UNIVERSIDADE FEDERAL DO PARANÁ

LUANA DE SOUZA COVRE

INFLUENCE OF AFRICAN MAHOGANY AGE ON DIVERSITY AND ATTACKS BY WOODBORING BEETLES (BOSTRICHIDAE, CERAMBYCIDAE AND CURCULIONIDAE)

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Tese apresentada ao curso de Pós-Graduação em Entomologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ciências Biológicas – Ênfase em Entomologia.

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RESUMO

O gênero *Khaya* A. Juss. (Meliaceae), conhecido como mogno-africano, compreende árvores de grande porte nativas das regiões tropicais da África e de alto valor econômico pela qualidade e durabilidade da madeira. No Brasil, o cultivo comercial de *Khaya* spp. tem se expandido como alternativa sustentável à exploração de madeiras nativas, mas ainda existem lacunas sobre as interações entre essas espécies e os insetos associados, especialmente besouros perfuradores de madeira. A introdução dessas árvores em novos ambientes trouxe desafios fitossanitários e ecológicos, demandando abordagens científicas integradas para compreender a dinâmica de pragas e propor estratégias sustentáveis de manejo. Esta tese investigou a influência da idade do mogno-africano (*Khaya grandifoliola*) sobre a diversidade e os ataques de coleobrocas, avaliando também o efeito das práticas silviculturais e das variáveis climáticas sobre a distribuição das árvores atacadas. O trabalho foi estruturado em três estudos complementares. O primeiro estudo consistiu em uma revisão crítica da literatura sobre insetos associados ao mogno-africano no Brasil, registrando 80 espécies de insetos e duas de ácaros, com predominância de Coleoptera (77,5%). Identificaram-se erros taxonômicos e diagnósticos incorretos de pragas, além da escassez de estudos que quantificam danos ou propõem medidas de manejo integrado. Evidenciou-se a necessidade de padronização metodológica e identificação por especialistas para consolidar o conhecimento sobre a entomofauna associada a *Khaya* spp. O segundo estudo abordou o monitoramento da diversidade de coleobrocas em plantios de diferentes idades e em fragmento de mata ciliar, totalizando 51.110 espécimes e 200 espécies identificadas. As guildas xilófagas e xilomicetófagas representaram a maior parte da riqueza e abundância, influenciadas pela idade dos plantios, práticas de manejo e proximidade com vegetação nativa. Talhões mais jovens e próximos ao fragmento apresentaram maior diversidade e uniformidade das comunidades. A presença da espécie exótica invasora *Euwallacea fornicatus* (Scolytinae) reforçou a importância do monitoramento e biossegurança em plantios comerciais. O terceiro estudo avaliou os ataques de *Euplatypus parallelus* (Platypodinae), relacionando-os à defesa das plantas, manejo e clima. A exsudação de goma atuou como defesa primária. Contudo, desbaste e desrama aumentaram a suscetibilidade ao ataque por favorecerem a emissão de voláteis atrativos e o acúmulo de resíduos. A precipitação reduziu a incidência de ataques, possivelmente por interferir na dispersão e comunicação química dos insetos.Os resultados indicam que a sustentabilidade do cultivo de mogno-africano depende da integração entre fatores bióticos, abióticos e de manejo. A manutenção de fragmentos florestais é essencial para conservar a diversidade e o equilíbrio ecológico. Estratégias de monitoramento contínuo e manejo adaptativo são fundamentais para prevenir surtos de pragas, otimizar a produção e garantir a sustentabilidade ambiental dos plantios de *Khaya* spp. no Brasil.

Palavras-chave: armadilhas; diversidade de insetos; *Euplatypus parallelus; Khaya grandifoliola*; monitoramento.

ABSTRACT

The genus *Khaya* A. Juss. (Meliaceae), known as African mahogany, comprises large trees native to tropical regions of Africa and of high economic value due to the quality and durability of their wood. In Brazil, the commercial cultivation of *Khaya* spp. has expanded as a sustainable alternative to the exploitation of native timber species, although there are still gaps in knowledge regarding the interactions between these trees and associated insects, especially woodboring beetles. The introduction of these trees into new environments has brought phytosanitary and ecological challenges, demanding integrated scientific approaches to understand pest dynamics and develop sustainable management strategies. This thesis investigated the influence of *Khaya grandifoliola* age on the diversity and attacks of woodboring beetles, also assessing the effects of silvicultural practices and climatic variables on the distribution of attacked trees. The research was structured into three complementary studies. The first study consisted of a critical literature review on insects associated with African mahogany in Brazil, recording 80 insect species and two mite species, with a predominance of Coleoptera (77.5%). Taxonomic errors and misdiagnoses of pest species were identified, as well as a lack of studies that quantify damage or propose integrated management measures. The need for methodological standardization and specialist identification was highlighted to consolidate knowledge about the entomofauna associated with *Khaya* spp. The second study addressed the monitoring of woodboring beetle diversity in plantations of different ages and in an adjacent riparian forest fragment, totaling 51,110 specimens and 200 identified species. The xylophagous and xylomycetophagous guilds accounted for most of the richness and abundance, influenced by plantation age, management practices, and proximity to native vegetation. Younger stands and those near the forest fragment showed higher diversity and community evenness. The detection of the invasive exotic species *Euwallacea fornicatus* (Scolytinae) reinforced the importance of monitoring and biosafety in commercial plantations. The third study evaluated attacks by *Euplatypus parallelus* (Platypodinae), relating them to plant defense, management, and climate. Gum exudation acted as a primary defense mechanism. However, thinning and pruning increased susceptibility to attack by promoting the release of attractive volatiles and the accumulation of woody residues. Rainfall reduced the incidence of attacks, possibly by interfering with the insects’ dispersion and chemical communication. The results indicate that the sustainability of African mahogany cultivation depends on the integration of biotic, abiotic, and management factors. The maintenance of forest fragments is essential to conserve diversity and ecological balance. Continuous monitoring and adaptive management strategies are fundamental to prevent pest outbreaks, optimize production, and ensure the environmental sustainability of *Khaya* spp. plantations in Brazil.

Keywords: traps; insect diversity; *Euplatypus parallelus*; *Khaya grandifoliola*; monitoring.

LIST OF FIGURES

CHAPTER III

LIST OF TABLES

SUMMARY

GENERAL INTRODUCTION AND OVERVIEW OF THESIS STRUCTURE

1 GENERAL INTRODUCTION

The genus *Khaya* A. Juss (Meliaceae), commonly known as African mahogany, comprises large tree species native to tropical regions of Africa (Lamb 1963; Pennington & Styles 1975). There are eight *Khaya* species: *Khaya agboensis* A.Chev., *Khaya anthotheca* (Welw.) C.DC., *Khaya euryphylla* Harms, *Khaya grandifoliola* C.DC., *Khaya ivorensis* A.Chev., *Khaya madagascariensis* Jum. & H. Perrier, *Khaya nyasica* Stapf ex Baker f., and *Khaya senegalensis* (Desr.) A. Juss. (Bouka et al. 2022). Among the most well-known and amongst the most planted species are *K. anthotheca, K. grandifoliola, K. ivorensis* and *K. senegalensis*, all of which hold significant commercial interest due to their high timber quality (Bouka et al. 2019). These trees exhibit rapid growth, reaching up to 50 meters in height, with straight trunks and reddish-colored wood, a characteristic that makes them highly valued in the timber market (Bouka et al. 2019; ITTO 2023). Their reproduction occurs through seeds, and their growth cycle involves juvenile stages that are particularly vulnerable to biotic and abiotic factors, including pest infestations and diseases (Reis et al. 2019).

African mahogany holds great economic and environmental relevance. Its wood is widely utilized in the furniture industry, civil construction, and the manufacturing of musical instruments due to its durability and mechanical resistance (Bouka et al. 2019; Ferraz Filho et al. 2021). Additionally, it has potential use in reforestation and the restoration of degraded areas, playing an important role in carbon sequestration, conservation, and nutrient cycling (Falesi & Baena 1999; Caldeira et al. 2023; Gomes et al. 2024). However, due to extensive exploitation over the past decades, natural populations of African mahogany (*Khaya* spp.) have been declining. As a result, all continental African species of the genus *Khaya* have been listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (CITES 2023). This listing does not indicate that the species are currently threatened with extinction, but it aims to regulate international trade to prevent further population declines and ensure their long-term conservation and sustainable management (CITES 2023).

Given the limitations on extractivism, the commercial cultivation of *Khaya* has expanded to various regions outside its natural distribution range, including countries in Latin America, Asia, and Oceania (Nikles et al. 2008; Bandara & Arnold 2018; Ferraz Filho et al. 2021). In Brazil, African mahogany plantations are expanding (Ferraz Filho et al. 2021). However, research on this tree crop remains limited. Many growers are unaware of the damage that might be inflicted by insects, including here woodboring species and the appropriate methods for controlling them. When infestations occur, chemical products are often applied, despite their known inefficacy and harmful effects on non-target insects. Most borer attacks in *Khaya* spp. are naturally aborted through gum exudation (Covre et al. 2018; Cristovam et al. 2018; Covre et al. 2025a), eliminating the need for insecticide-based control. However, factors such as tree age or an increase in woodboring populations within the area may compromise this defense mechanism in African mahogany trees.

The introduction of *Khaya* spp. into new environments has also led to phytosanitary challenges, as has already occurred with other forest cultivation introduced in Brazil (Andrade 1909; Iede et al. 1988), particularly concerning pest attacks and disease development, often favored by local ecological conditions (Covre et al. 2025b). Among the main reported issues are infestations by woodboring beetles, which can compromise tree growth and wood quality, ultimately reducing the economic viability of plantations on *Khaya* spp. (Covre et al. 2018; Cristovam et al. 2018; Covre et al. 2025a). Understanding how the woodboring beetle community behaves in African mahogany stands over the years and the species' defense capacity against insect attacks, as well as identifying the key borer species that damage the trunk and their seasonality, is crucial for developing sustainable monitoring and control strategies for this crop. Therefore, this thesis aimed to analyze the influence of African mahogany age on the diversity and attacks by woodboring beetles (Bostrichidae, Cerambycidae, and Curculionidae), as well as to evaluate the influence of management practices and climatic conditions on the distribution of attacked trees.

2 OVERVIEW OF THESIS STRUCTURE

This thesis will generate new insights, representing a pioneering study on the influence of tree age on woodboring attacks and beetle fauna in African mahogany plantations. Therefore, studies assessing the interaction between tree age and susceptibility to pest attacks are essential, enabling the development of effective management and control strategies.

This thesis is structured into three chapters, each presented as a manuscript. the chapters are presented following the format of the journals in which we intend to publish.

Chapter 1 titled “Correcting the record: insects of African mahogany (*Khaya* spp.) in Brazilian plantations” consists of a forum-style article that critically reviews the literature on insects associated with African mahogany in Brazil. It goes beyond a traditional review by integrating diverse sources and highlighting taxonomic and ecological inconsistencies. The most widely planted species in Brazil is *K. grandifoliola*, which was historically misidentified as *K. ivorensis*. This taxonomic confusion has caused significant inconsistencies in literature, directly affecting the accuracy of entomological studies and hindering integrated pest management strategies.

Therefore, this manuscript aims to consolidate and critically evaluate the available data (literature), contributing to the taxonomic and ecological understanding of insect-plant interactions with *Khaya* spp. and offering a foundation for sustainable pest management. This work is intended to support ecosystem health and guide stakeholders involved in African mahogany plantation.

Chapter 2 titled “Woodboring beetle diversity in *Khaya grandifoliola* C.DC. (Meliaceae) stands of different ages and adjacent riparian forest” presents an intensive, long-term monitoring study of woodboring beetles conducted over seven years in African mahogany plantations of varying ages, and three years in adjacent native vegetation. The goal is to identify and analyze population patterns of these beetles in both managed and natural ecosystems. The beetles were categorized into guilds (myelophagous, phloeophagous, spermophagous, xylomycetophagous, and xylophagous) to explore forest structural complexity. Emphasis is placed on biodiversity analyses, including species richness, presence, abundance, and identification of indicator species.

Chapter 3 presents a systematic, tree-by-tree monthly survey of woodboring attacks on tree trunks, conducted from May 2017 to December 2024. Titled "Spatiotemporal patterns of *Euplatypus parallelus* (Fabricius) attacks on *Khaya grandifoliola* C.DC.: insights for pest management", this chapter aims to assess the spatial distribution and temporal dynamics of *E. parallelus* infestations. Using geospatial analysis and statistical modeling, the study seeks to identify factors influencing infestation patterns. The results are expected to support the development of more effective pest monitoring protocols, enhance early detection strategies, and contribute to the sustainable management of *K. grandifoliola* plantations.

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CHAPTER I

CORRECTING THE RECORD: INSECTS OF AFRICAN MAHOGANY (*Khaya* spp.) IN BRAZILIAN PLANTATIONS

“Look deep into nature, and then you will understand everything better."

Albert Einstein

Correcting the record: insects of African mahogany (*Khaya* spp.) in Brazilian plantations

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Abstract

The interaction between exotic African mahogany species (*Khaya* spp.) and their associated insects in Brazilian plantations holds scientific and economic significance, and Brazil hosts one of the largest cultivated areas of these trees worldwide. The most widely planted species in the country, *Khaya grandifoliola*, has often been misidentified as *K. ivorensis*, causing confusion in the literature and compromising entomological research and pest management efforts. We also found several misidentifications of associated insects in the literature, further complicating the understanding of these interactions. While studies typically focus on the mahogany shoot borer (*Hypsipyla grandella*), records of numerous other insects reported by growers remain unpublished or are linked to incorrect tree species names. This reveals a critical knowledge gap, with few studies accurately documenting insect occurrences or confirming their pest status. This review article compiles and analyzes the current literature on insects associated with African mahogany in Brazil, contributing to the taxonomic and ecological understanding of these interactions. The findings provide a foundation for sustainable plantation management and improved pest management, offering guidance to researchers and producers involved in African mahogany cultivation.

Key words: insect pests, species misidentification, *Hypsipyla grandella*

Resumo

A interação entre espécies exóticas de mogno-africano (*Khaya* spp.) e insetos associados aos plantios no Brasil tem relevância científica e econômica, especialmente porque o país abriga uma das maiores áreas plantadas dessa árvore no mundo. A espécie mais cultivada no Brasil é *Khaya grandifoliola*, frequentemente identificada erroneamente como *Khaya ivorensis*, o que tem gerado confusões na literatura científica e comprometido estudos entomológicos e estratégias de manejo integrado de pragas. Além disso, há várias literaturas sobre insetos associados ao mogno africano que foram identificados errados complicando ainda mais a compreensão dessas interações. Embora a literatura enfatize a broca-das-meliáceas (*Hypsipyla grandella*), outros insetos relatados por produtores permanecem sem publicação ou são associados a nomes incorretos das espécies de *Khaya*. Essa situação revela uma lacuna crítica no conhecimento, com poucos estudos documentando adequadamente a ocorrência de insetos ou confirmando seu status como pragas economicamente relevantes. Este artigo de revisão reúne e analisa a literatura disponível sobre insetos associados ao mogno-africano no Brasil, contribuindo para o entendimento taxonômico e ecológico dessas interações. Os resultados oferecem subsídios essenciais para o manejo sustentável dos plantios e aprimoramento no manejo de pragas, além de orientar pesquisadores e produtores envolvidos com o cultivo da espécie.

Palavras-chave: insetos pragas, identificação equivocada, *Hypsipyla grandella*

1 INTRODUCTION

African mahogany (Meliaceae: *Khaya* A. Juss) comprises a group of African-origin species valued for their high-quality timber and significant economic importance (Bouka et al., 2019; ITTO, 2023). There are eight known *Khaya* species, *K. agboensis* A.Chev., *K. anthotheca* (Welw.) C.DC., *K. euryphylla* Harms, *K. grandifoliola* C.DC., *K. ivorensis* A.Chev., *K. madagascariensis* Jum. & H.Perrier, *K. nyasica* Stapf ex Baker f., and *K. senegalensis* (Desr.) A.Juss. (Bouka et al., 2022). Beyond economic value, mahogany plantations play crucial roles in carbon storage, nutrient cycling, and conservation (Caldeira et al., 2023; Gomes et al., 2024).

