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Is *Megaplatypus mutatus* (Chapuis) (Curculionidae: Platypodinae) a threat to *Khaya grandifoliola* (Meliaceae)? Observations from Brazil

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ABSTRACT

The ambrosia beetle *Megaplatypus mutatus* (Chapuis) (Coleoptera: Curculionidae: Platypodinae) is native to South America and is an important forest pest in poplar plantations in Argentina as well as in Italy where it has been introduced. Unlike most platypodine ambrosia beetles, it targets specifically live and vigorous trees. We report for the first time an attack on African mahogany trees, *Khaya grandifoliola* C. DC., by *M. mutatus* in Brazil, indicating its preference for trees with larger diameters. Most attacked trees exhibited only one or two gallery entrance holes, primarily along the lower 2 m of the trunk. However, colonization was impeded by gummosis, a plant defense mechanism. Overall, the attack rate was low, with nearly all of them failing to produce progeny. *Megaplatypus mutatus* exhibited a multivoltine life cycle in the study region, and most specimens captured in traps baited with the beetle's sex pheromone were females. Adults of neither sex responded to traps baited with ethanol. Although successful reproduction was not evidenced in *K. grandifoliola,* gallery initiation could still affect timber quality. Therefore, regular monitoring of *Khaya* plantations for potential *M. mutatus* infestations is recommended to mitigate potential impacts on tree health and timber value. Additionally, we proposed here a novel classification of Platypodinae species into 'A' and 'B' categories, based on their behavioral patterns and ecological interactions.

Introduction

Plantations of African mahogany (*Khaya* spp., Meliaceae) have expanded in Brazil in recent decades due to the high quality and economic value of the timber being used in the furniture industry (plywood, paneling, interior trim, flooring), and even for musical instruments and boatbuilding (Ribeiro et al., 2019). Most of Brazil's African mahogany timber is currently sold domestically, with a small percentage exported, mainly to Caribbean countries (ITTO, 2023).

However, many groups of insects can threaten African mahogany production in Brazil, both by their direct impact on the trees as well as by affecting international timber markets if the insects are considered quarantine pests by the importing countries. For example, leaf-cutting ants, *Atta* and *Acromyrmex* (Formicidae), and the mahogany shoot borer, *Hypsipyla grandella* (Zeller) (Pyralidae), are often mentioned in the literature as African mahogany pests in Brazil (Falesi, 2012; Zanetti et al., 2017; Covre et al., 2018a). In addition, beetle species of Scolytinae and Platypodinae (Curculionidae) have been reported to infest various *Khaya* species both in nurseries and plantations in several states of Brazil (Covre et al., 2018b, 2018c; Cristovam et al., 2018; Pelozato et al., 2018; Lunz and Reis, 2019).

Most Scolytinae are secondary pests, attacking their hosts when the plants are weakened by environmental stress, such as drought, fire, lightning and various silvicultural treatments (Wood, 1982; Mattson and Haack, 1987; Flechtmann et al., 1995). This is also the case with most Platypodinae (Roberts, 1977a; Milligan, 1979; Inoue et al., 1998; Bellahirech et al., 2019). However, some Platypodinae can infest apparently live and healthy trees (Browne, 1961; Santoro, 1963; Alfaro et al., 2007).

Among the few Platypodinae known to attack live and apparently healthy trees, a specific group of species, *Austroplatypus incompertus* (Schedl), *Dendroplatypus impar* (Schedl), *Megaplatypus mutatus* (Chapuis) and *Platypus tuberculosus* Strohmeyer. These species attack and develop exclusively in hosts that are in apparently good health (Santoro, 1957; Browne, 1961; Santoro, 1963; Kent and Simpson, 1992; Kent, 2001; Alfaro et al., 2007), and will be hereafter designated as 'A1'. In contrast, another group, hereafter designated as 'A2', *Notoplatypus elongatus* Lea and *Trachyostus ghanaensis* Schedl, includes species

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that will attack live trees that are however under some sort of stress (Roberts, 1960; Kent, 2001).

For all Platypodinae species known to have live trees as hosts, collectively referred to as group ‘A’ (‘A1’ plus ‘A2’), there is a tendency to attack only trees with a diameter at breast height (DBH) greater than 19 cm (Roberts, 1960; Browne, 1961; Kent, 2001). The reasons for this preference remain unclear; however, it may be attributed to two factors, acting together or individually: the shape of the gallery system, and the body size of the beetle. For certain species the gallery system requires considerable space. This is particularly true for *D. impar* and *M. mutatus*, where the gallery is built in a transverse plane, and curves gradually in a spiral close to the center of the heartwood (Santoro, 1957; Browne, 1961). This should also be the case with *A. incompertus*, a eusocial species with multiple generations in the same gallery system, in which the gallery system grows over the years, and where there is a positive relationship between tree size and the volume of wood available to support the colonies (Kent and Simpson, 1992; Kent, 2001; Smith et al., 2018). Thus, it is possible that *M. mutatus* has a preference for larger DBH host trees because these trees also provide more space for offspring development (Marquina et al., 2006), which can be as high as ca. 200 emerging adults on average in one single parental gallery (Santoro, 1963).

In contrast to group ‘A’, the vast majority of Platypodinae species attack only stressed, dying or felled trees – hereafter classified as ‘B’ species, and in this group there is no apparent preference for a particular minimum tree DBH, which may vary, often within a single species, from twigs a few centimeters wide to tree trunks as large as 15 – 20 cm in diameter. Some examples of ‘B’ species include *Crossotarsus externedentatus* (Fairmaire), *Dinoplatyus calamus* (Blandford), *Euplatypus parallelus* (Fabricius), *Platypus apicalis* White, *Platypus gracilis* Broun, *Platypus subgranosus* Schedl and *Treptoplatypus caviceps* (Broun) (Elliott et al., 1987; Roberts, 1977a; Milligan, 1979; Hijii et al., 1991; Li et al., 2018). However, three notable exceptions among the ‘B’ species are *Platypus cylindrus* (Fabricius), which attacks hosts with a DBH greater than 20 cm (Bellahirech et al., 2019), *Platypus gerstaeckeri* Chapuis (DBH > 14 cm; Roberts, 1977a) and *Platypus quercivorus* (Murayama) (DBH > 14 cm; Hijii et al., 1991), where the minimum DBH reported in the literature for attacked hosts exceeds 14 cm.

