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A double defensive mutualism? A case between plants, extrafloral nectaries, and trophobionts

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Defensive mutualisms are common in tropical plants (Rosumek et al. 2009). In these interactions, ants can reduce plant herbivory through a combination of direct predation on herbivores and/or aggressive behavior toward herbivores that avoid ant-infested plants or are expelled when they arrive (Rosumek et al. 2009). Plants often attract ants by offering food resources such as extrafloral nectaries (EFNs), beltian bodies, or shelters such as domatia (Bronstein et al. 2006). Another type of protection is provided by trophobiosis, which is the interaction between ants and phytophagous hemipterans that secrete sugary exudates. The main benefit provided by the attendant ants to their trophobionts is protection from predators and parasitoids. In contrast, the damage that herbivores cause to their host plants can be minimized by the suppressive effect of predatory ants that forage on foliage (Styrsky and Eubanks 2007). In all of these interactions, ants patrol the plants reducing herbivore abundance, increasing plant defenses, and benefiting plants through increased vigor and reproduction (Rosumek et al. 2009).

A very particular case involving different biotic defenses occurs in an endemic plant from Brazil that occurs in the Cerrado region (Fig. 1). This species, *Zeyheria montana* Mart. (Bignoniaceae, Fig. 2A), has EFNs on the leaf blade

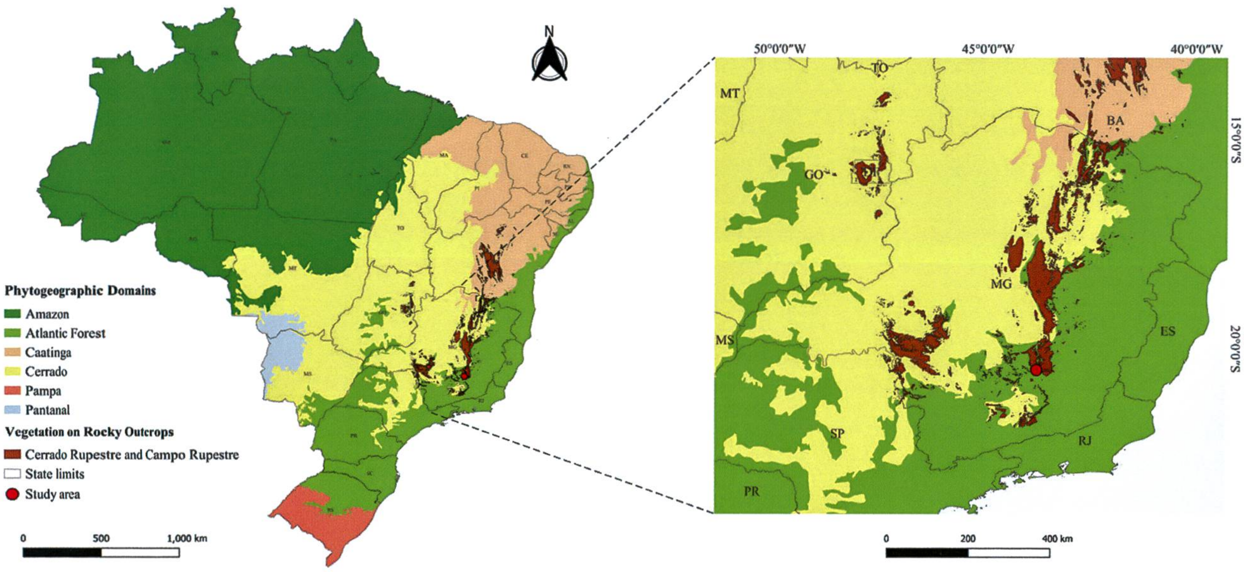

Figure 1. Map of the geographic location of the population of *Zeyheria montana* Mart. studied in the Cerrado Rupestre of Minas Gerais, Brazil. The boundaries of Brazilian phytogeographic domains were adapted from shapefiles available from the Instituto Brasileiro de Geografia e Estatística (2022) and the global ecoregions of Dinerstein et al. (2017). The vegetation on rocky outcrops is the combination of shapefiles from the rupestrian grasslands by Newton Barbosa and the iron outcrops of Serra dos Carajás in the State of Pará provided by Fernando Santos. Map design: Cássio Cardoso Pereira.