The introduction of African mahogany (*Khaya* spp.) to Brazil dates to the 1970s, with the first recorded introduction occurring at Brazilian Agricultural Research Corporation (Embrapa Amazônia Oriental) in Belém, in the state of Pará (Falesi & Baena, 1999). Initially, the introduced species was misidentified as *K. ivorensis* (Falesi & Baena, 1999). However, later studies confirmed that it was *K. grandifoliola* (ABPMA, 2020; Ferraz Filho et al., 2021). Seeds from these trees were distributed to producers by Embrapa, but some growers appear to have also independently imported seeds (Falesi & Baena, 1999). As a result, the exact timeline and pathways of *Khaya* species introductions into Brazil remain uncertain. This taxonomic misidentification has led to persistent confusion in the literature, particularly in entomological studies (Falesi & Baena, 1999; Lunz et al., 2008; Farias et al., 2011; Matrangolo et al., 2016; Nascimento et al., 2016; Ceu et al., 2017; Moura et al., 2017; Silva et al., 2017; Zanetti et al., 2017; Fialho Júnior et al., 2019; Lemes et al., 2019; Santos, 2019; Silva et al., 2020; Silva et al., 2022), where incorrect species identification makes it difficult to ascertain the accuracy of reports on insect-plant interactions.

The introduction of African mahogany species in Brazil was primarily driven by economic incentives, as these trees produce high-value timber with strong market potential. Additionally, the adaptability of *Khaya* species to diverse Brazilian climatic and edaphic conditions, excluding areas with frost or severe water deficits, further facilitated their expansion (Oliveira & Franca, 2020). African mahogany also emerged as a viable alternative to native Brazilian mahogany (*Swietenia macrophylla* King), which faces logging restrictions due to its endangered status in Brazil (CITES, 2024). Moreover, the monoculture of *S. macrophylla* is unfeasible due to severe infestations by the shoot borer *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) (Ohashi et al., 2008). Initially, it was believed that being an exotic species, African mahogany might exhibit some level of resistance to shoot borer attacks, making it an attractive substitute for the native species (Falesi & Baena, 1999).

The 2010s marked a significant boom in African mahogany plantations in Brazil leading to a substantial increase in cultivated areas (Taguchi, 2013). A 2021 survey estimated that approximately 50,000 hectares were planted with

African mahogany in Brazil, with *K. grandifoliola* representing 66% of the total area and *K. senegalensis* another 33% (Ferraz Filho et al., 2021). These two species are currently the most relevant for commercial forestry in Brazil (Reis et al., 2019). Other species, such as *K. anthotheca* and *K. ivorensis*, are also cultivated, but on a much smaller scale. African mahogany plantations are primarily concentrated in the Southeast (50%), followed by the Mid-West (25%), North (13%), Northeast (6%), and South (6%) regions (Ferraz Filho et al., 2021). Most stands are less than 10 years old, reflecting the species' relatively recent expansion in the country.

Although recently introduced in Brazil, African mahogany has gained commercial relevance, yet scientific research remains limited and largely restricted to conference proceedings and technical reports. Furthermore, initial misidentification of the most planted species as *K. ivorensis* instead of *K. grandifoliola* has led to persistent confusion in literature, particularly in entomological studies, where it compromises the accuracy of insect association records.

With that scenario in mind, we thus aimed to analyze the existing scientific literature (articles, books, thesis, dissertations, and conference proceedings) on insects associated with African mahogany (*Khaya* spp.) in Brazil. The objectives included: (1) identifying the insect orders and species reported, (2) determining the most studied *Khaya* species and evaluating the insect-affected plant parts, (3) quantifying the available publications and ways of publications, (4) examining cases of *Khaya* misidentification before and after correction clarification, and (5) map the geographic distribution of study locations.

2 PREFERENCE AND ASSOCIATED SPECIES OF *Khaya* spp. IN BRAZIL

The term “*agricultural pest*” refers to organisms (insects, nematodes, mites, etc.) that cause damage to plants, resulting in economic losses for humans (Hill, 1997). An analysis of publications on insects in African mahogany reveals that most species described as “*pests*” should instead be classified as insects associated with the crop, based on this concept. While the most of the publications describe damage to different plant parts, this damage is rarely quantified. Therefore, the more accurate term would be *associated insects*, with some potentially becoming pests of African mahogany.

The literature reports 80 insect species and two mite species associated with African mahogany in Brazil (Table 1). Regarding the insects, 62 species belong to the order Coleoptera (77.5%), seven species to Lepidoptera (8.8%), five species to Hymenoptera (6.3%), five species to Hemiptera (three in Sternorryncha, and two in Auchenorrhyncha), and one species to Orthoptera (1.3%) (Table 1). The two mite species belong to the family Tetranychidae.

At least 35% of the reviewed literature does not clearly indicate whether the insect species associated with African mahogany were identified by trained taxonomists or whether the authorship included specialists in the relevant taxonomic groups. This omission raises the doubt of possible misidentifications. For instance, Pinto (2020) reported the occurrence of *Xylothrips* sp., an exotic beetle not previously recorded in Brazil. However, upon direct inquiry, the author disclosed that the identifications were based solely on photographic comparisons from online sources. Given the potential implications of this uncertain record, the author kindly provided one of us (CAHF) with Bostrichidae specimens collected in *Khaya* wood used in the study. Upon examination, none of the specimens were *Xylothrips*; they were identified as *Xylionulus transvena* (Lesne) and *X. picea*, both of which may resemble *Xylothrips* to researchers without taxonomic training. Similarly, Falesi & Baena (1999) referred to a beetle boring into petioles as *Xyleborus* (misspelled as "*Xyleboros*") or *Xylosandrus* (misspelled as "*Xylosandros*"). Based on our experience, only *Hypothenemus* spp. and *Xylosandrus compactus* bore into petioles in Brazil (unpublished data), and inexperienced researchers might confuse one for the other.

A comparable issue appears in Gonçalves et al. (2023), who reported *X. compactus* attacking petioles but included photographs that clearly depicted *Hypothenemus*, leaving the actual identity of the reported species uncertain. These examples underscore the need for insect identifications to be confirmed by qualified taxonomists - particularly for ecologically and economically significant species - to ensure the reliability of records and the validity of ecological and management-related inferences.

The most frequently attacked part of the tree was the trunk, followed by branches and leaves (Table 1). African mahogany contains toxic secondary compounds, which are more concentrated in the leaves than in the trunk (Paritala et al., 2015). This may explain the higher number of insect species associated with trunks and branches compared to leaves.

Among insects, Coleoptera and Lepidoptera are particularly important in forestry due to the high number of phytophagous species (Frost, 1954). The order Lepidoptera plays a significant role in the forestry sector due to its presence across a wide range of forest crops in Brazil (Kowalczuck et al., 2012). Lepidoptera presence is easily spotted due to the visible defoliation their caterpillars inflict to leaves. However, so far only two defoliator species have been reported in the two most planted African mahogany species in Brazil, *K. grandifoliola* and *K. senegalensis* (Covre et al., 2025b), and only recently. Lepidoptera represent only 8.8% of all insect records in African mahogany plantations. Notably, most Lepidoptera species in these systems are associated with damage to trunks, seeds, and shoots or tips, rather than leaf defoliation (Table 1). However, we were made aware of a report of leaf damage on five-year-old *K. grandifoliola* trees in Ipueiras, state of Tocantins, caused by caterpillars of *Acharia* sp. (Limacodidae) (personal communication, agronomist Rodrigo Rafael de Deus Machado, 2025).

Although some insects, such as leaf-cutting ants and termites (Lemes & Zanuncio, 2021), are commonly found in forest plantations, there are few studies addressing these insects in African mahogany plantations in Brazil (Table 1). However, it is known that these insects are frequent in Brazilian African mahogany plantations, and the lack of studies may be explained by the fact that growers are already familiar with these pests and routinely incorporate their control into plantation management practices.

In Coleoptera, the families Bostrichidae, Cerambycidae, Curculionidae sensu stricto (*note: these represent the 'former' Curculionidae, excluding Scolytinae), and Scolytinae (Curculionidae sensu lato) are of forestry importance, primarily due to their association with wood (Penteado et al., 2009). As a matter of fact, these families have been prominent in studies of insects associated with African mahogany in Brazil. Scolytinae alone accounts for the majority of the reports (59.7%), followed by Bostrichidae (17.7%), Curculionidae: Platypodinae (9.7%), Curculionidae: Entiminae (4.8%), Cerambycidae (4.8%) and Anthribidae (3.2%) (Table 1).

Table 1. Orders (COL: Coleoptera, HEM: Hemiptera, HYM: Hymenoptera, LEP: Lepidoptera, ORT: Orthoptera, and mites: TRO: Trombidiformes), families, and species of insects and mites associated with African mahogany (*Khaya* spp.) in Brazil, and respective plant parts attacked (PPA) (BR = branches, FR = fruits, LE = leaves, PE = petioles, RO = roots, SE = seeds, SW = sawn wood, ST= shoot tips, TR = trunks), and their respective literature references.

Order	Family	Species	PPA	References
COL	Anthribidae	*Phaenithon curvipes* (Germar)*	TR	9
COL		*Phaenithon semigriseus* (Germar)*	TR	9
COL	Bostrichidae	*Apate terebrans* (Pallas)	TR	13, 39, 42
COL		*Dominikia uncinata* (Germar)	TR	3, 14, 58
COL		*Micrapate brasiliensis* (Lesne)	TR	58
COL		*Micrapate germaini* (Lesne)	TR	9, 14
COL		*Micrapate horni* (Lesne)	TR	58
COL		*Micrapate obesa* (Lesne)	TR	9
COL		*Minthea squamigera**	SW	51
COL		*Sinoxylodes curtulus* (Erichson)	TR	3
COL		*Tetrapriocera longicornis* (Olivier)	TR	9
COL		*Xyloperthella picea* (Olivier)	BR, TR	3, 9, 14, 15, 58
COL		*Xylothrips* sp.?	SW	51
COL	Cerambycidae	*Chlorida festiva* (Linnaeus)	TR	9
COL		*Neoclytus pusillus* (Castelnau & Gory)	TR	9
COL		*Trachyderes succintus* (Linnaeus)	TR, BR	9, 28
COL	Curculionidae: Entiminae	*Zygops mexicanus* Boheman*	TR	9
COL		*Zygops* sp.*	TR	9
COL		*Naupactus optatus* (Herbst)	LE, BR, RO	56
COL	Curculionidae: Platypodinae	*Euplatypus parallelus* (Fabricius)	BR, TR	3, 9, 14, 15, 20, 48, 58
COL		*Euplatypus segnis* (Chapuis)	TR	3, 58
COL		*Megaplatypus dentatus* (Dalman)	TR	3
COL		*Megaplatypus mutatus* (Chapuis)	TR	17, 58
COL		*Megaplatypus olivieri* (Chapuis)	TR	58
COL		*Teloplatypus ratzeburgi* (Chapuis)	BR	15

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COL		*Ambrosiodmus obliquus* (LeConte)	TR	3
COL		*Ambrosiodmus* hagedorni (Iglesias)*	TR	3
COL		*Cnestus retifer* (Wood)	TR	9
COL		*Cnestus retusus* (Eichhoff)	BR, TR	2, 15
COL		*Coptoborus semicostatus* (Schedl)*	BR	15
COL		*Coptoborus vespatorius* (Schedl)	BR	3
COL		*Coptoborus villosulus* (Blandford)	TR, BR	3
COL		*Corthylus antennarius* Schedl	TR	3
COL		*Corthylus pharax* Schedl	BR, TR	3, 15, 58
COL		*Corthylus theobromae* Nunberg	TR	3
COL		*Cryptocarenus heveae* (Hagedorn)	TR	3
COL		*Dryocoetoides cristatus* (Fabricius)	BR, TR	3, 58
COL		*Hylocurus dimorphus* (Schedl)	TR	14
COL		*Hypothenemus bolivianus* (Eggers)	TR	3
COL		*Hypothenemus eruditus* Westwood	BR, TR	3, 15, 58
COL		*Hypothenemus obscurus* (Fabricius)	TR	3, 9
COL	Curculionidae: Scolytinae	*Hypothenemus opacus* (Eichhoff)	TR	3
COL		*Hypothenemus plumeriae* (Nordlinger)	TR	9
COL		*Hypothenemus setosus* (Eichhoff)	TR	3
COL		*Microcorthylus minimus* Schedl	BR	15, 58
COL		*Microcorthylus quadridens* Wood	TR	3, 58
COL		*Microcorthylus ?parvidus**	TR	58
COL		*Premnobius ambitiosus* (Schaufuss)	TR	58
COL		*Premnobius cavipennis* Eichhoff	BR, TR	3, 1, 58
COL		*Sampsonius dampfi* Schedl	TR	3, 58
COL		*Sampsonius pedrosai* Schönherr	TR	3
COL		*Scolytopsis toba* Wichmann	TR	58
COL		*Xyleborinus linearicollis* (Schedl)	BR, TR	9, 15
COL		*Xyleborinus reconditus* (Schedl)	TR	58
COL		*Xyleborus or Xylosandrus* sp. ?	PE	22
COL		*Xyleborus affinis* Eichhoff	BR, TR	3, 9
COL		*Xyleborus ferox* Blandford	TR	58
COL		*Xyleborus ferrugineus* (Fabricius)	TR	3
COL		*Xyleborus spinulosus* Blandford	BR, TR	3, 15, 58

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COL	Curculionidae: Scolytinae	*Xyleborus squamulatus* Eichhoff	BR, TR	15, 58
COL		*Xylosandrus compactus* (Eichhoff) [?]	PE, ST	30
COL		*Xylosandrus crassiusculus* (Motschulsky)	TR	16
HEM	Aleyrodidae	*Aleurocanthus woglumi* Ashby	LE	23
HEM	Coccidae	*Parasaissetia nigra* (Nietner)	LE, PE, BR, TR	25, 59
HEM	Lecanodiaspididae	*Lecanodiaspis dendrobii* Douglas	TR, BR	57
HEM	Cicadidae	*Dorisiana noriegai* Sanborn & Heath	RO	19
HEM		*Taphura maccagnani* Sanborn	RO	19
HYM	Apidae	*Trigona spinipes* Fabricius	ST	43
HYM		*Trigona* sp.	ST	22
HYM	Formicidae	*Atta laevigata* Smith	LE	60
HYM		*Atta sexdens rubropilosa* Forel	LE	62
HYM		*Atta* sp.*	LE	4
LEP	Apatelodidae	*Apatelodes pandara* Druce	LE	18
LEP	Cosmopterygidae	*Pyroderces rileyi* (Walsingham)	TR	12
LEP	Geometridae	*Glena bipennaria bipennaria* (Guenée)	LE	18
LEP	Limacodidae	*Acharia* sp.	LE	41
LEP	Pyralidae	*Caphys biliniata* (Stoll)	TR	12
LEP		*Ectomyelois muriscis* (Dyar)	TR	11, 12
LEP		*Hypsipyla grandella* (Zeller)	TR, LE, SE, ST	12, 21, 37, 52, 55, 64
ORT	Acrididae	*Stenopola bohlsii* Giglio-Tos	LE	40
TRO	Tetranychidae	*Mononychellus* sp.	LE	44
TRO		*Oligonychus* sp.	LE	44

*Taxonomic identification refined by the authors after publication of the original source; [?]questionable determination

The most frequently reported species include *Euplatypus parallelus* (Fabricius) (Coleoptera: Curculionidae: Platypodinae), *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae), and *Xyloperthella picea* (Olivier) (Coleoptera: Bostrichidae) (Table 1).

Euplatypus parallelus (Figure 1) is a Neotropical species and it is considered one of the most widespread and destructive Platypodinae in the world (Wood & Bright, 1992). It is a polyphagous beetle that attacks standing trees, logs, or freshly cut wood (Beaver, 2013). This beetle is commonly found in most African mahogany plantations in Brazil and has been reported attacking standing trees, logs, and freshly cut branches. However, there are no published studies quantifying the damage caused by this insect in the crop. Cristovam et al. (2018) associated its attack with the thinning of *K. grandifoliola* trees, but did not provide no damage quantification or control recommendations, especially since the publication is an abstract from a scientific meeting, which limits the level of detail regarding the occurrence of this insect in the crop. Similarly, Covre et al. (2018d) mention that this species is related to pruning activities, and recommend the prompt removal of pruned branches to avoid trunk infestation by wood-boring beetles, including *E. parallelus*. Nevertheless, only infestation percentages were reported, and the trees were able to defend themselves against the borers through gum exudation. Therefore, it remains uncertain whether such attacks may impact the future quantity or quality of the wood.

Figure 1. *Euplatypus parallelus* (Fabricius) (Coleoptera: Curculionidae: Platypodinae), male (left) and female (right). (Source: L. S. Covre).

Hypsipyla grandella (Figure 2B) is a moth native to South and Central America, commonly known as the shoot borer or mahogany shoot borer, and it is a major pest of cedars (*Cedrela* spp.) and mahoganies (*Swietenia* spp.) (Griffiths, 2001). In Brazil, this species is a significant pest of Brazilian mahogany, and it has been observed attacking seeds, bark, and shoot tips of African mahogany. This moth has been reported to damage seeds of *K. grandifoliola* (Lemes et al., 2019). However, the authors did not perform any quantitative or qualitative assessment of the seeds, such as seed weight or germination tests; they only documented the occurrence and included photographs of the damage. Based on this, the insect should be regarded as a potential pest, particularly when seed-based propagation is used by producers for seedling production.