Body size of beetles may also play an important role in determining host diameter selection. For at least some Scolytinae species, body size is directly correlated with host diameter preference (Beaver, 1977). All ‘A’ species can be classified as large, with a body length of 5 mm or more (Chapuis, 1865; Lea, 1910; Strohmeyer, 1910; Schedl, 1936, 1959, 1968), when compared to ‘B’ species, which have an overall body length of less than 5 mm (Milligan, 1979; Candy, 1990; Hijii et al., 1991).

Megaplatypus mutatus is native to South America, where it is known to occur in Argentina, Bolivia, Brazil, French Guiana, Paraguay, Peru, Uruguay and Venezuela (Reichardt, 1964; Ceriani-Nakamurakare et al., 2022). In Brazil, it has been reported in the states of Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo (Schedl, 1950; Reichardt, 1964; Schönherr and Pedrosa-Macedo, 1981; Zanuncio et al., 2010; EPPO, 2020). Outside its native range so far, *M. mutatus* has been introduced only into Italy (Tremblay et al., 2000; Griffo et al., 2012). The addition of *M. mutatus* in the EPPO Alert List in 2004 and its inclusion as an EPPO A2 quarantine pest in 2007 resulted from its introduction into Italy and the risk it posed to trees in other European and Mediterranean countries (EPPO, 2004, 2007).

Megaplatypus mutatus is highly polyphagous, infesting several species of live forest, nut, fruit, and ornamentals trees, and is especially damaging to eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) and hazelnut trees (*Corylus avellana* L.) in Argentina and Italy (Giménez and Etiennot, 2003; Allegro and Griffo, 2008). Additionally, this beetle has also been reported to infest various Meliaceae species, including *Melia azedarach* L., *Cedrela fissilis* Vell. and other *Cedrela* species (Schedl, 1950; Santoro, 1960; Giménez and Etiennot, 2003). In Brazil specifically, reports indicate that *M. mutatus* infests both native and some exotic tree species (Schedl, 1950; Reichardt, 1964; Schönherr and Pedrosa-Macedo, 1981; Santana and Santos, 2001; Girardi et al., 2006; Queiroz and Garcia, 2007; Carvalho Filho et al., 2008; Zorzenon et al., 2008), including eastern cottonwood (Flechtmann, unpublished results), and various *Eucalyptus* species (Pinheiro, 1962; Zanuncio et al., 2010), such as *Eucalyptus saligna* Smith (Flechtmann et al., 2004).

Infestations primarily occur in live, apparently healthy trees, with a trunk DBH of at least 15 cm-(Santoro, 1957; Casaubon et al., 2006; Lucia et al., 2014). Direct damage to the tree results from the galleries that *M. mutatus* adults and larvae create in the wood, making the trees prone to wind throw when infestations are high (Santoro, 1957). Indirect damage results from the staining of the wood caused by the beetle’s symbiotic fungi that spread from their galleries (Santoro, 1957; Guerrero, 1966).

Platypodines often fail to establish successful broods because they are not able to overcome tree defenses. Roberts (1968) listed several reasons for brood failure in platypodines, including failure to attract a mate, host resistance, failure to grow the symbiotic ambrosia fungi, and natural enemies. One mechanism of host resistance involves the production of gum, which occurs in tree families, including Meliaceae (Pennington and Styles, 1975). In *Khaya* species (Meliaceae) gum is found in phloem vessels (Panshin, 1933), pores (Donkor, 1997) and in the secondary xylem (Pennington and Styles, 1975). There are several factors that cause the exudation of gum, or gummosis, and among those are injuries inflicted by insects (Jones, 1959; Taylor, 1960; Irvine, 1961; Roberts, 1969, 1977b; Nussinovitch, 2010). Gum exudation acts as a physical defense against invading insects, encircling and embalming them when they bore through the bark (Jones, 1959). The chemical constituents of *Khaya* gum contain several secondary metabolites (Konno, 2011), and have been extensively studied, including those of *Khaya grandifoliola* C.DC. (Aspinall et al., 1956; Aspinall and Bhattacharjee, 1970; Banerji and Nigam, 1984; Guimarães, 2007). These secondary metabolites may constitute a secondary line of defense, a chemical one, against insect borers (El-Aswad et al., 2004; Konno, 2011). Gummosis as a defense mechanism against platypodines is well known. Some examples include *A. incompertus*, *C. externedentatus*, *P. apicalis*, *T. caviceps*, *P. gracilis*, *Trachyostus aterrimus* (Schaufuss), *Trachyostus carinatus* Schedl, *T. ghanaensis* and *Trachyostus schaufussi schaufussi* Strohmeyer (Roberts, 1968; Wright and Harris, 1974; Roberts, 1977a; Milligan, 1979).

Like other ambrosia beetles, *M. mutatus* has a cryptic lifestyle, spending most of its life cycle hidden and protected within its host trees (Santoro, 1957). For this reason, the effectiveness of insecticides is generally low (Griffo et al., 2012). The pheromone of *M. mutatus* has been identified and could be useful as a monitoring tool or possibly as a mating-disruption technique (Funes et al., 2011; Gonzalez-Audino et al., 2013; Funes et al., 2016; Ceriani-Nakamurakare et al., 2017) and as a monitoring tool (Funes et al., 2009; Gonzalez-Audino et al., 2011).

Recently, in the state of Minas Gerais *M. mutatus* was found infesting commercial plantations of *K. grandifoliola*. Our objectives were to (1) assess the efficacy of semiochemicals to attract this beetle, (2) to study its flight activity and seasonality, and (3) to measure the success rate of *M. mutatus* attacks on *K. grandifoliola*.

