2004. Twenty-five thousand fruits were collected, 4 fruits per individual, to guarantee maximum genetic variability in the sample of the tested seeds. The ripe fruits were collected directly from the inflorescences selecting only the yellow staining ones. After harvesting, the fruits were taken to the laboratory and the epicarp and mesocarp were mechanically removed with a knife. A manual selection was performed to discard wilted and damaged seeds, and then the samples were homogenized. Those that did not reach 1.2 cm in width were discarded, since this was the limit found by Leite (1990) for aborted and unviable seeds.

Field experiments

Germination rate of *A. arenaria* was determined under four conditions: either seeds with or without mesocarp were placed on the soil surface or buried 5 cm deep. This burial depth was selected, as temperature 5 cm below the soil surface does not exceed 30 °C at midday (Scarano 2002). We used 8 replicates of 25 seeds each, totaling 1600 seeds.

Experimental plots were protected by wire mesh to avoid predation and seeds were not surface-sterilized. Buried seeds were extracted every two weeks along a 150-day period to determine germination status; non-germinating seeds were buried again. The germination criterion used was the emergence of the 1 mm-long cotyledonary petiole. At the end of the experiment, seeds that did not germinate were sectioned to look for the presence of Bruchinae larvae.

To test for the Janzen-Connell effect we collected five fresh fruits with mesocarp from under 20 *A. arenaria* individuals and five seeds from 20 dung piles of dispersers animals selected 50 m far from the nearest *A. arenaria* individual. Predation criteria were either the presence of Bruchinae larvae or exit holes.

Lab experiments

Four thousand *A. arenaria* seeds were collected in November 2004 from approximately 800 individuals. Mesocarps were removed manually using a knife, and old seeds and those damaged by insects were discarded; seeds less than 1.2 cm wide were also excluded as non-viable (Leite 1990).

To examine the combined effects of temperature and light on germination, seeds were exposed to five treatments at steady temperature (15, 20, 25, 30 and 35 °C) under constant white light (fluorescent light at 30 $\mu mol\ m^{-2}\ s^{-1}$) and dark conditions, using five replicates of 16 seeds each (800 seeds in total). Before the experiment, seeds were surface-sterilized by soaking them three times for 3 min in 5 % sodium hypochlorite solution and then rinsed three times for 3 min with deionized water. Seeds were subsequently sown onto sterilized sand in germination boxes and periodically watered with distilled water. Seeds were checked for germination on a weekly basis for 150 days.

Data analyses

We used t-test and Analysis of Variance (ANOVA), followed by Tukey test to compare mean number of germinated and infested *A. arenaria* seeds when data conformed to parametric premises either before or after transformation. If data did not conform to parametric premises, we compared mean number of germinated and infested *A. arenaria* seeds with the randomization test suggested by Pillar & Orlóci (1996). Post-hoc tests to evaluate significance of differences between means compared with the randomization procedure were done using contrasts between levels of factors (Pillar & Orlóci 1996). Randomization and post-hoc (contrasts) tests were conducted with the MULTIV software package (Pillar 1997). Data are presented as mean ± sd throughout the manuscript. Parametric analyses were performed using the basic interface of the software R v3.0.1 (R Development Core Team 2013)

Results

Seed germination in the field

Seed germination of *Allagoptera arenaria* in the field depended on the presence of mesocarp ($Q = 165.8$; $P = 0.001$, Fig. 1) being the germination rate greater when mesocarp was absent than when it was present (3.7 ± 5.5 vs. 0.5 ± 1.0, respectively). Position was also a determinant for *A. arenaria* germination ($Q = 276.4$; $P = 0.001$), being higher when seeds were buried than when they were on the soil surface (4.2 ± 5.2 vs. 0, Fig. 1). Finally, light condition also influenced germination ($Q = 118.3$; $P = 0.001$), and seeds fully exposed to sunlight germinated more than those in shade (3.4 ± 5.6 vs. 0.7 ± 1.2). Interaction between factors was significant ($Q = 83.3$; $P = 0.006$) and showed *A. arenaria* germination rate was affected by the interaction between the three factors (presence of mesocarp, light condition and seed position [buried or not]). Optimal conditions for *A. arenaria* germination would then be buried seeds without mesocarp in areas fully exposed to sunlight (Fig. 1).