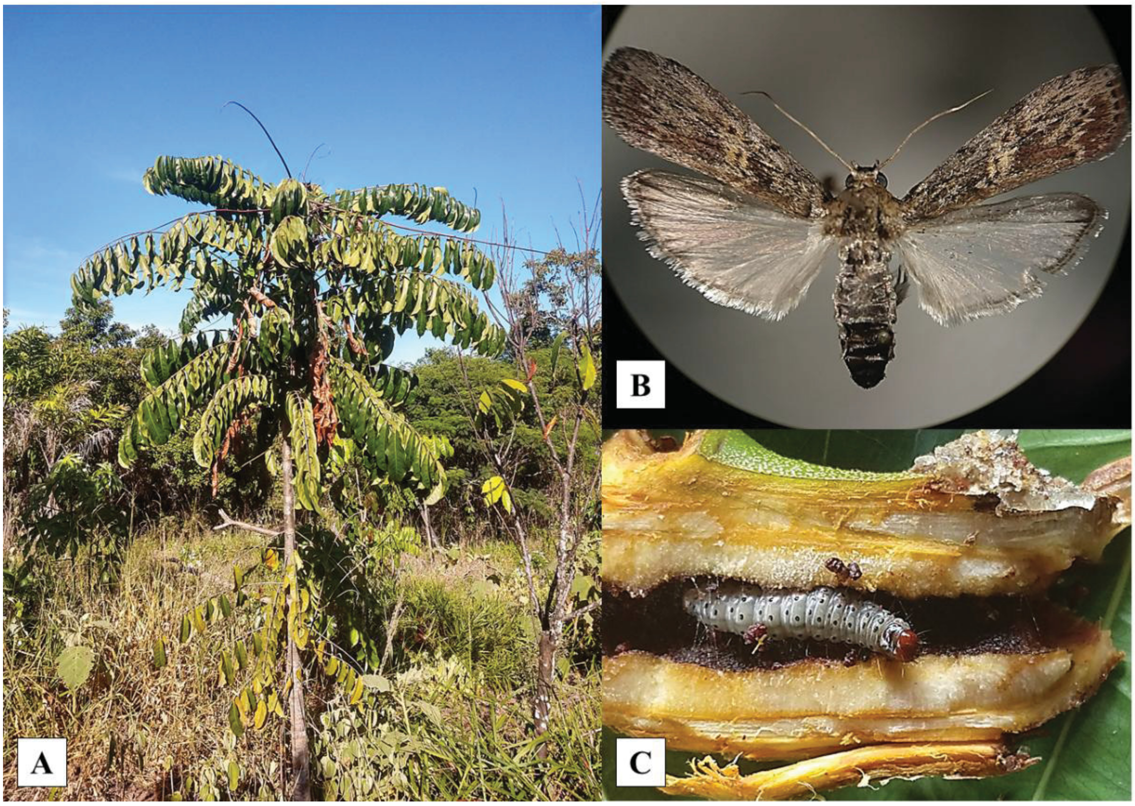

Figure 2. A) Damage to the shoot tip of *Khaya ivorensis*; B) adult and C) larva of *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) in Valença, Bahia. (Source: L. S. Covre).

Reports of *H. grandella* attacking shoot tips (Figure 2A, C) indicated low infestation levels, approximately three percent in *K. grandifoliola* (Zaneti et al. 2017). Damage has only been described for *K. senegalensis*, although infestation levels were not quantified (Queiroga et al. 2023). These studies report the occurrence of the insect and discuss possible impacts of the damage and control measures, drawing from literature on *H. grandella* damage in Brazilian mahogany (*S. macrophylla*). Therefore, it remains uncertain whether African mahogany trees affected by this insect will suffer any future economic impact in wood quality or commercial value. Moreover, *K. grandifoliola* appears to be less susceptible to shoot borer attack than K*. ivorensis* (Santos 2019; Ferraz Filho et al. 2021).

Hypsipyla grandella has also been reported, at low infestation levels (around 1% of trees), attacking the base of the trunk of *K. senegalensis* (Figure 3A) (Covre et al. 2018a; Dallacort et al. 2018), and appears to be associated with bark canker in *K. grandifoliola* (Covre et al. 2018a). However, no economic damage has been quantified and no control methods have been studied (Figure 3B) (Covre et al. 2018a).

Figure 3. A) Damage caused by *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) at the base of the trunk of *Khaya senegalensis* in Alpercata, Minas Gerais; and B) larva associated with bark canker on *Khaya grandifoliola* in São Roque de Minas, Minas Gerais. (Source: L. S. Covre).

Xyloperthella picea (Figure 4) is native to the African continent (Madagascar), and Arabia (Borowski & Wegrzynowicz, 2007). Although the exact date of its introduction to Brazil is uncertain, it likely occurred during the transatlantic slave trade (Lesne, 1903). This beetle is usually associated with dry wood (Kahuthia-Gathu et al., 2018), and as suggested by reports of other species within the same genus and tribe exhibiting similar behavior (Fisher, 1950; Roberts, 1967). However, in Brazilian African mahogany plantations, it has been reported infesting even trunks of apparently healthy tree, a behavior that is rather unusual for this species. Nevertheless, the extent of its damage was not quantified (Covre et al., 2018c). Despite the lack of detailed assessments, *X. picea* can be considered a potential pest of African mahogany, particularly in sawmills.

Figure 4. *Xyloperthella picea* (Olivier) (Coleoptera: Bostrichidae), lateral view (left) and dorsal view (right). (Source: L. S. Covre).

3 LITERATURE ON INSECTS ASSOCIATED WITH AFRICAN MAHOGANY IN BRAZIL

In our literature review, we found 36 publications on insects associated with African mahogany in Brazil, including two books, 16 peer-reviewed journal articles, 14 conference abstracts, and four theses/dissertations.

There are two additional books mentioning insects associated with African mahogany in Brazil (Pinheiro et al., 2011; Reis et al., 2019), but these were not included in our stats, as they primarily consist of literature reviews that cite previously published studies without presenting new data. Conference abstracts, theses, or dissertations that had subsequently been published as scientific articles were excluded from the literature census to ensure that the same insect records were not counted more than once.

The number of insect occurrence records we compiled from the reviewed publications was 14 for *K. grandifoliola*, 15 for *K. ivorensis*, and 12 for *K. senegalensis* (Table 2), with species names reproduced exactly as they appeared in the original studies. However, based on the geographic locations mentioned in these studies and the photographic documentation of insect damage provided in the methodology, we identified cases of misidentification between *K. grandifoliola* and *K. ivorensis*. Among the studies citing *K. ivorensis*, only that of Santos (2019) actually involved this species, while the remaining 14 studies were, in fact, conducted on *K. grandifoliola* (Table 2). It is worth mentioning that two articles (Fujihara et al., 2021; Silva et al., 2022) continued to use the incorrect species name *K. ivorensis* despite the official taxonomic clarification of African mahogany species provided by ABPMA (2020).

Table 2. Overview of the scientific literature published in Brazil regarding insect records associated with the African mahogany species *Khaya grandifoliola, Khaya ivorensis,* and *Khaya senegalensis.* Numbers in parentheses represent the total number of publications identified for each species.

***Khaya grandifoliola* (28)**		***Khaya ivorensis* (1)**	***Khaya senegalensis* (12)**
Falesi & Baena 1999*	Fialho Jr et al. 2019*	Santos 2019	Covre et al. 2018a
Lunz et al. 2008*	Lemes et al. 2019*		Covre et al. 2018b
Farias et al. 2011*	Santos 2019		Covre et al. 2018c
Matrangolo et al. 2016*	Pinto 2020		Dallacort et al. 2018
Nascimento et al. 2016*	Silva et al. 2020*		Texeira et al. 2018
Ceu et al. 2017*	Coelho et al. 2021		Benso 2019
Moura et al. 2017*	Fujihara et al. 2021*		Covre et al. 2021
Silva et al. 2017*	Souza et al. 2021		Bonfim et al. 2022
Zanetti et al. 2017*	Bonfim et al. 2022		Gonçalves et al. 2023
Covre et al. 2018a	Silva et al. 2022*		Queiroga et al. 2023
Covre et al. 2018d	Silva et al. 2024		Silva et al. 2024
Cristovam et al. 2018	Covre et al. 2025a		Covre et al. 2025b
Luna et al. 2018	Covre et al. 2025b		
Pelozato et al. 2018	Covre et al. 2025c		

*Literature in which the African mahogany species was misidentified as *K. ivorensis*

After these corrections, it becomes evident that *K. grandifoliola* is the most frequently studied African mahogany species in insect occurrence reports in Brazil (68.3%), followed by *K. senegalensis* (29.3%), and *K. ivorensis* (2.4 %) (Table 2). These figures closely mirror the proportion of plantation area occupied by each species, with *K. grandifoliola* covering ca. 66% of the total planted area and *K.senegalensis* about 33%, while *K. ivorensis* is limited to small experimental plots (Ferraz Filho et al., 2021).

Geographically, most records come from Minas Gerais, despite Pará being the pioneer in African mahogany cultivation (Falesi & Baena, 1999). Publications are distributed as follows, Southeast (66%), North (17%), Midwest

(10%), Northeast (7%), and none from the South (Figure 5). These proportions mirror the regional distribution of African mahogany plantations, with 50% in the Southeast, 25% in the Midwest, 13% in the North, 6% in the Northeast, and 6% in the South of Brazil (Ferraz Filho et al., 2021).

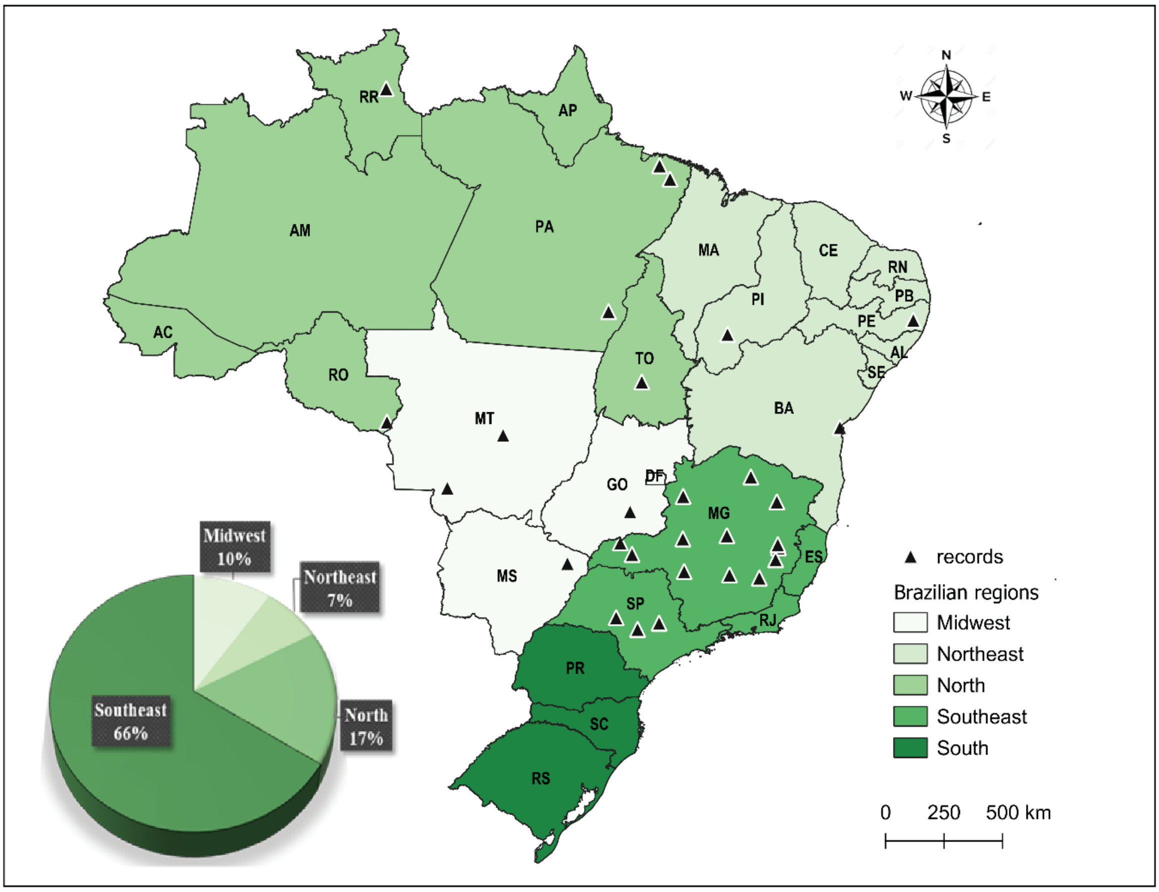

Figure 5. Records from the literature on insects associated with African mahogany (*Khaya* spp.) plantations by Brazilian region (1999–2025). (Source: author's elaboration).

4 CONCLUDING REMARKS

African mahogany, a valuable timber tree introduced to Brazil, faces challenges typical of exotic species, including pest threats. Difficulties in studying insect associations have been further complicated by the misidentification of the introduced species (*K. grandifoliola*). Recognizing the crucial role of accurate species identification and pest association in sustainable forestry, this manuscript critically evaluates the literature, corrects recurring taxonomic and entomological errors, and consolidates reliable data to support informed management and conservation decisions.

Most existing studies are occurrence reports that describe insect damage to plant parts but do not quantify economic losses. Consequently, the pest status of associated insects remains uncertain. In fact, only two publications have addressed both damage quantification and pest management strategies (Fialho Jr. et al., 2019; Covre et al., 2025b), leaving a significant gap in practical recommendations.

Therefore, future research should prioritize quantifying economic damage, developing integrated pest management techniques such as biological and chemical control, resistant or tolerant clones, and regular monitoring, and ensuring accurate species identification in publications. Additionally, facilitating access to research findings, particularly for African mahogany producers, is essential to promote informed decision-making.

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CHAPTER II

WOODBORING BEETLE DIVERSITY IN *Khaya grandifoliola* C.DC. (MELIACEAE) STANDS OF DIFFERENT AGES AND ADJACENT RIPARIAN FOREST

"To understand ecology is to see the invisible threads that bind life together."

David Attenborough

Woodboring beetle diversity in *Khaya grandifoliola* C.DC. (Meliaceae) stands of different ages and adjacent riparian forest

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Abstract

African mahogany (*Khaya* spp.) plantations have expanded considerably in Brazil over recent decades, yet their sustainability is increasingly challenged by woodboring beetles, which can cause significant economic and ecological impacts. Understanding the diversity, trophic guilds, and ecological dynamics of these insects is essential for developing sustainable management strategies. In this study, we evaluated woodboring beetle assemblages in *Khaya grandifoliola* C.DC. stands of different ages (planting in 2013, 2014, and 2015) and in an adjacent riparian forest fragment (RF) in Capinópolis, Minas Gerais, Brazil. Beetles were trapped weekly with ethanol-baited flight intercept traps, starting in April 2017 in the plantations and in August 2021 in the RF, until March 2024. A total of 51,110 individuals representing 200 species in Bostrichidae (13 spp.), Cerambycidae (87 spp.), Scolytinae (93 spp.), and Platypodinae (7 spp.) were recorded. Species were classified into five trophic guilds: xylophagous, xylomycetophagous, phloeophagous, spermophagous, and myelophagous. Community diversity was assessed using Hill numbers (q = 0, 1, 2), while compositional differences were evaluated with Jaccard and Bray–Curtis dissimilarities. Indicator species analysis identified taxa associated with specific environments, most of which were polyphagous, and the number of indicator species suggested successional changes in community composition. Xylophagous and xylomycetophagous guilds dominated the stands, whereas myelophagous, spermophagous, and phloeophagous species were primarily transient visitors dispersing from RF without establishing populations in the African mahogany stands. Despite similar species richness among sites, community differences were driven by species abundances and guild composition, emphasizing the importance of analyzing guilds separately to understand ecological associations. Assemblage dynamics were influenced by a combination of resource continuity (stand age, self-pruning, proximity to RF), resource pulses (management activities such as thinning and pruning), and resource diversity (heterogeneity in RF). Temporal patterns revealed the influence of climatic variability and management practices, with transient increases in resources promoting diversity in younger stands and successional processes driving convergence toward RF-like communities. Spatially, proximity to native forest enhanced species immigration and community evenness, highlighting the importance of maintaining habitat connectivity. From a management perspective, practices that retain structural heterogeneity, such as dead wood and variable stand structure, can support diverse and ecologically valuable beetle assemblages. Overall, African mahogany plantations embedded within heterogeneous landscapes, including native forest fragments, can sustain complex, dynamic systems.