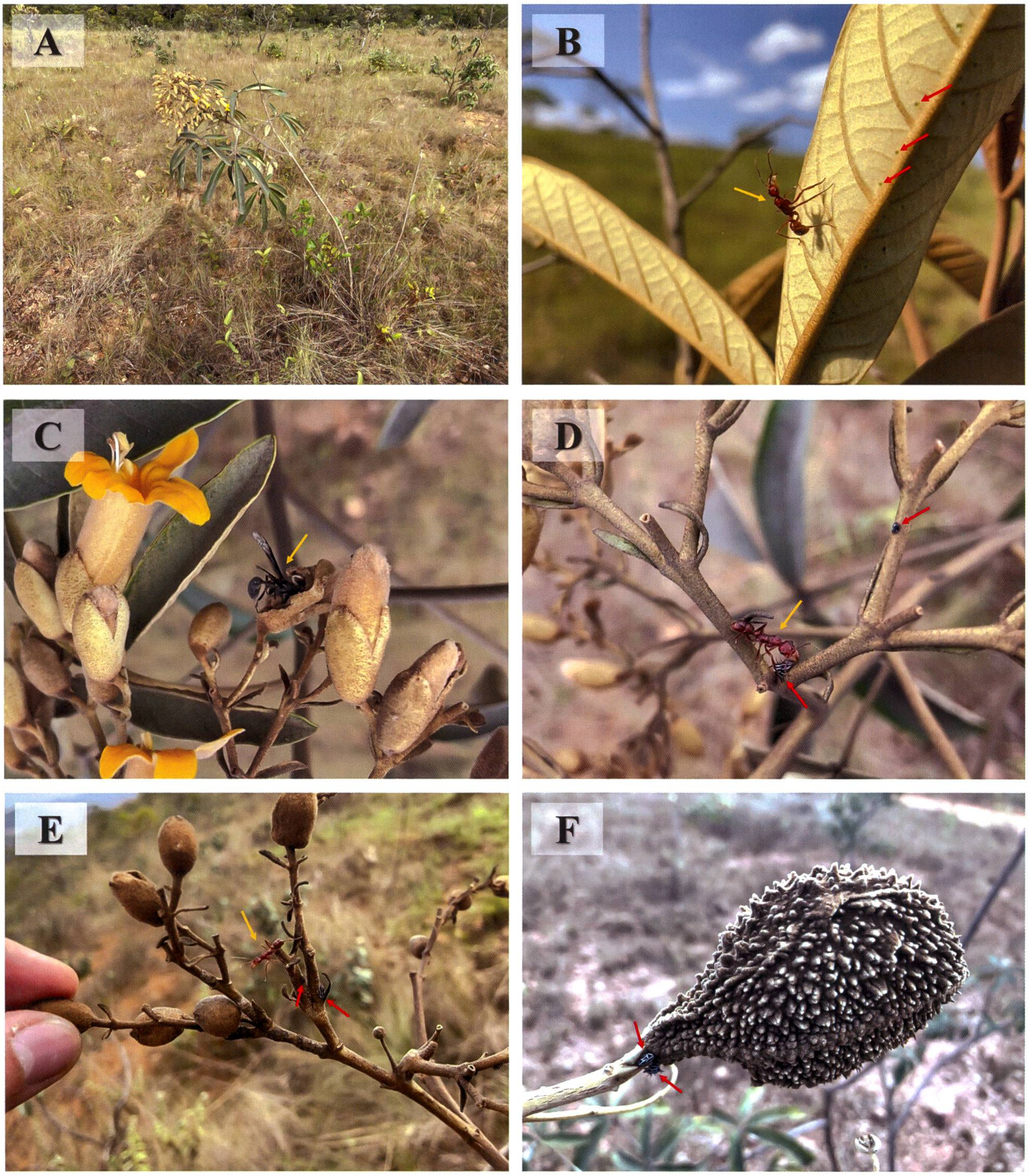

Figure 2. A. Individual of *Zeyheria montana* Mart. on rocky outcrops in Minas Gerais, southeastern Brazil; **B.** *Ectatomma tuberculatum* (Olivier, 1792) on the leaf blade of the *Z. montana*. The yellow arrow points to the ant and the red arrows point to the extrafloral nectaries; **C.** Wasp (yellow arrow) removing nectar inside the flower bud of *Z. montana*; **D.** Interaction between the ant *E. tuberculatum* and the treehopper *Guayaquila xiphias* (Fabricius, 1803), which provides honeydew in exchange for protection. The yellow arrow points to the ant and the red arrows point to the treehoppers; **E.** Reaction of the aggressive *E. tuberculatum* ant, which protects the treehoppers from attacking invaders. The yellow arrow points to the ant and the red arrows point to the treehoppers; **F.** The treehoppers *G. xiphias* (red arrows) at the base of *Z. montana* fruits.

(Machado et al. 2008). These EFNs attract patrolling ants such as the aggressive *Ectatomma tuberculatum* (Olivier, 1792), which in turn defends the leaves against herbivores (Fig. 2B). While EFNs are an important resource attracting ants to the leaves, they might also function to distract ants from the costly flowers and reproductive parts, preventing them from driving away visitors and potential pollinators (Villamil et al. 2019). Thus, keeping ants away from reproductive tissues can benefit florivores and nectar thieves that usually approach flowers (Fig. 2C).

This does not seem to be a problem for *Z. montana*. Surprisingly, in a population of this shrub that occurs in the Cerrado Rupestre, a rare ecosystem on rocky outcrops above 800 m altitude in Minas Gerais (Pereira and Fernandes 2022), southeastern Brazil (Fig. 1), we observed a second defensive mutualism occurring on these plants throughout 2021. The reproductive tissues of this shrub host the treehopper *Guayaquila xiphias* Fabricius, 1803 (Membracidae), which provides honeydew to *E. tuberculatum* in exchange for protection (Fig. 2D). This trophobiotic relationship persisted throughout the plant's reproductive period and seems to be effective