Materials and methods

Study Sites

The study sites were stands of different ages of African mahogany, *K. grandifoliola* (20°7’30.73”S 46°27’32.56”W) in São Roque de Minas, state of Minas Gerais, Brazil (Fig. 1, Table 1). Spacing between trees in all stands was 6 x 6 m, except for stand 6, where spacing was 6 x 12 m. The understory at all sites was generally clear of any competing woody species that could attract or sustain *M. mutatus* development.

Inspection of Trees Attacked by Megaplatypus mutatus

Trees with signs of *M. mutatus* attack were inspected from July 2016 until April 2021 (Table 2). The inspections varied among stands and years, but for each inspected tree, the number of active galleries (where frass and sawdust were actively being expelled; Figs. 2a, c), inactive galleries (i.e. where the gallery entrance hole was clogged with gum exuded by trees; Fig. 2d), and their height above the ground were recorded. We visually inspected the lower trunk on each tree up to the base of the crown and recorded data in the following intervals: (1) from ground level to 50 cm, (2) 51-100 cm, (3) 101-150 cm, (4) 151-200 cm, and (5) above 200 cm. Given that the trees were growing uniformly, we used timber stand inventory values for average DBH from 2016 to 2021 (Table 1).

Flight Seasonality and Semiochemical Assay

Flight intercept traps (modified from Berti Filho and Flechtmann, 1986) were placed at 1.5 m above ground and baited with either 96% ethanol or the *M. mutatus* sex pheromone, which consists of a blend of sulcatol, sulcatone and 3-pentanol (Gonzalez-Audino et al., 2005; Gatti-Liguori et al., 2008a). Each pheromone component was placed in an individual sachet and then suspended together in each trap. The pheromone-baited traps (N = 11) were deployed only in Stand 1, whereas the 35 ethanol-baited traps were dispersed among 9 stands (Table 1). The release rates of the three pheromonal components were 10.0, 7.8 and 40.0 mg/d at 25°C (ChemTica International, S.A., Costa Rica), respectively, while that of ethanol was 870 mg/d at 20°C. The pheromone dispensers were changed every three months and ethanol was replenished every week. The traps were checked weekly from 5 August 2017 until 28 September 2018, which equals 61 trapping weeks. For each trap and collection date, adult beetles were placed in labelled individual vials, returned to the laboratory, and identified based on specimens deposited in the MEFEIS collection. Voucher specimens of trapped beetles were deposited in the Museu

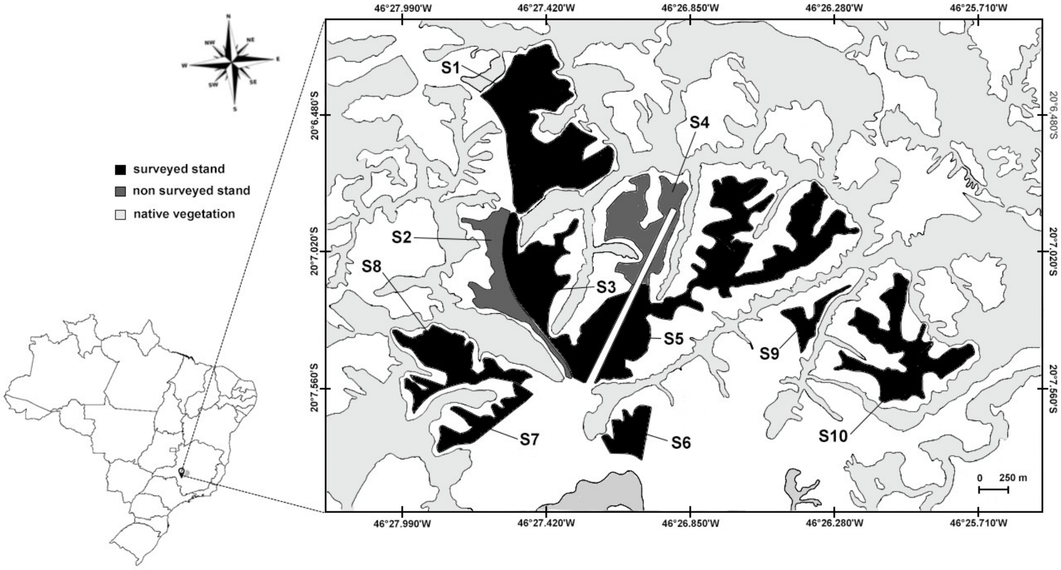

Figure 1 Delimitation of study areas. African mahogany (*Khaya grandifoliola*) stands (S1 to S10) and surrounding native vegetation in São Roque de Minas, Minas Gerais, Brazil.

Table 1. Stand number, planting date, stand age (as of June 2016), diameter at breast height (DBH; in cm) based on timber stand inventory data, and number of ethanol (Etoh) and pheromone (phero: sulcatol + sulcatone + 3-pentanol) baited flight intercept traps deployed in African mahogany (*Khaya grandifoliola*) stands in São Roque de Minas, Minas Gerais state, Brazil.

Stand number (planting date)	Stand age (months)	Area (ha)	Mean DBH (cm)						# Traps	
			2016	2017	2018	2019	2020	2021	Etoh	Phero
1 (Mar2010)	75	56.2	20.6	23.1	25.0	26.6	28.1	29.2	4	11
2 (Dec2012)	40–42	16.2	12.2	15.1	18.8	21.6	24.2	26.0	0	0
3 (Dec2012)		52.3							10	0
4 (Feb2013)		22.5							2	0
5 (Jan2013)		44.7							5	0
6 (Jan2013)		8.1							3	0
7 (Feb2013)		8.6							2	0
8 (Feb2013)		19.5							5	0
9 (Dec2013)	30	6.0	7.5	11.5	15.6	19.5	22.2	24.6	1	0
10 (Dec2013)		29.2							3	0

Table 2. Stands evaluated, inspection date, number of sampled trees, attacked trees, and total number of gallery entrance holes made by *Megaplatypus mutatus*.