Resumo

Os plantios de mogno-africano (*Khaya* spp.) expandiram-se consideravelmente no Brasil nas últimas décadas, mas sua sustentabilidade tem sido cada vez mais desafiada por insetos broqueadores de madeira, que podem causar impactos econômicos e ecológicos significativos. Compreender a diversidade, as guildas tróficas e a dinâmica ecológica desses insetos é essencial para o desenvolvimento de estratégias de manejo sustentável. Neste estudo, avaliamos as guildas de broqueadores de madeira em talhões de *Khaya grandifoliola* C.DC. de diferentes idades (plantios em 2013, 2014 e 2015) e em um fragmento adjacente de mata ciliar (RF) em Capinópolis, Minas Gerais, Brasil. Os besouros foram coletados semanalmente com armadilhas de interceptação de voo iscadas com etanol, iniciando-se em abril de 2017 nos talhões e em agosto de 2021 na RF, até março de 2024. O total de 51.110 indivíduos foi coletados, representando 200 espécies em Bostrichidae (13

spp.), Cerambycidae (87 spp.), Scolytinae (93 spp.) e Platypodinae (7 spp.). As espécies foram classificadas em cinco guildas tróficas: xilófagas, xilomicetófagas, floeófagas, espermófagas e mielófagas. A diversidade das comunidades foi avaliada utilizando números de Hill (q = 0, 1, 2), enquanto as diferenças de composição foram analisadas com dissimilaridades de Jaccard e Bray–Curtis. A análise de espécies indicadoras identificou táxons associados a ambientes específicos, a maioria deles polífagos, e o número de espécies indicadoras sugeriu mudanças sucessoras na composição das comunidades. As guildas xilófagas e xilomicetófagas dominaram os povoamentos, enquanto as espécies mielófagas, espermófagas e floeófagas foram principalmente visitantes transitórios dispersando-se a partir da RF, sem estabelecer populações nos plantios de mogno-africano. Apesar da similaridade na riqueza de espécies entre as áreas, as diferenças nas comunidades foram impulsionadas pelas abundâncias das espécies e pela composição das guildas, enfatizando a importância de analisar as guildas separadamente para compreender as associações ecológicas. A dinâmica das guildas foi influenciada por uma combinação de continuidade de recursos (idade do povoamento, desrama natural, proximidade da RF), pulsos de recursos (atividades de manejo como desbaste e desrama) e diversidade de recursos (heterogeneidade da RF). Padrões temporais revelaram a influência da variabilidade climática e das práticas de manejo, com aumentos transitórios de recursos promovendo diversidade em povoamentos jovens e processos de sucessão conduzindo à convergência para comunidades semelhantes às da RF. Espacialmente, a proximidade da floresta nativa aumentou a imigração de espécies e a equidade comunitária, destacando a importância de manter a conectividade do habitat. Do ponto de vista do manejo, práticas que mantêm a heterogeneidade estrutural, como a retenção de madeira morta e a variação na estrutura dos povoamentos, podem sustentar comunidades de besouros diversas. Em geral, os plantios de mogno-africano inseridos em paisagens heterogêneas, incluindo fragmentos de floresta nativa, podem sustentar sistemas complexos e dinâmicos.

1 INTRODUCTION

The diversity of woodboring beetles plays a crucial role in the management and ecological monitoring of forest plantations (Flechtmann et al. 2001; Allison et al. 2023). This is particularly important for high-value timber species such as *Khaya grandifoliola* C.DC. (Meliaceae), the main African mahogany *Khaya* species planted in Brazil (Ferraz Filho et al. 2021). Woodboring beetles broadly refer to beetles that have evolved to live and feed within woody tissue, encompassing species from several Coleoptera families, including Cerambycidae, Bostrichidae and Curculionidae, particularly the subfamilies Scolytinae and Platypodinae (Haack & Slansky 1987; Allison et al. 2023). These beetles occupy a variety of ecological niches and interact with woody substrates in distinct ways, contributing to wood decomposition and nutrient cycling (Dodds et al. 2023) and, in some cases, causing economic damage to commercial forests (Heber et al. 2021; Ceriani-Nakamurakare et al. 2022).

To better understand the ecological dynamics and potential impacts of these beetles, it is essential to group them into ecological guilds, that is, assemblages of species that exploit similar resources in similar ways, regardless of their taxonomic relationships (Root 1967). In the case of woodboring beetles, classifying species into trophic guilds such as xylophagous, xylomycetophagous, phloeophagous, spermatophagous, and myelophagous, provides valuable insight into their functional roles within forest ecosystems (Atkinson & Equihua-Martinez 1986).

Xylophagous beetles feed directly on woody tissue, playing a vital role in wood decomposition and nutrient cycling (Lesne 1911). Xylomycetophagous beetles, such as ambrosia beetles, cultivate symbiotic fungi within galleries excavated in wood, which they then consume (Hulcr & Skelton 2023). Spermatophagous beetles consume seeds, potentially affecting plant regeneration, while myelophagous beetles feed on the pith of twigs, petioles, and small stems (Wood 2007). Lastly, phloeophagous beetles, known as bark beetles, feed on the phloem of trees, potentially disrupting sap flow and causing significant damage in commercial forests (Atkinson & Equihua-Martinez 1986).

Understanding the composition and structure of woodboring beetle guilds is essential not only for pest management but also for assessing insect biodiversity and the health of forest ecosystems (Flechtmann et al. 2001; Allison et al. 2023). Additionally, such knowledge is important for detecting new or exotic introduced species (Covre et al. 2021, 2023, 2024). However, short-term studies may fail to capture the full extent of insect diversity or detect the subtle, long-term changes in the forest structure (Dolný et al. 2021; Noriega et al. 2021). Therefore, long-term monitoring is fundamental to detecting trends in species composition, the emergence of potential pests, and the impacts of environmental or anthropogenic changes on beetle assemblages (Escobar et al. 2008; Noriega et al. 2021; Gunggot et al. 2025).

Differences in insect diversity and community structure are expected between planted forests and adjacent native vegetation (Pacheco et al. 2009; López-Bedoya et al. 2021). Forest plantations, depending on species composition, management practices, and age, often present reduced structural complexity and diversity of microhabitats compared to native ecosystems, potentially influencing the richness and abundance of woodboring beetles (López-Bedoya et al. 2021; Allison et al. 2023).

Forest age and management practices play a crucial role in shaping the diversity of beetle species present in a given area (López-Bedoya et al. 2021). Younger plantations may exhibit different infestation patterns compared to older stands due to variations in tree physiology, bark texture, and the presence of natural enemies (Ryan et al. 2015). Similarly, native vegetation, which serves as a reservoir for insect species, may support a different community of woodboring beetles compared to commercial plantations, and may harbor a wider variety of beetles, including rare or specialized species, due to higher plant diversity, availability of deadwood, and less disturbance (Ferreira 2014; Leonel 2019; Allison et al. 2023).

Investigating the differences in beetle assemblages among *K. grandifoliola* plantations of varying ages and native forests can provide valuable insights into their population dynamics and interactions with the surrounding environment. The objective of this study was to assess the diversity of woodboring beetles in *K. grandifoliola* stands of different ages and adjacent native vegetation, a riparian forest fragment to be more specific. By analyzing the composition of beetle guilds across these environments, we seek to advance our understanding of how forest type, structure, and management influence the woodboring beetle diversity.

2 MATERIAL AND METHODS

2.1 Study sites

The study sites consisted of three *K. grandifoliola* stands (18°46’6.18”S 49°28’51.59”W), planted in November 2013 (S1), 2014 (S2), and 2015 (S3) in Capinópolis, state of Minas Gerais, Brazil (Figure 1). Stands S1 and S2 each covered 25 ha, while S3 measured 30 ha. The stands were surrounded by vegetation that included a backyard orchard (see Covre et al. 2025 for more details), a stand of black pepper (*Piper nigrum* L.) cv. Kottonandan and Bragantina, and a riparian forest fragment (RF) (Figure 1). The orchard covered an area of approximately 0.5 ha, the black pepper stand was about 1 ha, and the riparian fragment within the property was approximately 7 ha in size.

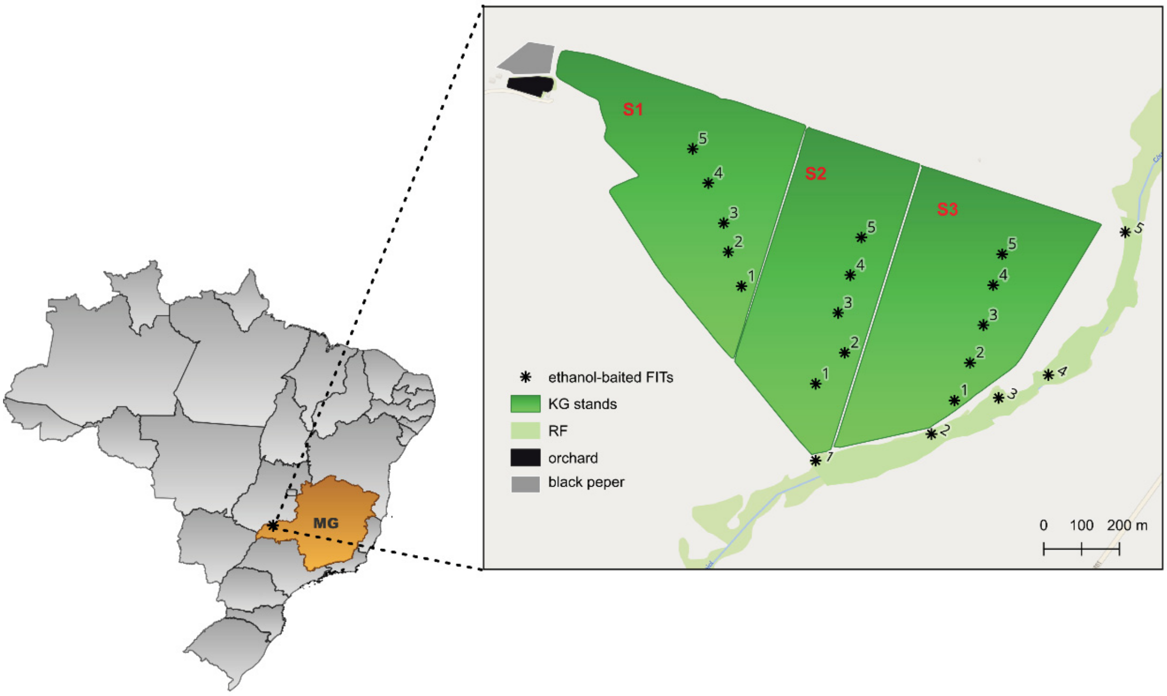

Figure 1. Study sites. Location of ethanol-baited FITs in *Khaya grandifoliola* (KG) stands, planted in November 2013 (S1), 2014 (S2), and 2015 (S3), and riparian forest fragment (RF). Fazenda Grama, Capinópolis, Minas Gerais, Brazil.

2.2 Woodboring beetle trapping and species determination

At roughly the center of each African mahogany stand, five flight-intercept traps (FIT) modified ESALQ-86 (Berti Filho & Flechtmann 1986) were deployed 100 meters apart in a transect on March 31, 2017. An additional five traps were deployed on August 5, 2021, in the riparian forest fragment (RF) adjacent to the stands (Figure 1).

The traps were suspended on steel rebar supports at a height of 1.5 meters and positioned between trees along the line to allow woodborer free access to the traps from any direction, while avoiding interference with mechanized forestry operations between rows. The bottom of the trap (collector) contained water with a few drops of detergent and a teaspoon of salt to help preserve the captured insects (Figure 2). The bait was 96% ethanol with a release rate of 870 mg/day at 20°C.

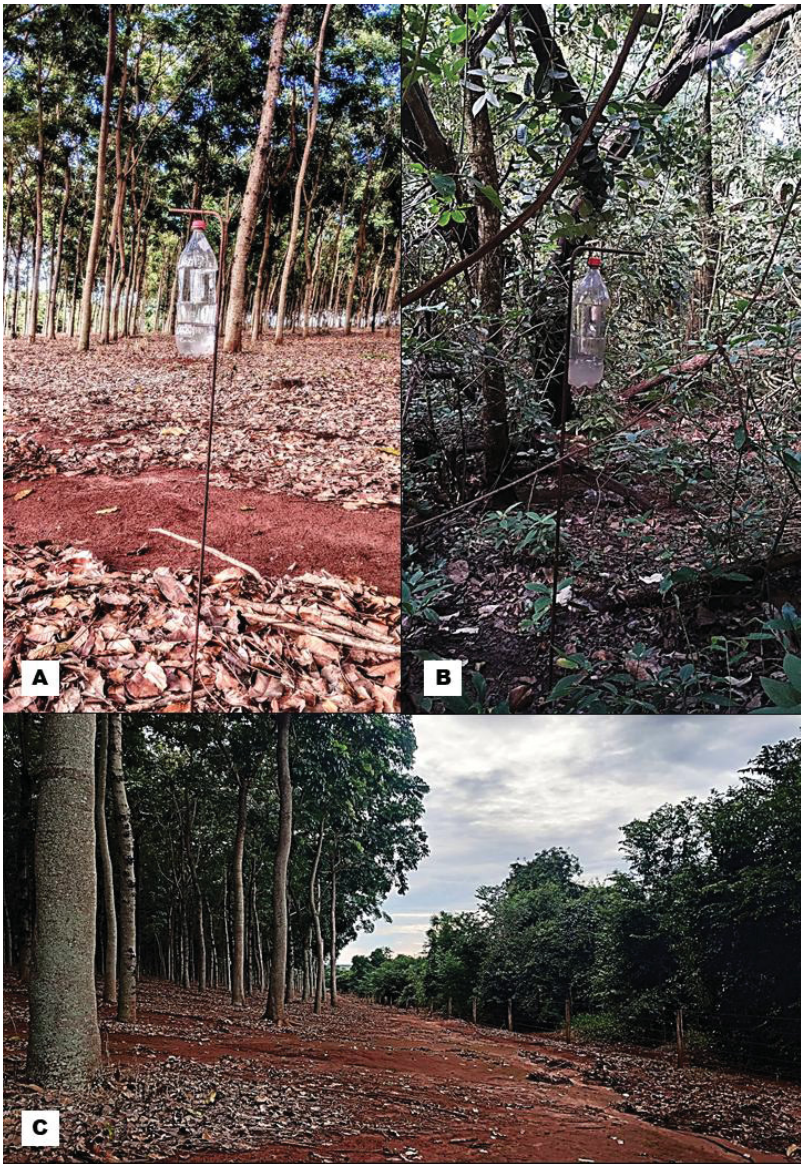

Figure 2. Ethanol-baited flight-intercept traps in (A and C-left) African mahogany (*Khaya grandifoliola*) stand and (B and C-right) in adjacent riparian forest. Capinópolis, Minas Gerais, Brazil. (Source: L.S. Covre).

Trapping frequency was weekly, with the first collection in the African mahogany stands made on April 10, 2017, and in the riparian forest on August 30, 2021. The final collections were made on March 28, 2024. In total, 365 trappings were carried out in the stands (7 years) and 136 in the riparian forest (ca 3 years).

Specimens of Curculionidae (Scolytinae and Patypodinae) and Bostrichidae were sorted and determined at the Entomology Laboratory of the São Paulo State University, Ilha Solteira campus (FEIS/UNESP), using the reference collection of the Entomology Museum of the the same campus

(MEFEIS). Cerambycidae specimens were determined by Dr. Antônio Santos-Silva from the Museum of Zoology of the University of São Paulo (MZUSP). Voucher specimens were deposited in the MEFEIS collection.

2.3 Data analysis

The analyses comprised trappings conducted exclusively in the *K. grandifoliola* stands (April 2017 to March 2024; seven years), and the adjacent riparian forest fragment was included in the analyses when traps were present in all four areas (S1, S2, S3 and RF) (August 2021 to March 2024; ca. three years).

All species were divided into guilds: (1) the entire woodboring beetle community (all guilds combined); (2) the xylophagous beetle community guild (all Bostrichidae, all Cerambycidae and two Scolytinae species); (3) the xylomycetophagous community guild (all Platypodinae and most Scolytinae – 46 species); (4) the phloeophagous community guild (part of Scolytinae – 30 species); and “others” (8 myelophagous and seven spermophagous Scolytinae species guilds) (Supplementary Tables S1 and S2). The proportion of woodboring species from each feeding guild was calculated based on the total number of species observed in each study site.

We evaluated if the species could be used as potential indicators by performing indicator species analyses using the package indicspecies (Cáceres & Legendre 2009). This approach combines measures of fidelity (the frequency of a species within a group) and specificity (its restriction to that group) to calculate an indicator value for each species. In the context of this study, the analysis was used to identify species that ecologically characterize each sampled stand and the adjacent riparian forest fragment.