Seed predation by bruchinae beetles

The frequency of seeds with Bruchinae larvae depended on the presence of mesocarp ($Q = 19.1$; $P = 0.01$) since the number of seeds with beetles was greater when mesocarp was present than when it was absent (2.4 ± 2.9 vs 1.3 ± 1.8). When seeds were laying on the soil surface, the presence of Bruchinae larvae were higher ($Q = 206.64$; $P = 0.001$) than when seeds were buried (3.7 ± 2.4 vs. 0.1 ± 0.3), and under shade ($Q = 15.01$; $P = 0.007$) than in fully exposed sunlight (2.4 ± 2.7 vs. 1.4 ± 2.2). There were significant interactions between seed position (sowing conditions) and light condition ($Q = 9.8$; $P = 0.03$) and between sowing conditions and presence of mesocarp ($Q = 13.1$; $P = 0.01$). *Allagoptera arenaria* seeds were more exposed to Bruchinae larvae when laying on the soil surface under shade and with mesocarp (Fig. 2A-B). There were no interactions between seed light condition and presence/absence of mesocarp ($Q = 1.3$; $P = 0.44$ – Fig. 2C) nor between all three factors ($Q = 0.14$; $P = 0.87$ – Fig. 2D). Additionally, we found that *A. arenaria* seeds laying on the soil surface next to the mother plant were more predated by beetles than seeds laying in dung piles 50 m apart from a mother plant ($t = 13.125$, $sd = 37.998$, p-value < 0.0001).

Laboratory seed germination

We found strong effects of mesocarp, light and temperature on *A. arenaria* germination rate in the lab. Seeds without mesocarp had greater germination rate than seeds with mesocarp ($t = -4.7$; $gl = 8$; p-value = 0.001, Fig. 3A);