Stand*	Inspection date	# Sampled trees	# Attacked trees	# Holes
1	Jul 2016	15625	37	56
10	Jan 2018	8125	1	1
9	Mar 2018	1675	0	0
5	Jul 2018	6200	3	4
8		5428	0	0
1	Dec 2019	7800	3	3
1	Mar 2021	10000	2	2
5		6000	0	0
7		1190	0	0
3	Apr 2021	6000	3	3
6		1000	2	3
7		1000	2	2
10		3000	8	13

*See stand locations in Fig. 1.

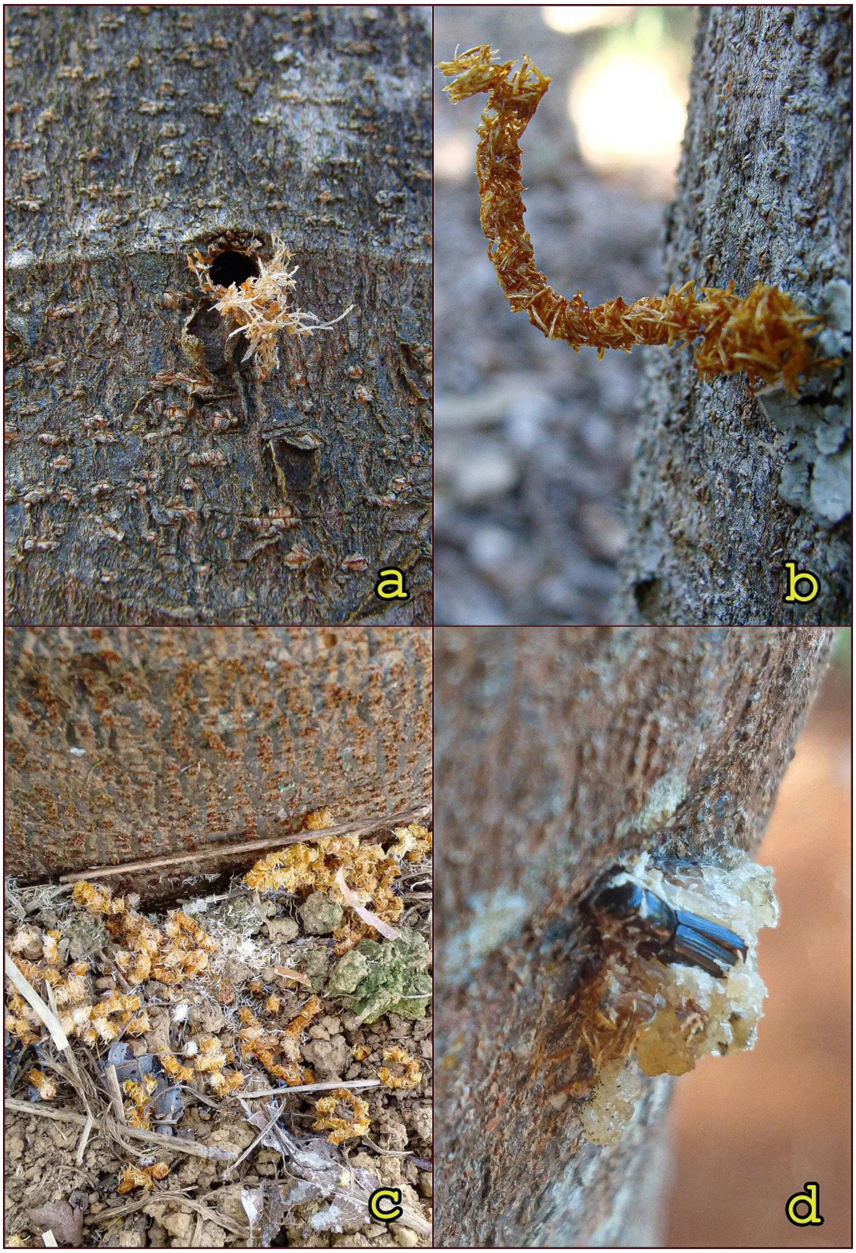

Figure 2 *Megaplatypus mutatus* in *Khaya grandifoliola* trunks. (a) entrance hole, (b) “toothpick” (frass aggregate); (c) frass pellets on the ground; (d) gummosis (pitched-out male beetle). São Roque de Minas, state of Minas Gerais, Brazil.

de Entomologia da FEIS/UNESP (MEFEIS), Ilha Solteira, state of São Paulo, Brazil.

Climatic data, including daily air temperature (maximum, minimum and mean), and mean weekly air relative humidity and rainfall data were obtained from the Meteorological Station "A565" (20°1'52"S 46°0'3"W) of The Instituto Nacional de Meteorologia (INMET) in Bambuí, Minas Gerais. This weather station was the nearest to our study site, although about 48 km away.

We divided the collection periods into a "rainy season", with generally higher temperatures and more rainfall, and a "dry season", with generally cooler temperatures and less rainfall (Flechtmann et al., 1995; Covre et al., 2021). The "dry season" corresponded to the periods of 5 August to 22 September 2017 and 13 April to 28 September 2018, while the "rainy season" fell between 23 September 2017 and 12 April 2018.

The meteorological variables and *M. mutatus* trapping data (catches between "seasons" and lures) were compared using the generalized linear model (Proc GLM) and separated by the Tukey test with an alpha level of 0.05 (SAS Institute, 1990). Differences in attack frequency by height above ground were compared with the Kruskal-Wallis test (proc NPAR1WAY Wilcoxon) (SAS Institute 1990).

Results

Inspection of Trees Attacked by Megaplatypus mutatus

We began site visits in June 2016, when damage by *M. mutatus* on *K. gradifoliola* trees was first observed. Damage was limited to Stand 1 (Fig. 1), which was the oldest stand in the plantation with the largest trees (Table 1). Trees in Stand 1 had undergone branch pruning during March and April of 2016 with the branches left on the forest floor. During this first site visit, we cut down one tree with three active *M. mutatus* galleries that were located at 0.8, 1.5, and 1.6 m above ground. The galleries at 0.8 m and 1.6 m each contained a male and a female parent adult, while the third gallery had only a male adult. All adults were alive and located at the end of short galleries, indicating that the attacks were recent.