Rarefaction and extrapolation curves were generated for each guild in the four study areas (stands 1, 2, 3, and RF) using Hill numbers, which incorporate a parameter ‘q’ that modulates sensitivity to species relative abundances: q = 0 corresponds to species richness; q = 1 is the exponential of Shannon entropy, weighting species proportionally to their abundance; and q = 2 corresponds to the inverse Simpson index, emphasizing dominant species (Chao et al. 2014). Statistical significance was inferred based on the overlap or separation of their

95% confidence intervals, calculated with the iNEXT package (Hsieh et al. 2016).

A Principal Coordinate Analysis (PCoA) was performed using both the Jaccard and Bray–Curtis dissimilarity indices with the vegan package (Oksanen et al. 2020) to evaluate community structure and to visualize potential differences in community composition among the study areas (Legendre & Cáceres 2013).

All statistical analyses described above were conducted in R (R Core Team 2024), and all graphics were created using the ggplot2 package (Wickham 2016).

3 RESULTS

3.1 Woodboring beetle communities

A total of 51,110 specimens (200 species) were trapped, 13 in Bostrichidae, 87 in Cerambycidae (Supplementary Table S1), 93 in Scolytinae and 7 in Platypodinae (Supplementary Table S2). We also trapped over 800 specimens of woodborer natural enemies in the families Cleridae, Histeridae and Trogossitidae.

The composition of insect guilds, based on the proportion of species in each study area, showed a consistent dominance of xylophagous and xylomycetophagous species in all four study sites. Xylophagous species accounted for approximately half of the species richness in each area, followed by xylomycetophagous species, which represented about one third of the total richness. Spermophagous, phloeophagous, and myelophagous guilds showed lower proportions throughout sites (Figure 3).

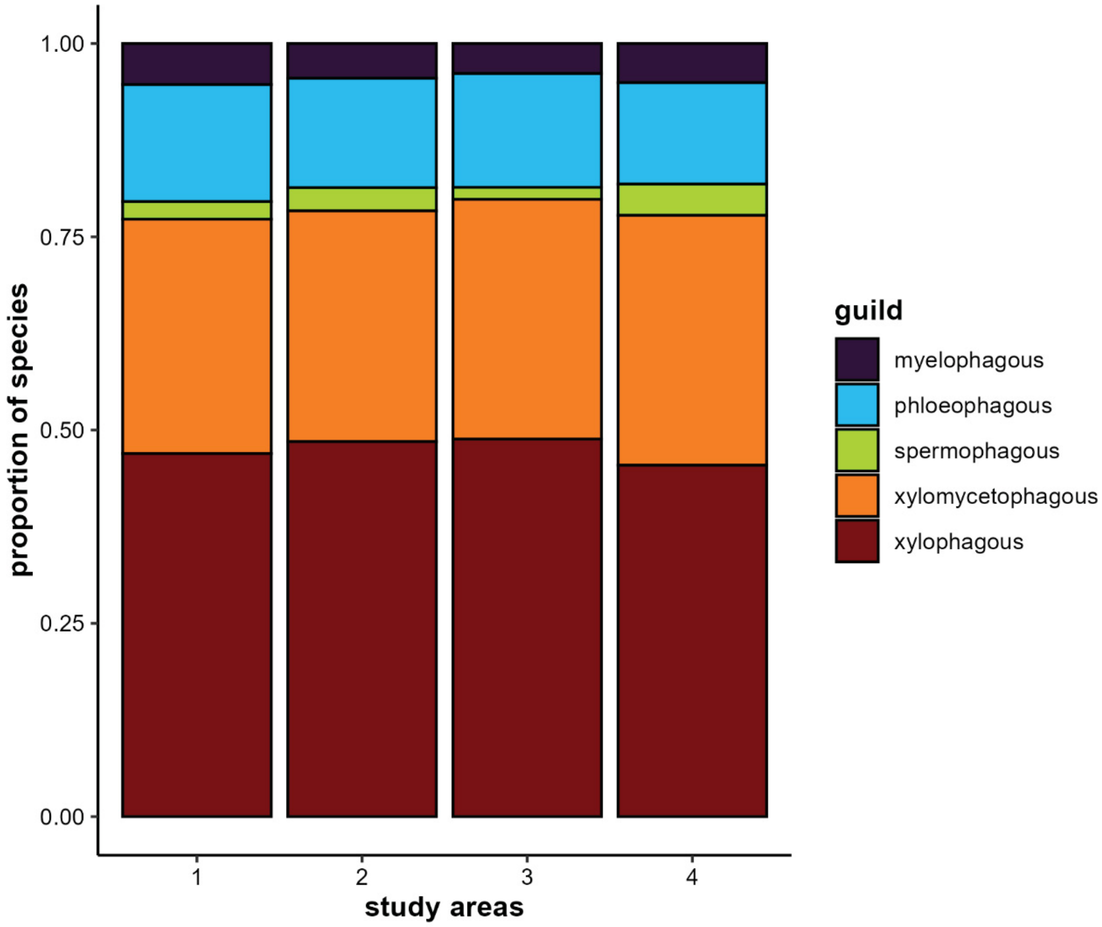

Figure 3. Proportion of woodboring species for each feeding guild in the four study areas: S1, S2, S3 (African mahogany stands) and 4 (riparian forest). Capinópolis, Minas Gerais, Brazil.

3.2 Indicator species

The indicator species analysis identified fifteen species significantly associated with specific stands (Table 1). The indicator species analysis revealed that *Hypothenemus setosus* (Eichhoff) and *Xyleborus spinulosus* Blandford were associated only with S1, *Xyleborus affinis* Eichhoff and *Xyloperthella picea* (Olivier) with S2, and *Cryptocarenus heveae* (Hagedorn), *Cryptocarenus seriatus* Eggers, *Dinoderus minutus* (Fabricius), *Hypothenemus subsulcatus* Atkinson & Flechtmann, *Premnobius perezdelacrucei* Petrov & Atkinson and *Sampsonius dampfi* Schedl with S3. While *Aglaoschema concolor* (Gounelle) was associated with both stands 1 and 3, *Euplatypus parallelus* (Fabricius), *Neoclytus pusillus* Laporte & Gory, and *Premnobius cavipennis* Eichhoff were associated with stands 2 and 3, and *Micrapate cribripennis*

(Lesne) with stands 1 and 2. Only one species, *Amphicranus* sp. 02, was exclusively associated with RF (Table 1).

Table 1. Indicator species analysis (in parenthesis, indicator value for each species) of woodboring beetles in African mahogany (*Khaya grandifoliola*) stands planted in November 2013 (S1), 2014 (S2), and 2015 (S3) and in adjacent riparian forest fragment (RF). Capinópolis, Minas Gerais, Brazil

site	indicator species
S1	*Aglaoschema concolor* (0.685) (**Cerambycidae**); *Micrapate cribripennis* (0.652) (**Bostrichidae**); *Hypothenemus setosus* (0.808), *Xyleborus spinulosus* (0.684) (**Scolytinae**)
S2	*Neoclytus pusillus* (0.792) (**Cerambycidae**); *M. cribripennis* (0.652), *Xyloperthella picea* (0.672) (**Bostrichidae**); *Premnobius cavipennis* (0.766), *Xyleborus affinis* (0.704) (**Scolytinae**); *Euplatypus parallelus* (0.695) (**Platypodinae**)
S3	*A. concolor* (0.685), *N. pusillus* (0.792) (**Cerambycidae**); *Dinoderus minutus* (0.769) (**Bostrichidae**); *Cryptocarenus heveae* (0.725), *Cryptocarenus seriatus* (0.684), *Hypothenemus subsulcatus* (0.658), *P. cavipennis* (0.766), *Premnobius perezdelacrucei* (0.853), *Sampsonius dampfi* (0.794), (**Scolytinae**); *E. parallelus* (0.695) (**Platypodinae**)
RF	*Amphicranus* sp.02 (0.683) (**Scolytinae**)

3.3 Species diversity yearly in *Khaya* stands and riparian forest

The xylophagous guild exhibited a progressive increase over the years, with a steady rise until year 3, followed by a decline in year 4. It then increased again, reaching a pronounced peak in all stands in year 6, before decreasing to levels similar to those of the xylomycetophagous guild. The richness of the xylomycetophagous guild, on the other hand, showed an increasing trend from year 1 to year 3 in the plantation stands, decreasing roughly until year 5, then showing an increase until year 7, while in the RF it showed a steady increase over time (Figure 4). The richness of the myelophagous, phloeophagous, and spermophagous guilds showed comparatively a low and relatively constant species richness throughout the study period across all sites (Figure 4).

Regarding Shannon diversity (q = 1), the xylomycetophagous guild was predominant in all sites, especially during the early years of the study, which was clearest in stands S2 and S3. Overall, the xylophagous guild showed values similar to the myelophagous and phloeophagous guilds in all stands, except for year 6, while remaining stable in the RF. The spermophagous guild showed the lowest diversity in all sites (Figure 4).

For the inverse Simpson diversity index (q = 2), the xylomycetophagous guild presented the highest values in the stands, showing an increase in the first years followed by a decrease in S2 and S3, while in S1 there was a continuous increase up to year 6, followed by a decrease. As for all other guilds, diversity values did not vary significantly over the years, where the myelophagous guild stood out as the one with the second highest one. In the RF, the highest values were observed for the myelophagous and xylomycetophagous guilds, which did not vary notably over the years, in stark contrast with the phloeophagous guild, which decreased over time. In RF, diversity decreased in phloeophagous and slightly in the xylomycetophagous guilds, while in increased slightly in the xylophagous guild (Figure 4).

Overall, the xylomycetophagous guild was the one with the highest diversity (Shannon and Simpson), which decreased over time, while the xylophagous guild increased in richness and slightly in diversity over the years, in the African mahogany stands (Figure 4).

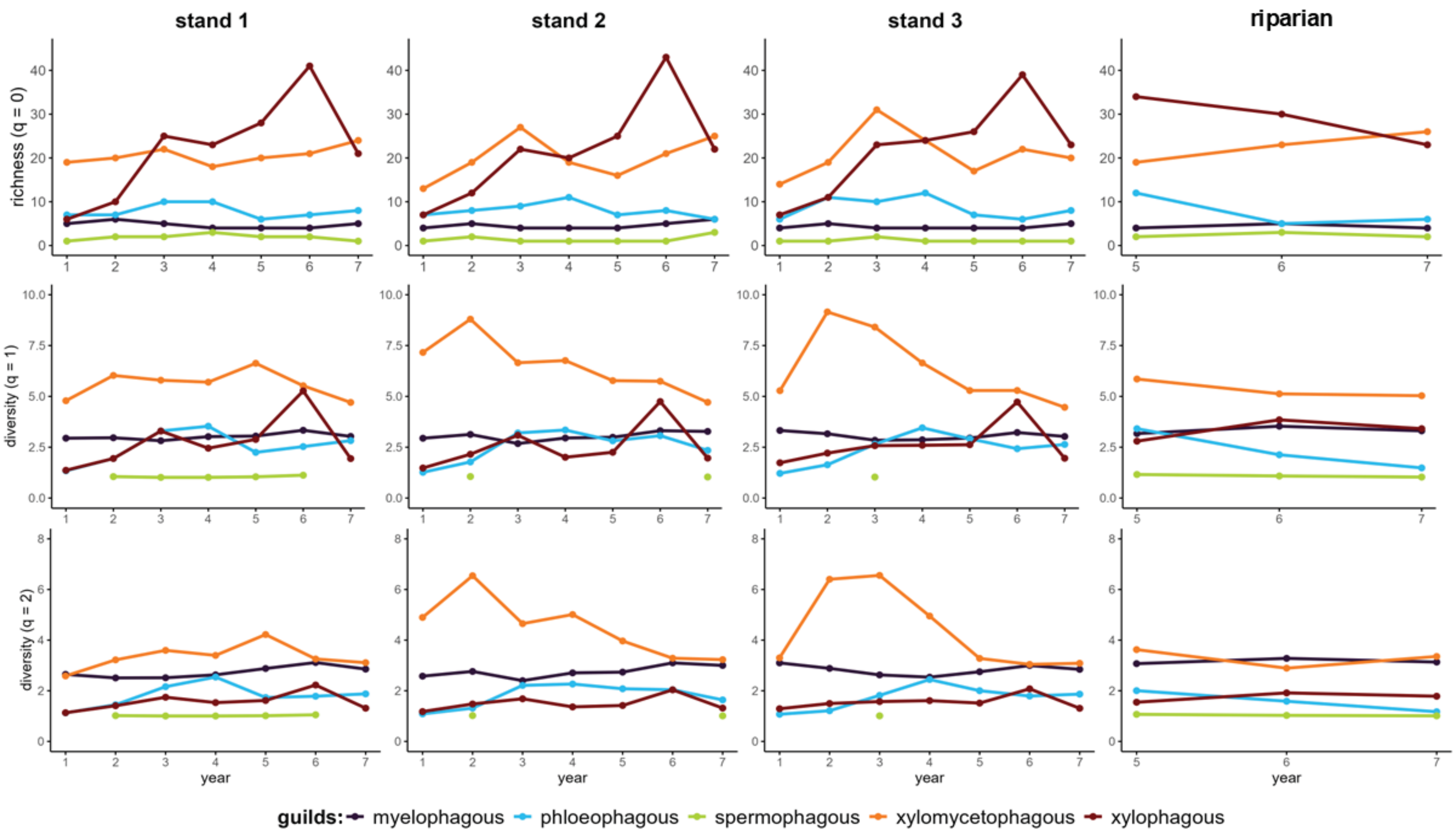

Figure 4. Hill numbers (q = 0, 1 and 2) for woodboring beetles' guilds trapped with ethanol-baited FITs in *Khaya grandifoliola* stands planted in November of 2013 (stand 1), 2014 (stand 2), and 2015 (stand 3), and riparian forest fragment (riparian) among study years. Capinópolis, Minas Gerais, Brazil, from April 2017 to March 2024.

3.4 Rarefaction and extrapolation curves in *Khaya* stands

Rarefaction and extrapolation diversity curves, based on Hill numbers, were generated for the woodboring beetle guilds. For species richness (*q* = 0), the confidence intervals along the curves showed considerable overlap among stands in all guilds, indicating no significant differences in species richness. Therefore, the stands can be considered similar regarding species richness (Figure 5).

Considering Shannon diversity index (*q* = 1), a distinct pattern was observed. When all guilds were analyzed together, stand S3 exhibited a slightly higher diversity. However, when analyzed separately by guilds, the xylophagous community was lowest in S2 whereas S1 and S3 exhibited similar levels (Figure 5). Xylomycetophagous and combined myelophagous/spermophagous species were more diverse in S2 and S3 compared to S1 (Figure 5). In contrast, the phloeophagous beetle community was more diverse and distinct in S1, while stands S2/S3 exhibited similar patterns for this guild (Figure 5).

Finally, for inverse Simpson diversity index (*q* = 2), stand S3 exhibited a distinct community with the highest overall diversity when all guilds were considered together (Figure 5). However, when analyzing the guilds separately, *q* = 2 was highest in S3/S1 for the xylophagous community, with a smaller value for S2. The xylomycetophagous guild was similar in S2 and S3, and higher than in S1, while for phloeophagous beetles it was higher and S1, with no differences in S2 and S3. For the combined myelophagous/spermophagous guild, distinct communities were observed, with a highest diversity in S3, followed by S2 and then by S1 (Figure 5).