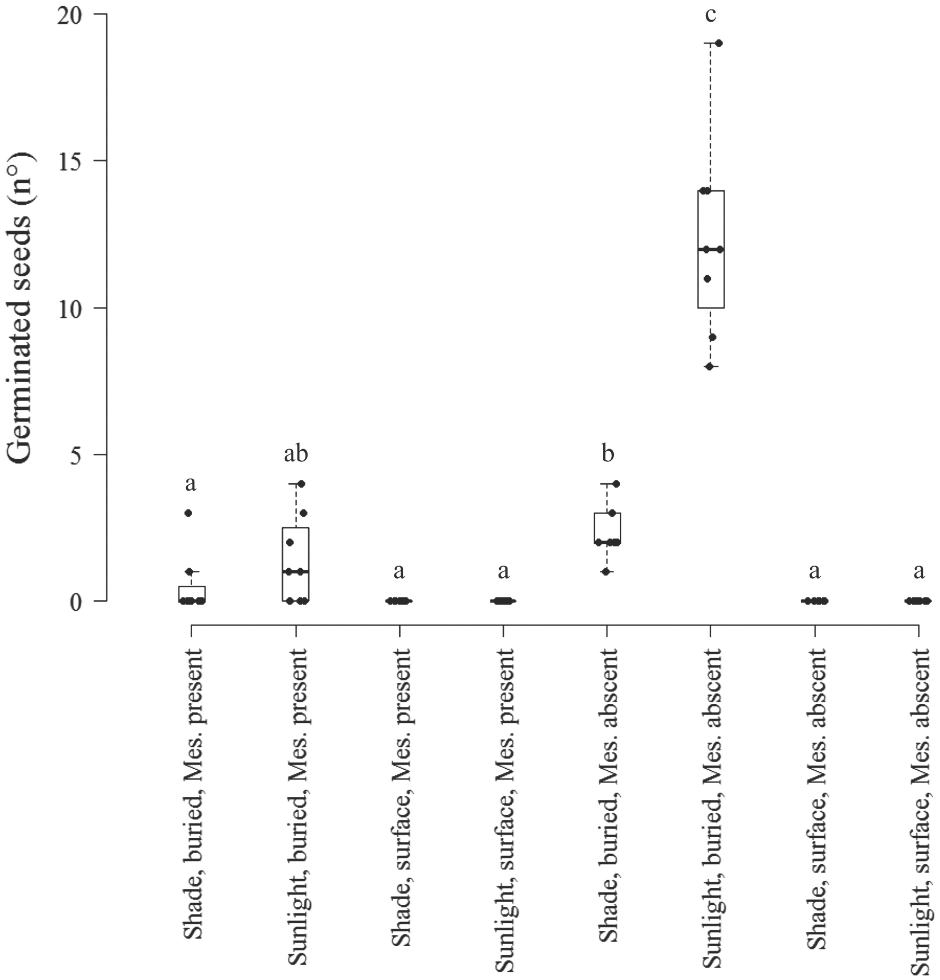

Figure 1. Germination rate of *Allagoptera arenaria* according to habitat, presence of mesocarp and environmental factors. Bars with the same letters are not significantly different (P > 0.05).

seeds germinated more in light than in the dark (Q = 4.8; P = 0.005, Fig. 3B), and germination rate increased linearly with temperature (Q = 74.4; *P* = 0.001, Fig. 3C). The interaction between light and temperature was not significant (Q = 2.2; *P* = 0.398).

Discussion

As expected, seeds of *Allagoptera arenaria* strongly depended for germination and establishment on environmental conditions and interactions with dispersers. In both, field and laboratory experiments, the absence of mesocarp, exposure to light, and temperature were critical for seed germination. Field experiments showed that *A. arenaria* seeds placed directly onto the soil surface had poor germination rates, both in the open and under the canopy. In addition, the presence of mesocarp likewise limited germination. Temperature oscillations may trigger the germination process by breaking the testa in some seeds and in palms could interfere with the process of clearing the germ pore, weakening the pore plate or the operculum (Henderson 2006; Baskin & Baskin 2014). Thus, and even though there is greater water availability beneath tree canopies (Pugnaire *et al.* 1996; Zaluar & Scarano 2000) the buffering of temperatures did not favor seed germination. This pattern is typical of pioneer species (*sensu* Swaine & Whitmore 1988) such as *A. arenaria*, which prefer open areas even though seeds would be more exposed to predators (Grenha *et al.* 2008).

Allagoptera anrenaria, is often a critical component of the *restinga* community as it contributes to the survival of other species acting as facilitator (Menezes & Araujo 2000; Zaluar & Scarano 2000; Scarano 2002; Scarano *et al.* 2004). Facilitators are positively associated to other species and are instrumental in increasing vegetation complexity over time (Armas & Pugnaire 2005). This palm tree shows high recruitment rates on bare soil, becoming dominant and occupying a central position in vegetation patches that