not only as a defensive strategy for flower buds and flowers (Fig. 2E) but also for the fruit (Fig. 2F), which, although is a dry fruit and dispersed by wind, was attacked by weevils because it contains a significant amount of water during its development (personal observation). Finally, although these ants fight florivores, nectar robbers, and frugivores, they probably do not harm pollination because *Z. montana* is mainly pollinated by hummingbirds (Araújo et al. 2013), which, in addition to not landing on flowers and being larger, were not chased away by ants (personal observation).

This is the first case reported in the literature involving EFNs, ants, and trophobionts occurring simultaneously on a plant species. Future studies shall be carried out to assess whether this combination of defensive mutualisms can increase the fitness of these plants. We wonder how frequent simultaneous defensive mutualisms can be, which are generally not quantified or reported in the literature.

Common or not, we emphasize that insect–plant interactions such as those presented here are at serious risk of disappearing along with the rare environments in which they occur (Pereira and Fernandes 2022). Biodiversity has been increasingly impacted by climate change, pollution, habitat destruction, invasive alien species, and overexploitation of natural environments, which lead several species to population collapse (Cardinale et al. 2012). The extinction of a single species involved in mutualism can lead, in the long term, to the disappearance of other species dependent on the interaction, affecting other levels in the large network of relationships between species. This cascade effect can affect the functioning of ecosystems, leading to dramatic changes in community composition, including the loss of species, interactions, functions, and ecosystem services (Galetti et al. 2013). Therefore, in addition to preserving more natural areas, we urgently need measures to mitigate human impacts on biodiversity so that interactions such as those presented here can be maintained and preserved.

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