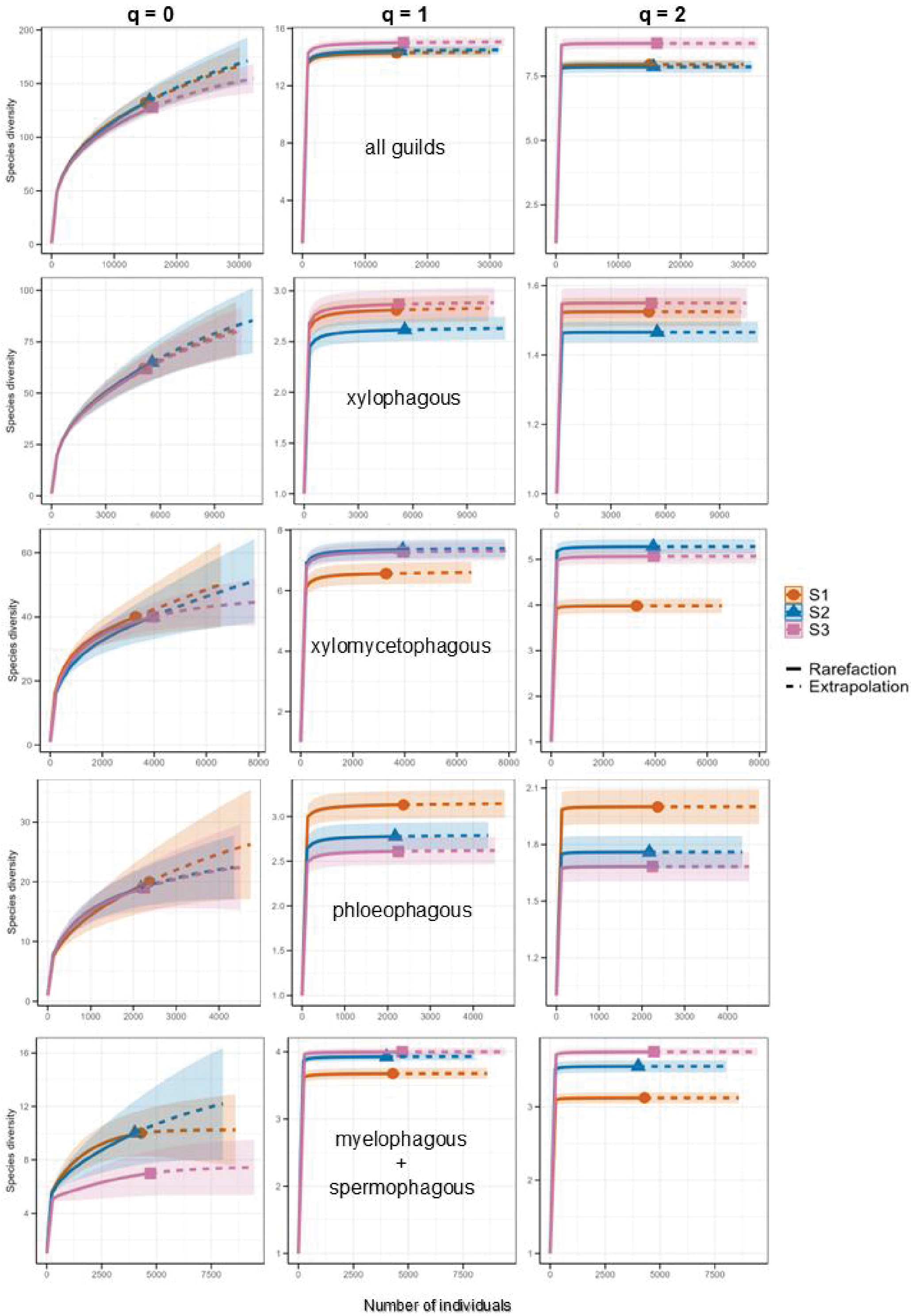

Figure 5. Rarefaction and extrapolation curves with Hill numbers of order q = 0 (species richness), q = 1 (exponential of Shannon entropy), and q = 2 (inverse of Simpson diversity) for woodboring beetles guilds trapped with ethanol-baited FITs in *Khaya grandifoliola* stands planted in November of 2013 (S1), 2014 (S2), and 2015 (S3), Capinópolis, Minas Gerais, Brazil, from April 2017 to March 2024. Solid and dashed lines depict the rarefaction and extrapolated number of individuals, respectively. Shaded areas indicate the 95% confidence interval. Non-overlapping confidence intervals indicate differences between stands.

3.5 PcoA Bray-Curtis and Jaccard indices in *Khaya* stands

The PCoA analysis based on the Bray-Curtis distance showed a clear separation among the African mahogany stands, particularly for S1, while S2 and S3 appeared more similar across all analyzed guilds. The only exception was the xylophagous guild, where there were no clear separations among stands. There were no clear separations among stands in Jaccard's PcoA, except for, combined myelophagous/spermophagous guild, where there was a particular community in S1, while S2 and S3 are similar (Figure 6).

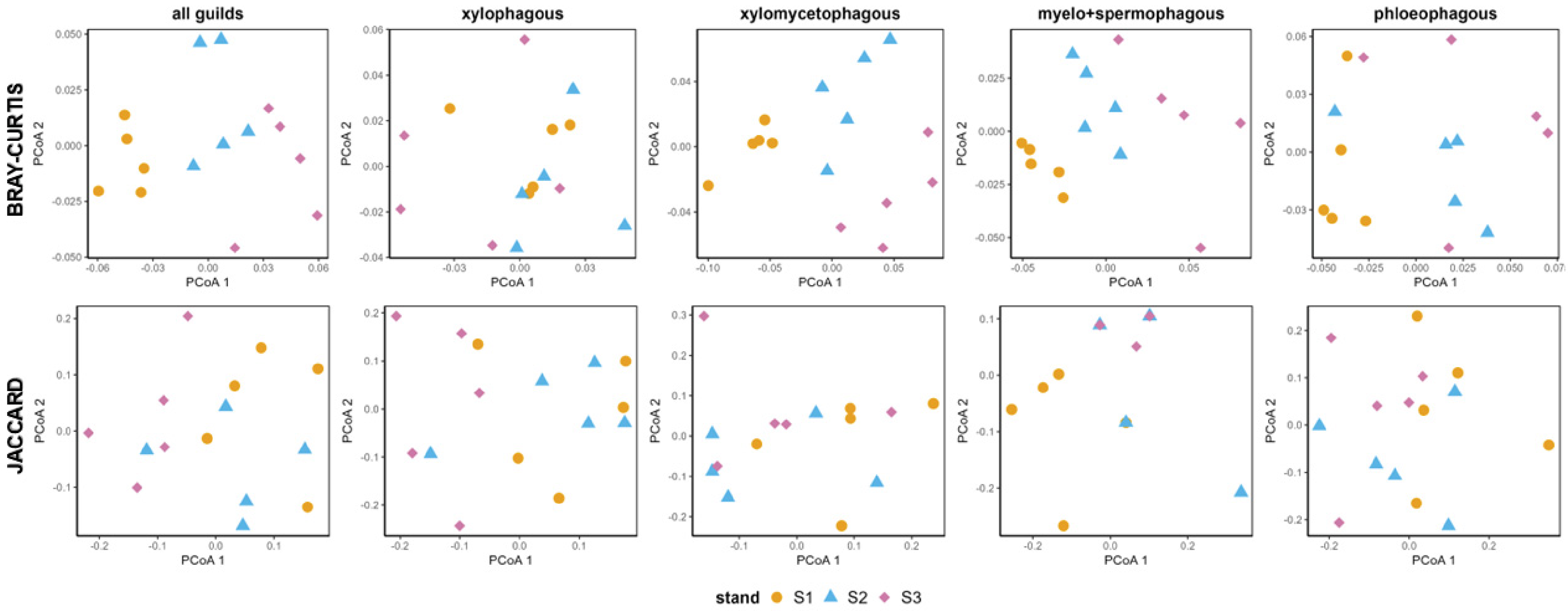

Figure 6. Principal coordinate analysis (PCoA) plot with Bray-Curtis and Jaccard for all woodboring guilds, xylophagous, xylomycetophagous, phloeophagous, and combined myelophagous/spermophagous trapped with ethanol-baited FITs in *Khaya grandifoliola* stands planted in November of 2013 (S1), 2014 (S2), and 2015 (S3), Capinópolis, Minas Gerais, Brazil, from April 2017 to March 2024.

3.6 Rarefaction and extrapolation curves comparison in *Khaya* stands *vs.* riparian forest fragment

In the following analysis, the RF was now included, albeit with fewer trapping dates. At this time, the African mahogany stands were 8, 7, and 6 years-old in S1, S2, and S3, respectively. Rarefaction and extrapolation diversity curves based on Hill numbers were generated for woodboring beetle guilds.

For species richness (q = 0), the confidence intervals showed substantial overlap among all study sites, indicating no statistically significant differences among them. An exception was observed in the combined myelophagous/spermophagous guild, where S3 exhibited a slightly reduced richness (Figure 7).

For all guilds combined, Shannon (q = 1) and inverse Simpson (q = 2) diversity indices were higher in RF. However, for the other guilds, there was no clear separation among sites, except in the xylophagous guild, where diversity in RF and S1 were similar and both were higher than in S2 and S3 (Figure 7).

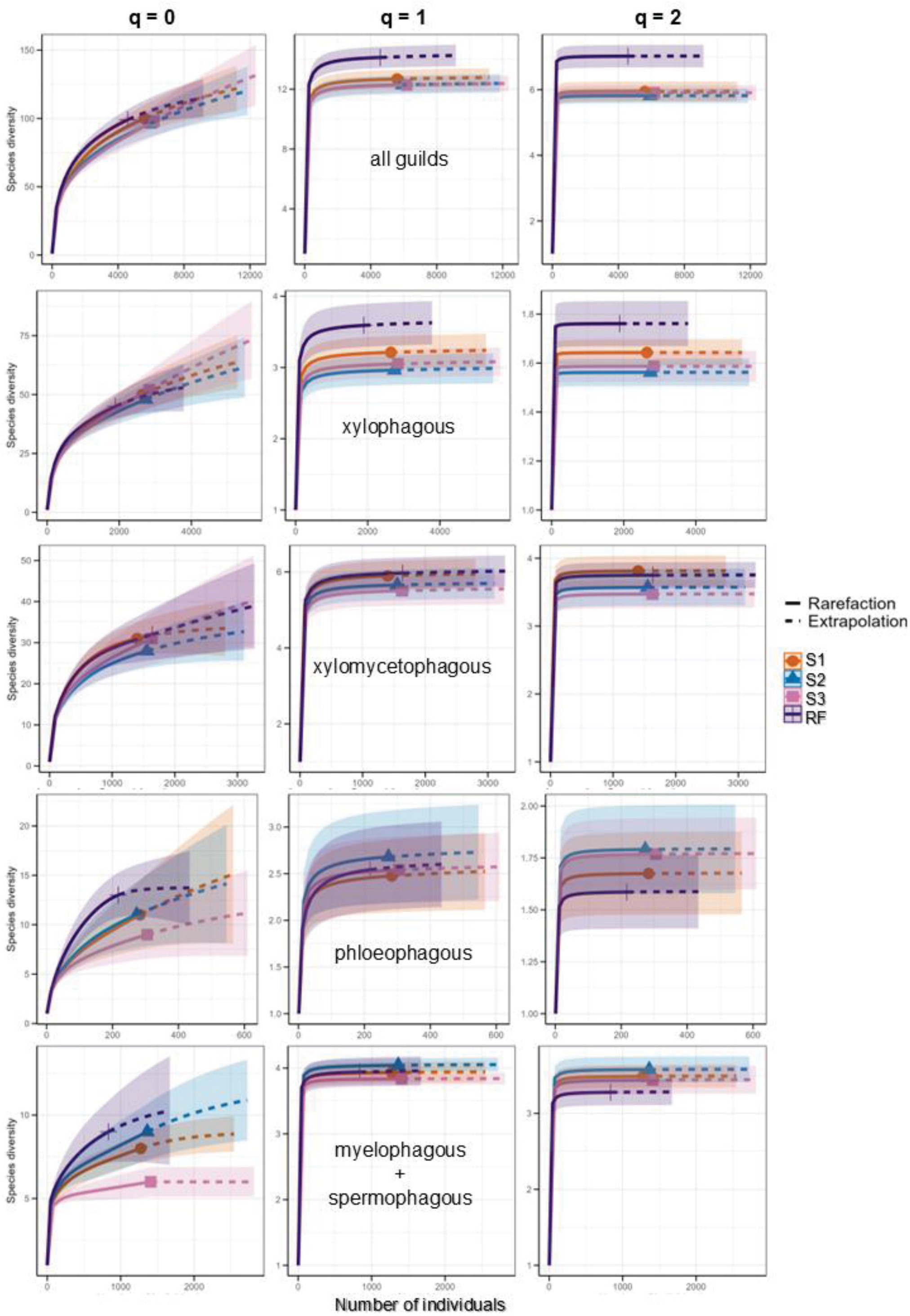

Figure 7. Rarefaction and extrapolation curves with Hill numbers of order q = 0 (species richness), q = 1 (exponential of Shannon entropy), and q = 2 (inverse of Simpson diversity) for woodboring beetles guilds trapped with ethanol-baited FITs in *Khaya grandifoliola* stands planted in November of 2013 (S1), 2014 (S2), and 2015 (S3), and riparian forest fragment (RF), Capinópolis, Minas Gerais, Brazil, from August 2021 to March 2024. Solid and dashed lines depict the rarefaction and extrapolated number of individuals, respectively. Shaded areas indicate the 95% confidence interval. Non-overlapping confidence intervals indicate differences between stands.

3.7 PcoA Bray-Curtis and Jaccard: comparison *Khaya* stands *vs.* riparian forest fragment

The PCoA analysis based on Bray-Curtis distance showed a clear separation between RF and all the African mahogany stands when all guilds combined and the myelophagous/spermophagous guild were considered. For all the remainder of the guilds, there was an overlap among sites, so the separation among the areas was not clear. When Jaccard's PcoA index was considered, there were no clear separations among sites. An exception was observed for the combined myelophagous/spermophagous guild, with potentially distinct communities in S1 and RF, and the complete absence of species from this guild in S3 (Figure 8).

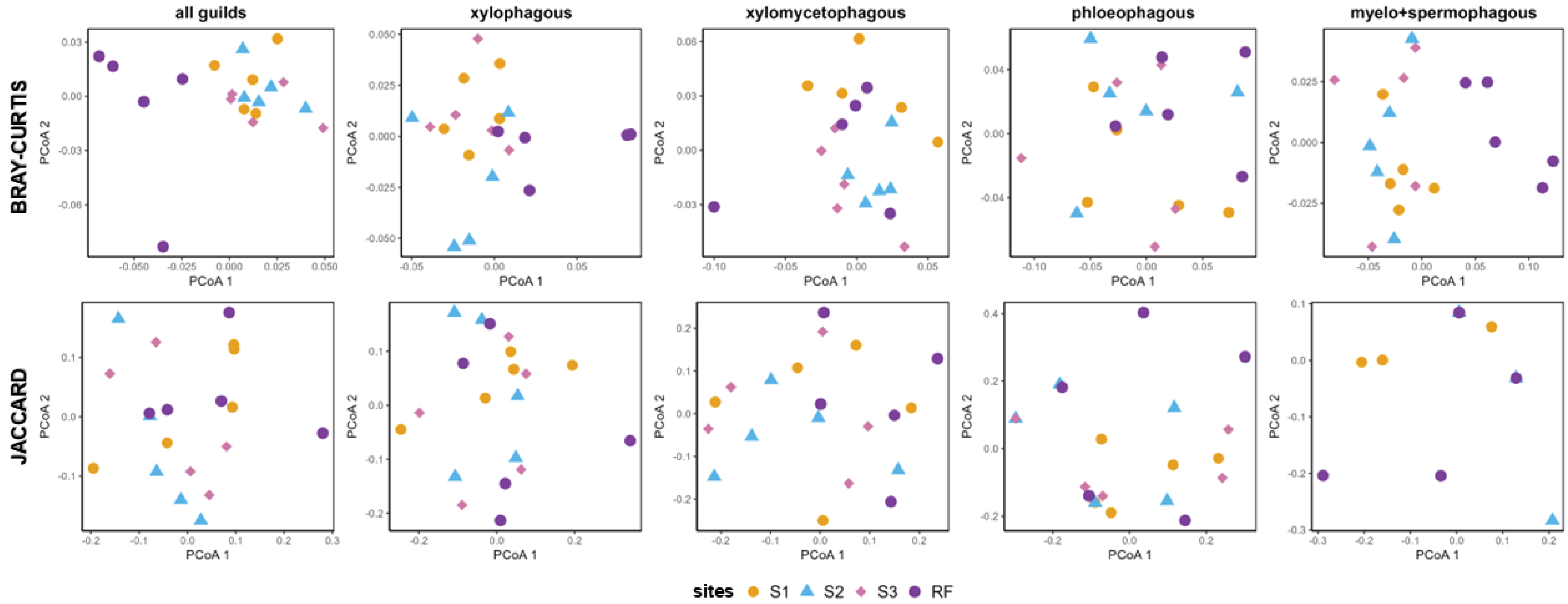

Figure 8. Principal coordinate analysis (PCoA) plot with Bray-Curtis and Jaccard for all woodboring guilds, xylophagous, xylomycetophagous, phloeophagous, and combined myelophagous and spermophagous trapped with ethanol-baited FITs in *Khaya grandifoliola* stands planted in November of 2013 (S1), 2014 (S2), and 2015 (S3), and riparian forest fragment (RF), Capinópolis, Minas Gerais, Brazil, from April 2017 to March 2024.

4 DISCUSSION

4.1 Woodboring beetle communities in African mahogany stands

In this study, we recorded a high number of Cerambycidade and Scolytinae species in African mahogany stands, including the detection of an exotic species, *Euwallacea fornicatus* (Schedl) (Curculionidae: Scolytinae) (Covre et al. 2024), which has been reported as an invasive ambrosia beetle in several parts of the world (Smith et al., 2019). The detection of this species highlights the importance of continuous monitoring and early detection programs in forest plantations, especially in non-native systems like African mahogany in Brazil (Covre et al. 2024). Such efforts are essential to prevent the establishment and spread of exotic pests that can pose serious threats to forest health and productivity.