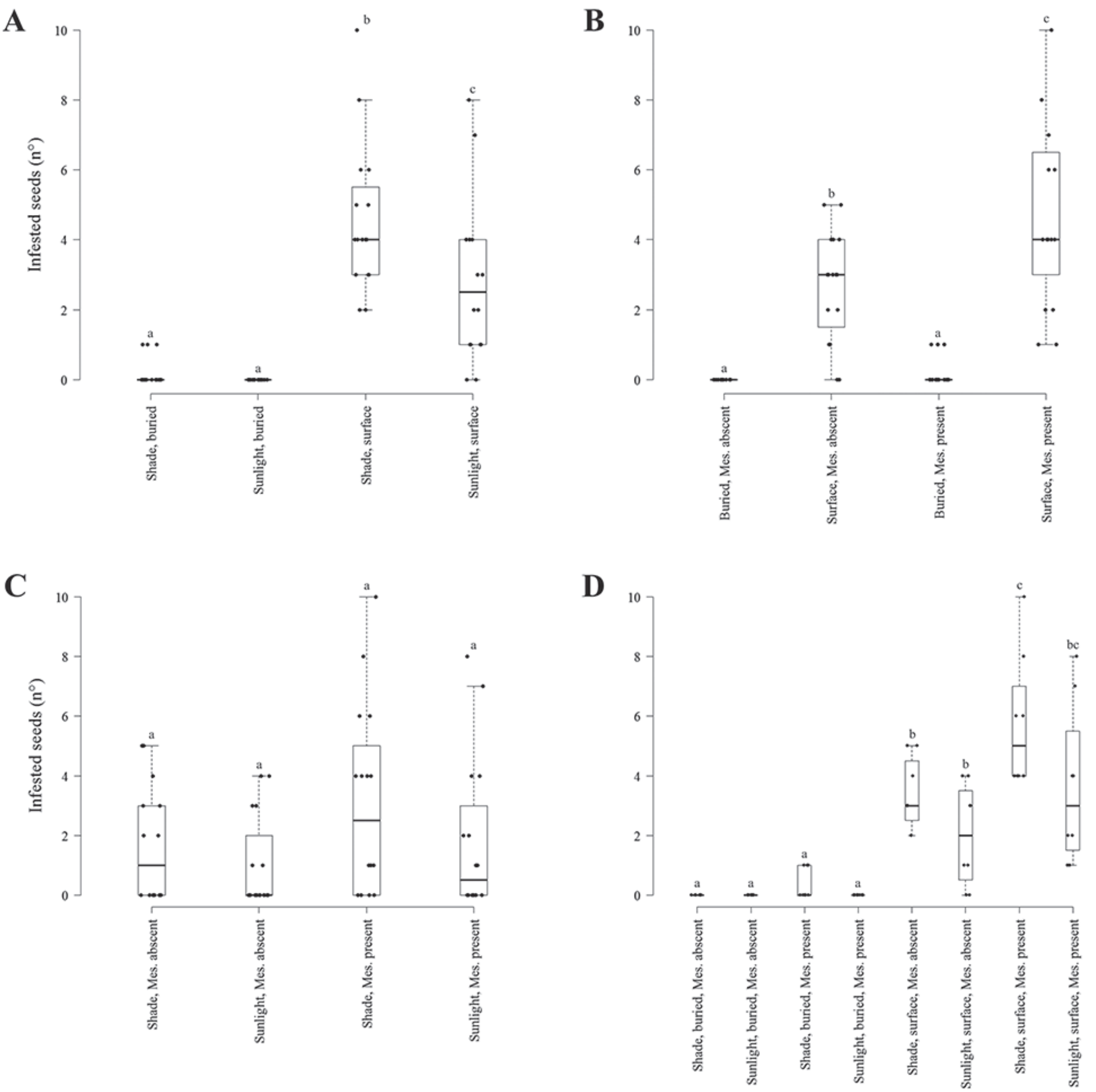

Figure 2. Mean incidence of *Allagoptera arenaria* seed predation by Bruchinae beetles under different conditions. First and second order interactions between environment, mesocarp and sowing condition are shown: **A.** between microhabitat and environmental condition, **B.** between sowing and mesocarp presence; **C.** between environment and mesocarp; **D.** between environment, mesocarp and sowing microhabitat. Bars with the same letters are not significantly different (P> 0.05).

thrive around them, showing a positive spatial association with seedlings of other species (Zaluar & Scarano 2000). Mature individuals act as facilitator species by modifying the environment under their canopy through accumulation of litter, increased soil nutrient content, lowering soil surface and air temperature as well as decreasing wind velocity (Menezes & Araujo 1999).