During the July 2016 inspection of Stand 1, 37 trees were found to be infested, which corresponded to less than 1% of all trees in the stand (Table 2). We found an average of 1.5 galleries per infested tree (range 1–5). For the 37 trees, 56 entrance holes were counted, with 83% classified as active (with fresh frass and sawdust), and 17% considered inactive (where gum had been secreted by the trees to "flood" the galleries, which apparently killed or expelled the invading beetles). Entrance holes were found along the trunks from 5 cm to 3 m above the ground, with 75% between 0.5 cm to 1.5 m. The attacks were all located in the interior of Stand 1, having a clumped distribution, and concentrated in the northern part of the plantation (Fig. 1).

In January 2018, we surveyed all trees in Stand 10, during which we found a single attacked tree with only one inactive gallery at 20 cm, filled with gum, and with one dead male *M. mutatus* just under the bark. In March 2018, we surveyed all trees in Stand 9, and none were attacked.

In July 2018, we surveyed about half of Stand 5 and all of Stand 8 trees (Table 2). In Stand 5, we found three attacked trees: one tree with one active gallery, another with one inactive gallery, and a third tree with two inactive galleries. All galleries were in the lower 1 m of trunk. No attacked trees were found in Stand 8.

In December 2019, we surveyed the southern part of Stand 1. Three new attacked trees were found, two had one inactive gallery each, and the third had one active gallery. One of the trees in Stand 1 that had two active galleries in July 2016, had no active galleries in December 2019 as well as no evidence in the bark of the previous entrance holes from 2016, indicating that the tree was able to overcome the attack and seal the holes.

Stand 1 was again surveyed, nearly in its entirety, in March 2021, as well as about half of Stands 5 and 7 (Table 2). In Stand 1, only two attacked trees were found, one tree with an inactive gallery (DBH = 32.5 cm, gallery at 1.3 m), and another with one active gallery (DBH = 45.0 cm, height = 0.4 m). No attacked trees were found in Stands 5 and 7.

In April 2021, we surveyed less than 50% each of Stands 3, 6, 7 and 10 (Table 2). In Stand 10, trees had been pruned five days prior to our survey, with the pruned branches removed on the same day of our evaluation. In all four of these stands, *M. mutatus* attacks were observed. In Stand 3 there were three attacked trees (average tree DBH = 28.9 cm), each with one inactive hole. In Stand 6, we found two attacked trees (average tree DBH = 30.6 cm), one with one inactive gallery, and another with two inactive galleries. There were two trees with one inactive hole each in Stand 7 (average tree DBH = 29.3 cm). In Stand 10 there were 8 attacked trees (average tree DBH = 28.3 cm); six trees with one inactive gallery each, one tree with six inactive galleries, and one tree with one active gallery that had been only recently initiated. All attacked trees in Stand 10 were in the interior of the stand and had a clumped distribution.

The average DBH of all attacked trees was 23.3 cm (15.6 cm – 45.0 cm, n = 62 trees). For any missing values, we used the average stand DBH based on inventory data from Table 1. However, if we consider only those trees whose DBH was actually measured, then the average DBH of the attacked trees was 27.8 cm (21 – 45 cm, n = 18 trees). For all 62 attacked trees, found in all surveys, the observed number of gallery entrance holes per infested tree varied from one to six, with most having just one (Fig. 3). Attack heights were found from 2 cm above ground up to a height of 3 m, with most below 2 m ($\chi^2 = 81.77$, df = 4, P < 0.0001, Fig. 4). Overall, of the 90 (three holes were added here from the tree that was cut in June 2016) *M. mutatus* attacks found in all stands during this study, 16 (18%) were considered active at the time of inspection while 74 (82%) were classified as inactive.

Seasonality and Semiochemical Assay

Average weekly climate values were significantly higher during the "rainy season" compared to the "dry season" for rainfall ($F_{1,59} = 23.46$, $P < 0.0001$), air relative humidity ($F_{1,59} = 7.50$, $P = 0.0081$) and maximum

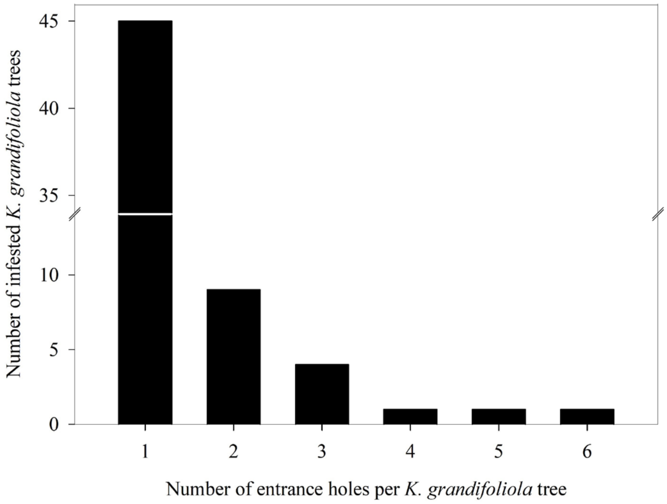

Figure 3 Number of *Megaplatypus mutatus* entrance holes. Number of gallery entrance holes of *Megaplatypus mutatus* found per number of infested *Khaya grandifoliola* trees in various stands in São Roque de Minas, Minas Gerais state, Brazil, during inspections from June 2016 until April 2021.