This number of species is considered high when compared to other studies conducted in both planted and native tropical forests in Brazil, which often report lower species numbers, possibly because our sampling period was longer than in most previous studies (e. g. Flechtmann et al. 2001; Leonel 2019; Martins e Silva et al. 2021). Moreover, the presence of a diverse woodboring beetle community, including multiple families and ecological guilds, highlights the ecological complexity of African mahogany plantations and their surrounding landscapes, reinforcing the importance of long-term monitoring to understand beetle diversity patterns and their potential impacts on forest health.

Our findings are consistent with previous studies from Brazil, which have reported a diversity of woodboring beetle species associated with African mahogany (*Khaya* spp.). According to chapter 1, the most frequently reported species belong to Scolytinae, Bostrichidae, Platypodinae and Cerambycidae respectively, representing several ecological guilds, including xylomycetophagous, xylophagous, phloeophagous, myelophagous, and spermophagous groups. Moreover, these species have been found attacking different plant parts, such as trunks, branches, stems, seedlings, and even petioles, reflecting the broad range of niches exploited by woodboring beetles in African mahogany systems.

The beetle community was classified into five feeding guilds as myelophagous, phloeophagous, spermophagous, xylomycetophagous and xylophagous species. Among these, the xylophagous and xylomycetophagous guilds were dominant, followed closely by the phloeophagous guild, with the myelophagous and spermophagous species present in smaller proportions (Figure 3). Both xylophagous and xylomycetophagous species rely on wood as their feeding and breeding substrate (Haack & Slansky 1987). However, they differ in their nutritional strategies: xylophagous species feed directly on wood tissue, whereas xylomycetophagous species cultivate symbiotic fungi within the wood, which serve as their main food source (Haack & Slansky 1987). These two guilds are typically polyphagous, exploiting a broad range of host plants and food resources (Raffa et al. 2015; Zhao et al. 2021).

In contrast, the phloeophagous, myelophagous, and spermophagous guilds occurred in lower proportions. These guilds generally consist of oligophagous or even monophagous specie with narrower and more specialized food niches (Atkinson & Equihua-Martinez 1986; Flechtmann et al. 1995). Phloeophagous insects feed specifically on the phloem of particular host trees, resulting in high specialization and limited food availability (Raffa et al. 2015). Notably, in our study, nearly half of the phloeophagous guild was composed of *Hypothenemus* species, which accounted for over 99% of all trapped specimens (Supplementary Table S2 and S3). Unlike 'true' phloeophagous species, *Hypothenemus* beetles are highly polyphagous (Wood 2007; Marchioro et al. 2023), displaying a feeding breadth comparable to that of the xylophagous and xylomycetophagous guilds. Myelophagous species specialize on medullary (pith) tissues within the wood (Raffa et al. 2015; Zhao et al. 2021), while spermophagous insects rely on seeds - an ephemeral and seasonally variable resource – highlighting their restricted and specialized dietary niche (Wood 1982).

Forest environments typically offer a greater abundance and continuous supply of woody resources, which favors the dominance of guilds dependent on wood for feeding and breeding – namely the xylomycetophagous, xylophagous and the *Hypothenemus*-dominated phloeophagous guilds. The African mahogany stands studied here have a sparse understory, lacking suitable plant hosts for the development of myelophagous and spermophagous species. Additionally, 'true' phloeophagous species (excluding *Hypothenemus*) are not known to feed or breed on live African mahogany trees and were never observed attacking these trees in our stands. This explains their lower relative abundance compared to the *Hypothenemus* group.

Considering this, it is likely that the spermophagous, myelophagous and 'true' phloeophagous, spermophagous, and myelophagous beetles recorded in the traps were not strongly associated with the African mahogany stands themselves but were merely transient visitors dispersing from surrounding native vegetation, a riparian forest fragment (RF), without establishing populations within the African mahogany stands.

4.2 Indicator species

As expected, most species selected as site indicators were typically polyphagous, belonging to either the xylophagous, xylomycetophagous, or the *Hypothenemus*-dominated phloeophagous guilds (Table 1; Supplementary table S1 and S2). Each site clearly harbors distinct beetle communities, as evidenced by the selection of different beetle groups within each stand. In the African mahogany plantations, the stands vary in age, with S1 being the oldest, S2 of intermediate age, and S3 the youngest. This age gradient is reflected in the number of selected species, which decreases as the stands get older—meaning the youngest stand (S3) had the highest number of selected species, followed by the intermediate stand (S2), and then the oldest stand (S1). This pattern likely reflects the intensity of forestry operations, which decreased from the youngest to the oldest stand (Supplementary Table S4). Consequently, the availability of slash - resulting from pruning and thinning - may have influenced species selection by providing breeding material. Additionally, the proximity of S3 to the riparian forest fragment (RF) likely allows for migrating species from native vegetation to contribute to the beetle assemblages, making the higher number of indicator species in S3 a combination of these factors.Interestingly, *E. parallelus* was selected as an indicator species in stands S2 and S3, where forestry activities were most intensive (Table 1; Supplementary Table S4). This aligns with previous findings that link this species' occurrence to pruning (Covre et al. 2018) and thinning (Cristovam et al. 2018) activities, supporting the idea that forestry operations may shape beetle assemblages. Additionally, a few myelophagous species (*C. heveae* and *C. seriatus*) were found in S3, the stand nearest to RF, a riparian forest fragment (Figure 1). These species may have been captured during their dispersal flights from the native vegetation, as suggested earlier.

There was considerable species overlap among stands, especially between S2 and S3 (Table 1), further emphasizing the combined role of slash availability and habitat connectivity among sites due to their close proximity, in selecting characteristic beetle species at these sites. Regarding the RF, its greater environmental heterogeneity and structural complexity contrast with the African mahogany monocultures. Here, resources and ecological niches are more evenly distributed, likely reducing dominance by any particular beetle group and resulting in the scarcity of strong indicator species (Ramey & Richardson 2017; Popescu et al. 2021). Rather than indicating ecological uniformity, this paucity of indicator species in RF probably reflects a well-balanced system where multiple species coexist without significant dominance.

Under these conditions, it is unsurprising that only one indicator species, *Amphicranus* sp. 02, was identified in RF (Table 1). All *Amphicranus* species are considered rare (Wood 2007), which supports the notion that naturally rare organisms are more sensitive to environmental changes and tend to be confined to habitats that preserve their optimal conditions (Ramey & Richardson 2017). Although RF is just a forest fragment, it likely serves as a refuge for *Amphicranus* sp. 02, underscoring its ecological importance as a key habitat for disturbance-sensitive and substrate-specialist species.

4.3 Woodboring guilds diversity yearly in *Khaya* stands and riparian forest

The analysis of trophic guilds over time and at all sites revealed distinct ecological dynamics that reflect species interactions and changing environmental conditions (Figure 4).

A temporal pattern was observed in the xylophagous guild in all African mahogany stands, characterized by an increase in species richness and the Shannon and inverse Simpson diversity indices from year 1 (Y1) to year 3 (Y3), followed by a decline in year 4 (Y4). Subsequently, species richness and the diversity indices steadily rose until year 6 (Y6) before decline again (Figure 4). This consistent pattern among stands suggests climatic factors as the primary drivers of the observed variation. Indeed, in Y4, there was a significant decrease in rainfall coupled with an increase in temperature relative to previous years. Rainfall and temperature levels returned to values comparable to Y1-Y3 in year 5 (Y5), and Y6 experienced a substantial increase in rainfall while temperatures remained similar to those in Y1-Y3.

In contrast, year 7 (Y7) saw another drop in rainfall to levels akin to Y4, accompanied by temperatures exceedingly even those recorded in Y4 (Supplementary Table S5).

Xylophagous beetles exhibit a strong seasonal flight behavior influenced by climate (Sittichaya et al. 2013; Keszthelyi et al. 2017; Oliveira et al. 2021). The results presented here corroborate this seasonality, showing that their activity related to host selection and dispersal is largely influenced by climatic variables (Sittichaya et al. 2013; Dang et al. 2021). Our findings suggest that a combination of below-average rainfall and simultaneously elevated temperatures suppresses flight activity, whereas above-average rainfall and moderately lower temperatures stimulate it.

Richness and diversity indices of xylophagous beetles did not differ significantly among stands (Figure 4), indicating similar availability of food resources are similar in all stands. This aligns with the phenology of *K. grandifoliola*, whose natural self-pruning desiccates and sheds lower branches (Opuni-Frimpong et al. 2008), thereby ensuring a stable resource supply for these beetles.

The xylomycetophagous guild showed a broadly similar temporal pattern in species richness in all African mahogany stands, with parallel rises and falls over the years (Figure 4). This indicates that landscape-scale factors, such as the availability of breeding substrate, microclimatic conditions, and seasonal periods when many individuals disperse simultaneously, were influencing the number of species present, affecting all plantation stands in a comparable manner. In contrast, the diversity indices that incorporate evenness (Shannon and inverse Simpson) revealed more site-specific trends.

In S1, Shannon and inverse Simpson diversity remained relatively stable over the monitoring period (Figure 4), indicating not only steady species richness but balanced relative abundances (Supplementary Table S2). This stability may reflect consistent resource availability and microhabitat conditions in this stand.

By contrast, S2 and S3 displayed pronounced diversity peaks in Y2, followed by gradual declines until around Y5, after which diversity stabilized at levels similar to S1 (Figure 4). The initial peak could result from temporary species influxes triggered by pruning activities (Supplementary Table S4), favorable climatic conditions (Supplementary Table S5) or other disturbances increasing resource heterogeneity and reducing dominance by a few species (Supplementary Table S2 and S3). The subsequent decline suggests increasing dominance by competitive or disturbance-tolerant species reduced evenness despite relatively stable species (Supplementary Table S3).

By Y5 and beyond, diversity indices converged in all stands (Figure 4) likely reflecting plantations reaching comparable structural stages, breeding substrate levels, canopy cover, and microclimatic stability, resulting in equilibrium community compositions.

The phloeophagous assemblage was overwhelmingly dominated by the highly polyphagous *Hypothenemus* species (> 99% of trappings; Supplementary Table S2 and S3), which exploit a wide variety of woody substrates and are not limited to fresh phloem (Wood 2007; Marchioro et al. 2023). Ecologically, these species likely behave more like xylophagous beetles, readily utilizing dry woody material (Fisher 1950; Roberts 1967; Sittichaya et al. 2013). The Shannon diversity index increased from Y1 to Y4 and then stabilized, with inverse Simpson values showing a similar trend (Figure 4). This pattern suggests that the increasing diversity was due to a more balanced species abundance distribution rather than rare species alone (Supplementary Table S2 and S3), mirroring trends in the xylophagous guild as woody substrates accumulated and diversified with stand age. Differences among stands after Y4 were small, consistent with converging resource availability and habitat conditions.

For the myelophagous and *Hypothenemus*-dominated phloeophagous guilds, the diversity indices showed little variation among the African mahogany stands and over time (Figure 4). This likely reflects their status as transient visitors that are not strongly associated with this monoculture environment, as previously discussed.

In the riparian forest fragment, the diversity indices for ‘all guilds’ remained overall relatively stable throughout the study, with minor year-to-year fluctuations (Figure 4). This stability probably reflects the structural complexity and floristic heterogeneity of the native vegetation, which supports a well-established, balanced beetles communities. Interestingly, diversity patterns in African mahogany stands for most guilds gradually converged toward those observed in the riparian forest from Y5 to Y7 (Figure 4). This suggests that, after several years of growth, the plantations achieved a level of habitat complexity and resource availability comparable to the native forest fragment, at least from the perspective of the beetle guilds examined.

However, not all guilds in the riparian forest fragment followed the same trajectory. Both xylophagous and *Hypothenemus*-dominated phloeophagous guild showed declines in richness and diversity over time (Figure 4), likely reflecting natural deadwood fluctuations. Episodic events like storms, branch falls, and tree mortality can create sudden increases in colonization opportunities followed by leaner resource periods, leading to declines in specialist populations. Although *Hypothenemus are* polyphagous (Wood 2007), their reliance on dry woody substrates makes them vulnerable to such resource variability. In contrast, xylomycetophagous diversity increased from Y5 to Y7 (Figure 4), possibly benefiting from storm-driven increases in breeding material such as broken branches and trees.

The myelophagous and spermophagous guilds consistently displayed low and minimally variable diversity in both riparian forest fragment and African mahogany sites, with minimal temporal variation (Figure 4). These patterns suggest that these guilds consist mainly of transient individuals dispersing from surrounding vegetation rather than sustaining local populations within the plantation stands This pattern indicates less dependence on local resources and greater influence from dispersal and seasonal dynamics in their source habitats.

4.4 Diversity of woodboring guilds in *Khaya* stands

After seven years, the three adjacent African mahogany stands converged in species richness, with overlapping values among S1, S2, and S3 (Figure 5). This convergence is ecologically plausible given sufficient colonization and turnover time in adjacent, structurally similar stands lacking woody understory.

However, evenness patterns revealed differences. Although richness converged, species abundance distributions varied. S3 exhibited the highest evenness for ‘all guilds’ combined, indicating no single species was disproportionately dominant. S3’s proximity to the native forest fragment likely contributed to this pattern by facilitating steady influxes of visitor species from the adjacent native vegetation, combined with no single colonist finding uniquely favorable transient conditions, results in balanced abundances between residents and newcomers. Thus, S3 functions as an immediate edge habitat filtering species composition.

For xylophagous beetles, we expected there would be no differences in diversity among stands, because all have experienced comparable availability of deadwood resources, both in slash left from management and in self-pruning branches. However, it was lowest in S3. One plausible explanation is that substrate quality, not just quantity, differed. S2's slash may have been in less favorable microclimatic conditions (greater sun exposure, lower humidity, faster desiccation), making it less suitable for sustained development. Alternatively, colonization pressure may have differed: S1 and S3 may have received more immigrants from nearby source habitats (S3 from the forest fragment; S1 from the black pepper and/or orchard areas) (Figure 1), whereas S2's more "central" location limited immigrant inflow. Timing of fresh slash input relative to beetle dispersal periods may also affect colonization success.

The xylomycetophagous group had its lowest diversity in S1 (Figure 5), reflecting dominance by one or two ambrosia beetle species (Supplementary Table S2 and S3) that reduced evenness despite the presence of other taxa. By contrast, *Hypothenemus*-dominated phloeophagous beetles reached their highest diversity in S1 (Figure 5), suggesting wood resources there supported a more balanced community, even though this guild, like the xylophagous, breeds in dead wood. The myelophagous + spermophagous guild showed lowest diversity in S1 for both indices (Figure 5), consistent with its greater distance from native vegetation, limiting colonization by edge- or forest-associated specialists. S3, contiguous with the native riparian vegetation, recorded highest overall diversity and evenness, reflecting richer species pools more balanced abundances.

Among the African mahogany stands, inverse Simpson further highlighted guild- and site-specific responses. In all guilds combined, S3 showed highest values, reflecting communities with no overwhelming dominant species, consistent with influence from the adjacent native vegetation (Figure 5). This result aligns with S3's immediate proximity to native riparian vegetation, which likely serves as a continuous source of colonists and promotes a more balanced distribution of abundances.

The xylomycetophagous guild, by contrast, displayed its lowest inverse Simpson value in S1 (Figure 5). This outcome reflects the disproportionate numerical weight of a few species (Supplementary Table S2), which sharply reduced evenness despite the presence of other taxa. In S3, the same guild benefitted from a broader and more evenly distributed species set, again likely influenced by adjacency to native habitats. *Hypothenemus*-dominated phloeophagous beetles exhibited the opposite trend, with their highest inverse Simpson diversity in S1 (Figure 5), possibly due to microhabitat or woody substrate condition differences favoring diverse feeders

The myelophagous + spermophagous guild consistently recorded its lowest values in S1, echoing the Shannon index results (Figure 5) and reinforcing the idea that greater distance from native vegetation limits the arrival and persistence of species specialized on seeds, twigs, or pith. In S3, these guilds were comparatively more diverse and balanced (Supplementary Table S2 and S3), again pointing to the role of landscape context in shaping community structure.

Together, these patterns suggest that while woody substrate quantity was broadly similar among stands, proximity to native riparian vegetation and microhabitat heterogeneity strongly influenced the evenness component of diversity, with different guilds responding in contrasting ways to the same environmental gradients.

The similarity among insect communities in the three African mahogany stands varied depending on the guild and the way similarity was measured, either by species presence/absence (Jaccard index) or by species abundance (Bray–Curtis index). Overall, Bray–Curtis values tended to be higher than Jaccard values for the same guild and stand pair. This suggests that even when stands differed in which species were present, the dominant species usually had similar relative abundances. In contrast, lower Bray–Curtis values indicated changes not only in species identity but also in how abundances were distributed (Figure 6).