Our results suggest that a complex sequence of interactions is required for germination success of this *restinga* species. For instance, the high germination rate of naked *A. arenaria* seeds buried in open areas is consistent with dispersal by the Scarabaeidae *Ateuchus squalidus* (Leite 1990). These Scarabaeidae use mammalian dung and fruits as food and/or as oviposition sites (Cambefort & Walter 1991; Hanski 1991; Halffter & Matthews 1966). In *A. arenaria* seeds this beetle is essential for germination. Beetles remove fruits and bury them ca. 5 cm deep, where they feed on the pulp (Leite 1990). Just slightly below the soil surface, temperatures do not exceed 30 °C, close to the optimal germination range for this species. By contrast, seeds remaining on the soil surface in the open would rapidly be damaged by desiccation and

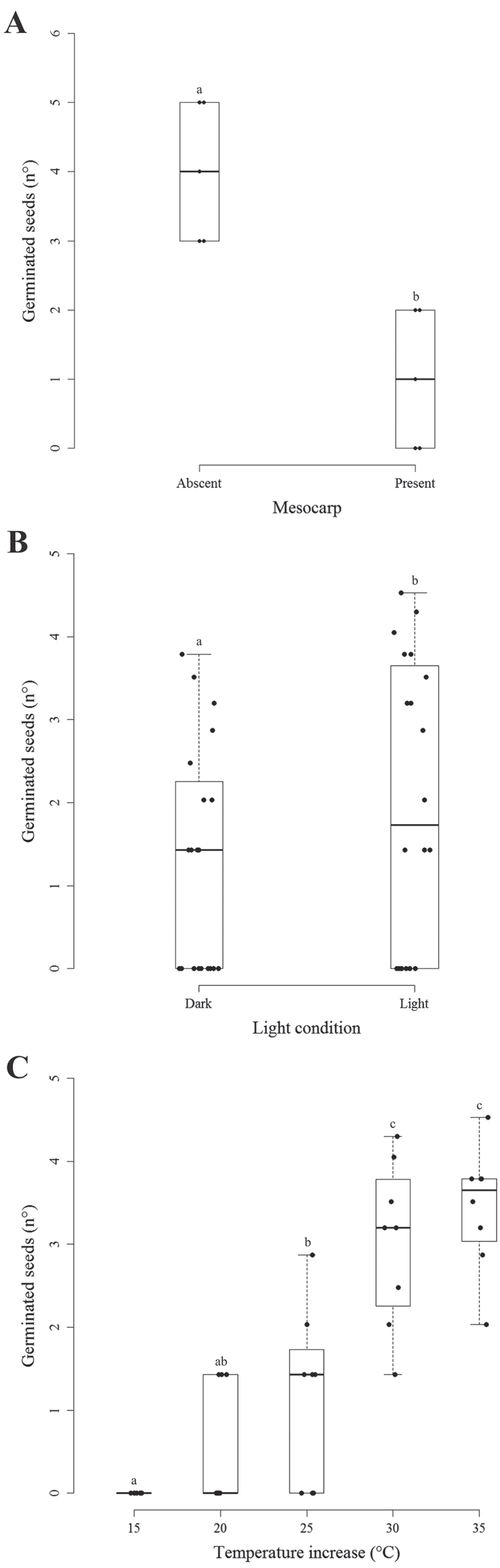

Figure 3. Mean number of seeds germinated in lab conditions **A.** with and without mesocarp, **B.** in conditions of light and dark; and **C.** in five temperature conditions. Black dots represent the dispersion of raw data for each treatment of temperature. Bars with the same letters are not significantly different (P > 0.05).

high temperatures, often reaching 70 °C (Scarano 2002). Therefore, reproductive success of *A. arenaria* strongly depends on the feeding behaviour of *A. squalidus*, an interaction that could be termed as mutualistic. While mutualistic relationships are often difficult to recognize, they are very important in terms of plant population and community structure (Price 1997).