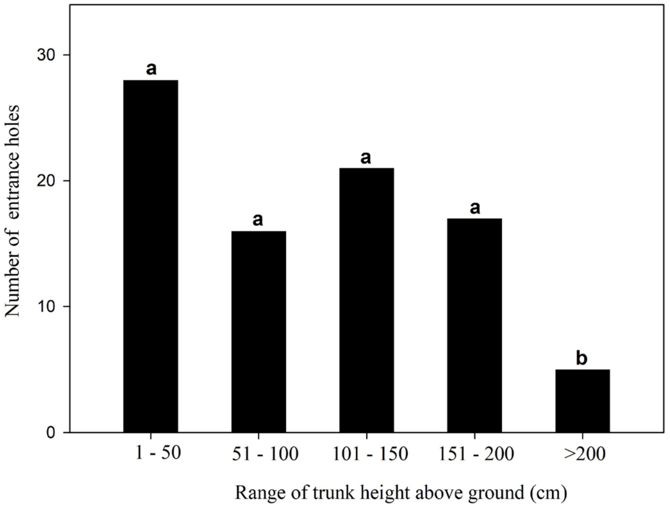

Figure 4 Frequency of height of *Megaplatypus mutatus* entrance holes. Frequency diagram of the number of *Megaplatypus mutatus* gallery entrance holes located at various heights along the trunk height above ground of *Khaya grandifoliola* trees in São Roque de Minas, Minas Gerais state, Brazil, during inspections from June 2016 until April 2021. Range of trunk height above ground with the same letter are not significantly different from each other (P < 0.0001, Kruskal-Wallis test).

($F_{1,59}$ = 18.87, P < 0.0001), minimum ($F_{1,59}$ = 111.31, P < 0.0001) and mean daily temperatures ($F_{1,59}$ = 123.29, P < 0.0001) (Fig. 5).

Over the 61 trap-weeks, we caught a total of only 8 males and 73 females, of which all were collected in the pheromone-baited traps. There was no significant difference in weekly trap catches of *M. mutatus* between seasons ($F_{1,887}$ = 2.55, P = 0.1109).

Discussion

Our study presents the first report of *M. mutatus* attacking a *Khaya* species, specifically *K. grandifoliola*, in a commercial plantation in Brazil.

We surveyed for *M. mutatus* attacks six times, evenly distributed between the dry and rainy seasons. All attacks occurred on apparently healthy trees; none showed clear signs of stress or disease, classifying *M. mutatus* as an 'A1' species. However, we observed males initiating attacks at scars on the trunks possibly from forest implement damage or trunk cankers, suggesting a potential classification as an 'A2' species.

Megaplatypus mutatus exhibits a strong preference for trees with a diameter at breast height (DBH) of 15 cm or greater (Santoro, 1957; Casaubon et al., 2006; Girardi et al., 2006; Marquina et al., 2006; Lucia et al., 2014). Roughly, trees reached a minimum of 15 cm DBH

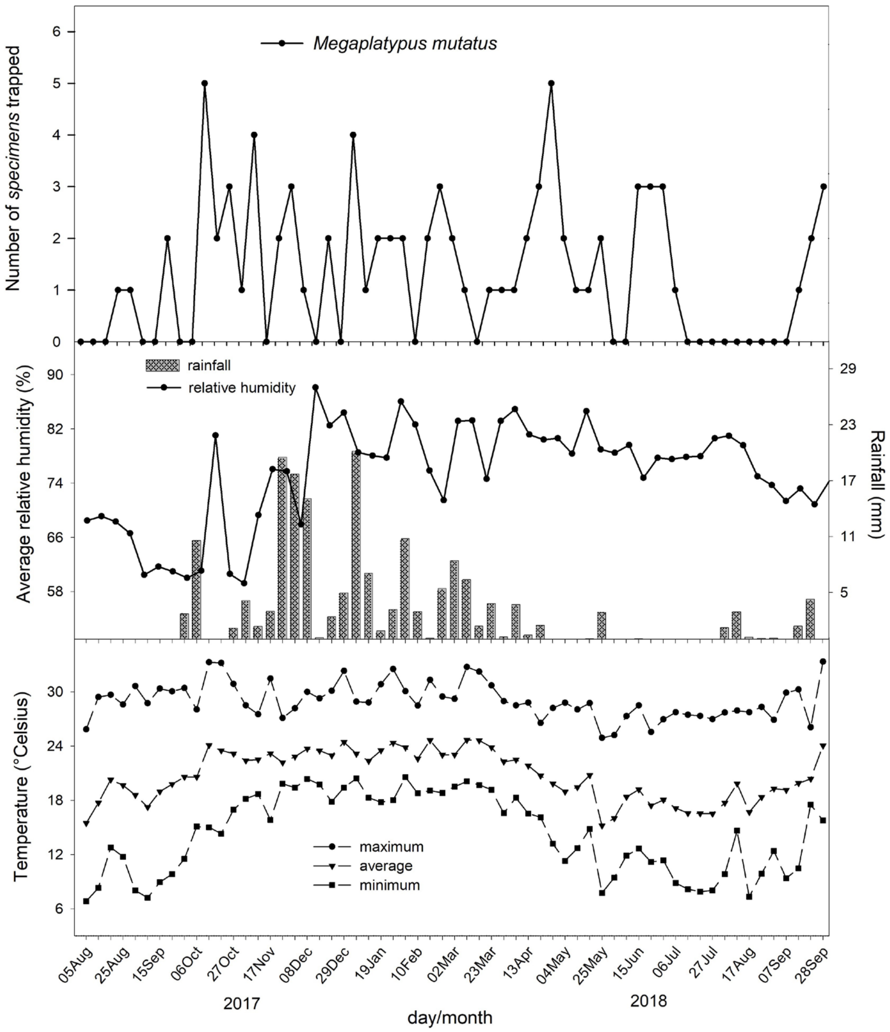

Figure 5 Weekly trapping of *Megaplatypus mutatus* and weather data. Total number of *Megaplatypus mutatus* adults trapped weekly in 11 pheromone-baited flight intercept traps in Stand 1 of an African mahogany, *Khaya grandifoliola* plantation in São Roque de Minas, Minas Gerais state, Brazil, and weekly values of mean rainfall, relative humidity, and temperature (maximum, average, minimum), from August 2017 until September 2018.