Our results show that *A. arenaria* seeds in dung piles away (50 m) were less predated than those near the parent tree, evidencing the Janzen-Connell effect. Species of the Pachymerini beetle tribe (Bruchinae) feed almost exclusively on palm seeds (Johnson *et al.*1995), being fruit exposure the main cause of bruchinae predation (Silvius & Fragoso 2002). We recorded that mesocarp presence increased seed predation rate. There is a misconception that palm fruits only become predated by Bruchiane beetles after their consumption by frugivores (Wright 1983). However, in our case intact mesocarps significantly contributed to greater Bruchinae predation rates.

Predation by invertebrates is density-dependent, so that the greater accumulation of seeds the greater number of beetles (Wilson & Janzen 1972; Shepherd & Chapman 1998; Galetti *et al.* 2001). However, Bruchinae beetles generally have low dispersal capacity and move short distances between plants, so that individuals are often restricted to the understory of a palm tree for their whole life (Janzen 1971). Frugivores, by contrast, take fruits away from the mother plant, preventing the accumulation of fruits and thus reducing Bruchinae predation. Therefore, dung piles deposited by dispersers somehow are a way of seed protection against Bruchinae while helping dispersal of seeds to significant distances from the mother plant (Fragoso 1997; Quiroga-Castro & Roldán 2001; Fragoso *et al.* 2003) avoiding competition for resources (Janzen 1970; Pimentel & Tabarelli 2004; Rios & Pacheco 2006). Bruchinae predation can reach up to 100 % of exposed seeds in some palm species (Wenny 2000; Russo & Augspurger 2004) in contrast to low predation rates in dung piles (Quiroga-Castro & Roldán 2001; Rios & Pacheco 2006). For instance, only 2 % of *Attalea maripa* seeds in dung piles were predated by Bruchinae beetles as compared to 77 % of seeds lying under parent palm trees (Fragoso 1997); and only 6 % of *Attalea phalerata* seeds in mammalian dung piles were predated, against 61 % of seeds under parent trees (Quiroga-Castro & Roldán 2001).

Long-distance dispersal of *A. arenaria* seeds in *restinga* environments depends on two vertebrates, *Cerdocyon thous* and *Procyon cancrivorus*, in which more than 80 % of scats contain palm seeds (Gatti *et al.* 2006; Andreazzi *et al.* 2009). They are also responsible for the clumped distribution of *A. arenaria*. Dung beetles use both fruits and mammalian dung as fodder and oviposition sites (Cambefort & Walter 1991; Hanski 1991; Halffter & Matthews 1966), acting as secondary dispersers and positively affecting seed survival by preventing predation (Wicklow *et al.* 1984; Estrada & Coates-Estrada 1991; 1996). The minimum temperature for *A. arenaria* germination was 20 °C (2.7 %), with the greatest germination rate at 35 °C (40 %), unusually high compared to other tropical species (Mello & Barbedo 2007; Cardoso & Pereira 2009; Pires *et al.* 2009; Pimenta *et al.* 2010). Optimum temperature for germination corresponds to temperatures usually experienced at the time of seedling emerge (Baskin & Baskin 2014; Bell *et al.* 1993) which in *A. arenaria* is the summer period, when water availability is greatest. Temperature control of germination could determine the geographical range of many plant species (Thompson 1973; Probert 1992) and for *A. arenaria* may represent a limiting factor as temperatures decrease further south.

Conclusion

Our results show that *A. arenaria* colonizes open areas in *restinga* systems mostly through mutualistic interactions that help escape both, unfavorable conditions and predation, thus confirming our hypotheses. On the one hand, vertebrates contribute to long-distance dispersal and the protection of seeds within dung piles, crucial against Bruchinae beetles, the main predators of *A. arenaria* seeds. On the other hand, secondary dispersal by the beetle *Ateuchus squalidus* contributes to germination success. Then, establishment of *A. arenaria* in open areas of *restinga* is the outcome of a complex interaction network between dispersers and predators, which place seeds in the best possible microhabitat for establishment. This interactions network is essential to maintain *restinga* community dynamics.

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