when they were five years old, under local site conditions in Brazil. In our study, the average DBH of attacked trees was over 23 cm, consistent with literature reports. The preference of *M. mutatus* for larger trees, characteristic of a large Platypodinae species, may stem from the increased space these trees offer for offspring development, with up to 200 adults emerging from a single parental gallery (Santoro, 1963). Over 73% of attacked trees had only one entrance hole, and those with up to two holes comprised about 89% of infested trees (Fig. 3). Typically, 'B' species show higher attack frequencies compared to 'A' species (Roberts, 1968; Milligan, 1979; Lee et al., 2011; Bellahirech et al., 2019). It is noteworthy that while sex pheromones are involved in attacks of 'A' species (reported only for *A. incompertus*, *M. mutatus*, and *T. ghanensis*), aggregation pheromones are absent in this group (Roberts, 1968; Kent, 2001; Gonzalez-Audino et al., 2005). In contrast, 'B' species commonly utilize aggregation pheromones, as reported for *Myoplatypus flavicornis* (Fabricius), *P. apicalis*, *P. cylindrus*, *P. gracilis*, *Platypus koryoensis* (Murayama) and *P. quercivorus* (Madrid et al., 1972; Milligan, 1982; Milligan et al., 1988; Algarvio et al., 2002; Tokoro et al, 2007; Kim et al., 2009). Sex pheromones typically attract primarily the opposite sex of the beetle releasing them, whereas aggregation pheromones attract conspecifics of both sexes in larger numbers (Symonds and Gitau-Clarke, 2016 and references therein). This apparent absence of aggregation pheromones in 'A' species may explain their tendency to attack trees in lower numbers, while 'B' species often attack in much higher numbers when colonizing their hosts.

We found *M. mutatus* attacks on tree trunks up to heights of 3 m, similar to patterns observed on Brazilian native trees (Girardi et al., 2006) and *Eucalyptus* clones in Brazil (Zanuncio et al., 2010), and *Populus deltoides* in Argentina (Landi et al., 2011) and Brazil (Flechtmann, unpublished results). However, attacks can occur as high as 12 m in Argentina (Marquina et al., 2006). Most attacks in our study were concentrated from ground level up to 2 m high, particularly along the lower trunk (first 50 cm) where diameter is greatest. Such results are similar to those reported for *P. koryoensis* (Lee et al., 2011) and *P. quercivorus* (Igeta et al., 2004). This concentration may be due to a higher tree diameter near the base.

One strategy to overcome tree resistance by colonizing beetles is mass attack, a well-known phenomenon in Scolytinae bark beetles (Six, 2020 and references therein). However, no such behavior has been reported for 'A' species of Platypodinae (Browne, 1961; Roberts, 1968; Kent, 2001), given that trees are usually attacked by a low number of individuals. In our study, *M. mutatus* fits the general pattern reported in the literature for 'A' species (Santoro, 1957, 1963; Girardi et al., 2006), as most attacked trees had only one or two entrance holes (Fig. 3). Conversely, mass-attacks on host trees appear to be the rule for 'B' species (Roberts, 1977b; Milligan, 1979; Hijii et al., 1991; Lee et al., 2011; Bellahirech et al., 2019).

Limited information exists regarding the distribution of Platypodinae infestations within forests or plantations. *Platypus apicalis*, *P. gracilis* (Milligan, 1979) and *P. quercivorus* (Yamasaki et al., 2014), all 'B' species, are reported to infest trees in a clumped distribution. *Platypus subgranosus*, another 'B' species, also shows a clumped distribution, but apparently this species is just following the distribution of its diseased host trees, which typically have a clumped distribution (Elliott et al., 1987; Candy, 1990). Our observations revealed a clumped distribution of infested trees in two instances when sufficient data were available (Stand 1 in June/July 2016 and Stand 10 in April 2021), possibly influenced by pruning treatments that released kairomones attracting *M. mutatus*. These kairomones were likely used by males as chemical cues for host location, as reported before in *M. mutatus* (Lucia et al., 2014), ultimately concentrating attacks within the interior of the stands. Roberts (1977b) noted that platypodines generally attack at stand borders unless influenced by forest operations. In Argentina however, the distribution of *M. mutatus* attacks appears to be at random (Gonzalez-Audino et al., 2005).

When platypodines attempt to colonize trees there is always a certain percentage of attacks that fail to produce brood. We observed a high rate of aborted attacks (85%), characterized by gum exuding from entrance holes, where dead males were either pitched out (Fig. 2d) or surrounded by gum, suggesting that gummosis is the primary resistance factor against *M. mutatus*. Gummosis has been reported as a defense mechanism against *M. mutatus* in several tree species, in different tree families (Santoro, 1957, 1960; Zanuncio et al., 2010), and we can now add *K. grandifoliola* to this list. In one instance, a tree cut after two recorded holes showed no evidence of prior attacks, indicating potential secondary plant defenses that could have killed the attacking beetles and allowed the tree to overgrow entrance wounds.

As for other factors that might affect tree colonization, given that *M. mutatus* has a 1:1 sex ratio (Santoro, 1963), it seems fair to assume that a pheromone-calling male would be able to attract a mate. Although several fungi associated with *M. mutatus* have been documented (Guerrero, 1966; Ceriani-Nakamurakare et al., 2016, 2018, 2020), brood failure is unlikely due to symbiotic fungi not establishing since male galleries were often aborted or they died in the early stages of tree colonization. Moreover, all adult beetles found during gallery dissection were intact, ruling out the presence of natural enemies.

The tree's resistance to *M. mutatus* appears to involve two distinct layers of defense: an initial response marked by the exudation of gum when the beetle bores into the phloem, followed by a secondary defense mechanism that utilizes potentially toxic secondary compounds to target beetles reaching the sapwood.

The total number of *M. mutatus* collected in pheromone traps was low, suggesting a low density of beetles in the stand. In our study, using sex-pheromone baited traps, we observed flight activity year-round (Fig. 5), with no significant differences in catch rates across seasons. This indicates that monitoring for this species should ideally occur throughout the year. The only similar study in Brazil focused on beetle activity within live *Paubrasilia echinata* (Lam.) trees, which also appears to occur year-round, although it lacked specific seasonality data (Girardi et al., 2006).

In contrast, our findings differ from the seasonal patterns observed in northeastern (Entre Rios and Buenos Aires) and southern (Rio Negro) Argentina, where *M. mutatus* exhibits distinct flight activity. In northeastern Argentina, flight activity peaks during the warmer, rainier months (September to February), particularly between November and December (Santoro, 1957, 1963; Funes et al., 2011, 2016). Beetles may also fly during fall and winter when temperatures are unusually high (Toscani, 1990). In southern Argentina, the flight period extends from November to May (spring through fall) (Thomas, 2011). In Italy, where *M. mutatus* was introduced (Tremblay et al., 2000; Griffo et al., 2012), flight activity occurs from May to September in the southwestern region of Campania (Funes et al., 2011, 2013; Gonzalez-Audino et al., 2013).

Voltinism in *M. mutatus* varies by region. In our study, *M. mutatus* exhibited a multivoltine behavior, as it was present year-round (Fig. 5). In contrast, studies in Argentina indicate it is primarily univoltine (Santoro, 1957, 1963; Toscani, 1990; Thomas, 2011), although it may occasionally be bivoltine under certain conditions (Gatti-Liguori et al., 2008b; Gonzalez-Audino et al., 2011). In Italy, while some overlapping generations were noted at specific sites, the species appears to be bivoltine overall (Funes et al., 2011; Gonzalez-Audino et al., 2013).

Temperature plays a crucial role in regulating insect development and voltinism patterns (Annila, 1969). In northeastern Argentina, average winter temperatures range from 11-12°C (Casaubon et al., 2006), while southwestern Italy reports similar temperatures, between 9-11°C

(Fato et al., 2004). In contrast, our study site in Brazil has an average winter temperature of approximately 18°C. Generally, insect species with broad geographic ranges tend to be univoltine in colder climates and multivoltine in warmer ones (Schebeck et al., 2017). Therefore, if future studies were conducted in a colder region of Brazil (further south), we might expect *M. mutatus* to shift from a multivoltine to a univoltine or bivoltine life cycle, similar to the predominant patterns observed in Argentina and some Italian sites.

While *M. mutatus* specimens have been successfully trapped in ethanol traps at other locations (CAHF, personal communication), none were captured in the African mahogany stands of our study. However, our results align with expectations. Ethanol serves as a key olfactory cue for locating suitable host plants in several Scolytinae and some Platypodinae species, particularly less aggressive ones that colonize stressed hosts (Elliott et al., 1983; Cavaletto et al., 2021). More aggressive Scolytinae species that frequently attack live trees show minimal response to ethanol (Miller and Rabaglia, 2009; Kendra et al., 2014; Rabaglia et al., 2019; Mendel et al., 2021), a trend also observed in the platypodine *P. quercivorus* (Tokoro et al., 2007). *Megaplatypus mutatus* fits this pattern as an aggressive species attacking live trees (Santoro, 1957, 1963; Alfaro et al., 2007). Additionally, the influence of pruning suggests that other tree kairomones may attract males, which are the pioneer sex that initiates the gallery (Santoro, 1957; Gonzalez-Audino et al., 2013). In our traps baited with the *M. mutatus* sex pheromone blend, 90% of trapped beetles were females (8 males and 73 females), consistent with findings from Italy where circa 90% of trapped beetles were also females (67–100%; n = 9 study sites) (Gonzalez-Audino et al., 2013). Trapping non-target males in sex pheromone-baited traps is not uncommon (Borden and Stokkink, 1973; Hager and Teale, 1996; Miller et al., 2000; Allison et al., 2013). This behavior may occur because males utilize the male-produced sex pheromone as a cue to locate suitable hosts or potential mates (Müller and Eggert, 1987; Chemnitz et al., 2020).

Conclusions

This study presents a novel classification of Platypodinae species into 'A' and 'B' categories, based on their behavioral patterns and ecological interactions. We provide the first report of *M. mutatus* attacking *K. grandifoliola* in Brazil, classifying it as an 'A1' species due to its preference for healthy trees and low numbers of attacking individuals. The beetle favors larger trees with a DBH of 15 cm or greater and primarily targets the lower 2 m of the trunk. The high rate of aborted attacks indicates that tree defenses, particularly gummosis, are significant resistance factors against this beetle, and beetles that were able to overcome gummosis appeared unable to complete development in *K. grandifoliola* trees. Consequently, all specimens found in the *K. grandifoliola* trees and in the pheromone-baited traps in our study must have originated from the surrounding native vegetation, a cerrado/seasonal forest (IBGE, 2018). Our findings reveal that *M. mutatus* exhibits a multivoltine behavior in Brazil, contrasting with univoltine patterns seen in cooler regions like Argentina and Italy. Although we did not find evidence of successful reproduction of *M. mutatus* in *K. grandifoliola* trees, gallery initiation could still affect wood quality in some cases. Nevertheless, managers of *Khaya* plantations should monitor their trees for potential pests, including *M. mutatus*.

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Conflicts of interest

The author declares no conflicts of interest.

Author contribution statement

LSC: (Conceptualization [Equal], Formal analysis [Lead], Investigation [Lead], Methodology [Equal], Visualization [Equal], Writing—original draft [Lead], Writing—review & editing [Equal])

RAH: (Writing—review & editing [Equal])

JCPC: (Conceptualization [Equal] and Investigation [Equal])

JCZ: (Editing [Equal])

CAHF: (Conceptualization [Lead], Formal analysis [Lead], Investigation [Equal], Visualization [Equal], Writing—original draft [Lead], Writing—review & editing [Equal]), Project administration [Lead]).

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