Some guilds displayed clear, consistent patterns of similarity or difference among all stands. The xylophagous guild exhibited uniformly high Jaccard and Bray-Curtis values in all stand pairs. The *Hypothenemus*-dominated phloeophagous guild showed similarly high, though slightly more variable values; this indicates that the same core species were present everywhere and in roughly similar abundances. In contrast, the xylomycetophagous guild showed uniformly low similarities in both indices for every stand pair (Figure 6). This indicates that each stand had a unique set of species with different dominance patterns, likely due to microhabitat differences influencing where these species occur.

The myelophagous + spermophagous guild showed a somewhat mixed pattern, where S1-S3 contrasts were pronounced in both indices, while S1-S2 and S2-S3 showed only moderate dissimilarity (Figure 6). This means it would not fully correspond to the results to say that all stands were strongly different for this guild; instead, differences were largest where the distance from native vegetation was greatest (S1 vs. S3) (Figure 6).

Overall, it is reasonable to state that generalists with uniform resource availability tend to maintain similar communities among sites, whereas guilds associated with more specialized or variable microhabitats often form distinct assemblages. An intermediate case, such as the myelophagous + spermophagous guild, suggests that dispersal potential, proximity to the native riparian vegetation, and temporal resource dynamics interact to produce uneven similarity patterns.

4.5 Diversity of woodboring guilds in *Khaya* stands compared to riparian forest

When considering species richness, patterns were remarkably consistent for most guilds among the African mahogany stands and the riparian forest fragment. The overlapping confidence intervals indicate no significant differences among sites, with one notable exception: the combined myelophagous + spermophagous guild. Here, richness was lower in S3 than in the other stands and the riparian forest fragment (Figure 7). This suggests that these guilds, likely composed of transient visitors from the adjacent native forest, are less able to establish in the youngest stand, perhaps due to reduced resource diversity or microhabitat availability, as discussed before. For the other guilds, the lack of differences in species richness (Figure 7) suggests that suitable habitats or resources are widely available both in the planted stands and in the nearby forest fragment. This means that the overlap in species observed earlier among the African mahogany stands is extensive enough that their communities resemble those found in the native vegetation.

Shannon diversity mostly followed the same trends as richness, but showed some interesting small differences. In most cases, the overlap among Shannon values indicates that the sites were similar to one another. However, for both the ‘all guilds’ category and the xylophagous guild, Shannon values were higher in the riparian forest, reflecting a more even species distribution. For instance, in RF’s xylophagous guild, the dominance of *X. picea* was lower (~75% of individuals) compared to the stands (often >80–85%), with several less common species contributing more evenly to the community (Supplementary Table S1 and S3). The higher Shannon diversity for xylophagous beetles in RF is interesting, given that all stands provide abundant dry wood from self-pruning. This could mean that while resource quantity is similar, the native forest offers a wider variety of microhabitats or host plant species, fostering greater evenness. Conversely, the phloeophagous guild, dominated almost entirely by *Hypothenemus* species, did not mirror the xylophagous pattern, despite both relying on dead woody material (Figure 7). This divergence can be attributed to the overwhelming dominance of a single species, *Hypothenemus eruditus* Westwood, which comprised over 70-80% of the specimens at most sites (Supplementary Table S2 and S3). Such dominance indicates that evenness in *Hypothenemus*-dominated communities is inherently low and remains largely consistent regardless of stand type.

Simpson diversity reflected these patterns. For most guilds, there were no significant differences among sites, primarily due to the strong dominance of one or a few species, such as *X. picea* in the xylophagous guild (>80% in most stands), *H. eruditus* in the phloeophagous guild (70–90% in stands and RF), and *Hypothenemus obscurus* (Fabricius) in the spermophagous guild (>98% among all sites) (Supplementary Table S3), kept diversity values relatively low and made differences between sites hard to detect. The xylophagous and ‘all guilds' categories once again exhibited higher values in RF, reflecting the pattern seen in Shannon diversity and suggesting a slightly lower dominance in that environment. For example, in the xylophagous guild of RF, *X. picea* accounted for ca. 75% of individuals, compared to 80-85% in the stands (Supplementary Table S3). For myelophagous + spermophagous beetles, lower Simpson values in RF (Figure 7) reflected not only the reduced richness already noted but also the overwhelming dominance of *H. obscurus*, which alone made up roughly 90% of spermophagous individuals and was similarly dominant among myelophagous species, strongly skewing evenness despite the presence of other taxa (Supplementary Table S3).

Taken together, these results suggest that the African mahogany stands, at their current ages when these comparisons were made, provide broadly similar conditions for most beetle guilds. Resource type and availability, especially dead wood from self-pruning and slash derived from forestry operations, appear sufficient to support comparable levels of richness and diversity to those found in the native riparian forest fragment. The only consistent departure from this pattern concerns the myelophagous + spermophagous guild (Figure 7), whose members seem more tightly linked to resources in the native forest and less able to exploit the plantation stands, likely due to the scarcity of suitable host plants in the understory there, as previously discussed. Overall, the community structure appears to be shaped less by stand age (at these present stages) and more by the interplay between resource specialization, species dominance, and the availability of microhabitats among both planted and native environments.

When we analyzed the similarity among insect communities in the three African mahogany stands and the adjacent riparian forest, the combined analysis of “all guilds” showed considerable overlap among sites in both Bray-Curtis and Jaccard analyses, although in Bray-Curtis the riparian forest tended to stand slightly apart (Figure 8), likely reflecting its higher abundances of forest-associated species (about 10–15% more individuals than the stands over years 5–7; Supplementary Table S3).

Focusing on individual guilds revealed subtler trends. Xylophagous assemblages tended to separate the oldest stand (S1) and RF from younger stands, likely due to S1’s long-term buildup of seasoned wood and the forest’s greater botanical diversity. Within this group, S1 captured about 40% more individuals than S2 and S3, while RF numbers were intermediate. Xylomycetophagous beetles showed a similar pattern, with Bray-Curtis analysis separating S1 from other sites. This separation was likely driven by greater availability of breeding material, resulting from more intensive forestry operations, especially thinning, which provide additional breeding material, and possibly some influx from the nearby orchard and black pepper plantation (Figure 1). For this guild, S1 totals were about 50% higher than RF and about one-third higher than S2 and S3 (Supplementary Table S3). The *Hypothenemus*-dominated phloeophagous beetles closely followed the xylophagous pattern, consistent with their reliance on dry woody substrates, as discussed before (Figure 8).

The myelophagous + spermophagous beetles showed the clearest distinction: the riparian forest stood apart in Bray-Curtis analysis, reflecting the abundance of breeding material, largely absent from the plantations. The weaker separation observed in the Jaccard analysis (Figure 8) suggests occasional dispersal into the stands without successful establishment.

Overall, these assemblages were shaped by a combination of resource continuity (stand age, self-pruning, forest proximity), resource pulses (management activities), and resource diversity (native forest richness). This combination blurred site boundaries for generalist guilds but produced more distinct separations among those with specialized ecological requirements.

5 CONCLUSIONS

Our study provides a detailed assessment of woodboring beetle communities among African mahogany plantations of varying ages and an adjacent riparian forest fragment. The remarkably high species richness recorded, including the presence of the invasive ambrosia beetle *E. fornicatus*, underscores the ecological complexity and dynamic nature of these environments. Importantly, the plantations support diverse assemblages spanning multiple guilds, suggesting that even non-native monocultures can sustain substantial insect biodiversity when resources and structural elements are sufficiently available.

The dominance of polyphagous guilds such as xylophagous and xylomycetophagous beetles among sites emphasizes their adaptability and resource flexibility, while the more specialized myelophagous, spermophagous, and ‘true’ phloeophagous guilds display tighter associations with native forest habitats. This differential association highlights the crucial role of landscape context and resource diversity in shaping community composition.

Temporal patterns in species richness and diversity further reveal the profound influence of climatic variability and forestry management practices on beetle communities. Occasional increases in available resources created by thinning and pruning contribute to transient increases in diversity, especially in younger stands, while longer-term successional processes drive convergence of community structure toward that seen in native riparian forest fragments.

Spatially, proximity to native forest emerges as a key driver of diversity patterns and community evenness, particularly evident in the youngest plantation stand closest to the riparian fragment. This connectivity facilitates species immigration and promotes more balanced species abundances, underscoring the importance of preserving native habitat patches adjacent to plantations for maintaining ecological functions and biodiversity.

From a management perspective, our findings suggest that sustainable forestry operations that maintain or mimic natural resource heterogeneity, such as retaining dead wood and managing stand structure, can support diverse assemblages of ecologically valuable woodboring beetles. Additionally, ongoing monitoring is essential to detect and mitigate potential invasive species incursions and to better understand the long-term ecological trajectories of plantation ecosystems.

In conclusion, African mahogany plantations, when embedded within heterogeneous landscapes that include native forest fragments, can harbor complex and dynamic woodboring beetle communities comparable in richness to natural forests. Balancing plantation productivity with biodiversity conservation requires integrated approaches that recognize the interplay between stand age, resource availability, habitat connectivity, and climatic factors shaping insect assemblages.

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SUPPLEMENTARY MATERIAL

Supplementary Table S1. List of guild (xylop: xylophagous), species and total specimens of Bostrichidae and Cerambycidae trapped in ethanol-baited flight-intercept traps in African mahogany (*Khaya grandifoliola*) stands planted in November of 2013 (S1), 2014 (S2), and 2015 (S3), and in adjacent riparian forest fragment (RF). Capinópolis, state of Minas Gerais, Brazil. Collections in the plantation stands were conducted from April 2017 to March 2024, and in the riparian forest from August 2021 to March 2024

Guild	**Family/Species**	**Study areas**				
		S1	**S2**	**S3**	**RF**	**Total**
	Bostrichidae					
xylop	*Bostrychopsis laminifer* (Lesne, 1895)	1	0	2	0	3
xylop	*Bostrychopsis uncinata* (Germar,1824)	64	52	60	23	199
xylop	*Dinoderus minutus* (Fabricius, 1775)	93	97	159	13	362
xylop	*Lichenophanes plicatus* (Guérin-Méneville, 1844)	0	0	2	0	2
xylop	*Melalgus parvidens* (Lesne, 1895)	1	0	1	0	2
xylop	*Melalgus* sp. 01	0	0	3	0	3
xylop	*Melalgus* sp. 02	2	0	0	0	2
xylop	*Micrapate atra* (Lesne, 1899)	4	11	6	2	23
xylop	*Micrapate brunnipes* (Fabricius, 1801)	0	1	1	0	2
xylop	*Micrapate cribripennis* (Lesne, 1899)	208	194	168	89	659
xylop	*Micrapate obesa* (Lesne, 1899)	0	1	0	0	1
xylop	*Micrapate spinula* Liu, 2024	0	0	1	0	0
xylop	*Xyloperthela picea* (Olivier, 1790)	3817	4391	3933	1371	13512
	Σ Bostrichidae specimens	4190	4747	4335	1498	14770
	Σ Bostrichidae species	**8**	**7**	**11**	**5**	**13**
	Cerambycidae					
xylop	*Achryson surinamum* (Linnaeus, 1767)	4	4	7	3	18
xylop	*Aegomorphus (Psapharochrus) jaspideus* (Germar, 1824)	20	17	15	14	66
xylop	*Aerenea brunnea* Thomson, 1868	9	9	11	8	37
xylop	*Aerenicopsis* sp.	0	1	1	0	2
xylop	*Aglaoschema concolor* (Gounelle, 1911)	26	14	28	17	85
xylop	*Ambonus distinctus* (Newman, 1840)	1	1	5	0	7
xylop	*Ambonus electus* (Gahan, 1903)	1	1	0	0	2
xylop	*Ambonus interrogationes* (Blanchard, 1847)	12	13	12	6	43
xylop	*Andraegoidus fabricii* (Dupont, 1838)	1	1	1	1	4
xylop	*Ancylocera cardinalis* (Dalman, 1823)	3	3	3	1	10
xylop	*Argyrodines aurivillii* (Gounelle, 1905)	0	1	0	0	1
xylop	*Ataxia operaria* (Erichson, 1849)	20	28	14	13	75
xylop	*Beraba decora* (Zajciw, 1961)	0	0	2	1	3
xylop	*Callia fulvocincta* Bates, 1866	1	0	0	0	1

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Xylop	*Callisema rufipes* Martins & Galileo, 1990	1	1	0	0	2
Xylop	*Cacostola zanoa* Dillon & Dillon, 1946	4	0	0	0	4
Xylop	*Chevrolatella tripunctata* (Chevrolat, 1862)	2	1	2	1	6
Xylop	*Chlorida festiva* (Linnaeus, 1758)	25	20	32	11	88
Xylop	*Chrysoprasis chalybea* Redtenbacher, 1868	0	0	0	1	1
Xylop	*Chydarteres dimidiatus dimidiatus* (Fabricius, 1787)	11	12	2	2	27
Xylop	*Colobothea poecila* (Germar, 1824)	0	0	1	0	1
Xylop	*Colobothea rubroornata* Zajciw, 1962	3	2	2	1	8
Xylop	*Compsa quadriguttata* (White, 1855)	25	16	15	11	67
Xylop	*Compsibidion faimarei* (Thomson, 1865)	3	7	0	6	16
Xylop	*Compsibidion truncatum* (Thomson, 1865)	0	1	0	0	1
Xylop	*Coremia plumipes* (Pallas, 1772)	0	1	0	0	1
Xylop	*Cosmoplatidius lycoides* (Guérin-Méneville, 1844)	1	0	0	0	1
Xylop	*Cupanoscelis heteroclita* Gounelle, 1909	0	1	0	1	2
Xylop	*Deltosoma lacordairei* Thomson, 1864	0	0	1	0	1
Xylop	*Distenia* (*Distenia*) *columbina* Audinet-Serville, 1828	0	1	0	0	1
Xylop	*Dorcacerus barbatus* (Olivier, 1790)	0	1	3	0	4
Xylop	*Drycothaea anteochracea* (Breuning, 1974)	1	0	0	0	1
Xylop	*Eburodacrys assimilis* Gounelle, 1909	7	14	10	5	36
Xylop	*Eburodacrys crassimana* Gounelle, 1909	0	0	1	0	1
Xylop	*Eburodacrys cunusaia* Martins, 1997	0	2	1	0	3
Xylop	*Eburodacrys punctipennis* White, 1853	1	0	1	2	4
Xylop	*Eburodacrys vittata* (Blanchard, 1847)	0	0	0	1	1
Xylop	*Epectasis juncea* (Newman, 1840)	49	31	32	19	131
Xylop	*Estola densepunctata* Breuning, 1940	0	1	0	0	1
Xylop	*Estola flavescens* Breuning, 1940	3	3	0	0	6
Xylop	*Estola* sp.	0	0	1	0	1
Xylop	*Eutrypanus dorsalis* (Germar, 1824)	1	3	1	1	6
Xylop	*Gorybia veneficella* Martins, 1976	1	1	0	0	2
Xylop	*Hamaederus glaberrimus* (Martins, 1979)	1	1	0	2	4
Xylop	*Hesychotypa subfasciata* Dillon & Dillon, 1945	2	2	0	0	4
Xylop	*Hylettus seniculus* (Germar, 1824)	5	13	8	6	32
Xylop	*Hyperplatys cana* (Bates, 1863)	1	0	0	0	1
Xylop	*Hyperplatys melzeri* (Gilmor, 1965)	39	29	33	11	112
Xylop	*Hypsioma chapadensis* Dillon & Dillon, 1945	1	0	0	0	1
Xylop	*Hypsioma fasciata* (Thomson, 1860)	0	0	1	0	1
Xylop	*Jupoata rufipennis* (Gory, 1831)	1	0	1	1	3
Xylop	*Leptostylus perniciosus* Monné & Hoffmann, 1981	0	1	0	0	1

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Xylop	*Lepturges (Chaeturges) inscriptus* Bates, 1863	3	1	0	1	5
Xylop	*Lophopoeum carinatulum* Bates, 1863	1	3	3	6	13
Xylop	*Lypsimena fuscata* Haldeman, 1847	2	2	1	0	5
Xylop	*Megacyllene falsa* (Chevrolat, 1862)	14	17	18	9	58
Xylop	*Mionochroma electrinum* (Gounelle, 1911)	1	0	1	2	4
Xylop	*Neoclytus pusillus* Laporte & Gory, 1838	178	229	247	112	766
Xylop	*Nesozineus lineolatus* Galileo & Martins, 1996	0	2	2	0	4
Xylop	*Nyssodrysternum rubiginosum* Monné, 1975	0	0	2	0	2
Xylop	*Opsibidion albifasciatum* Giesbert, 1998	0	1	0	0	1
Xylop	*Opsibidion albinum* (Bates, 1870)	1	1	0	1	3
Xylop	*Oreodera aerumnosa* Erichson, 1847	7	2	8	4	21
Xylop	*Oreodera bituberculata* Bates, 1861	1	0	0	2	3
Xylop	*Orthostoma abdominale* (Gyllenhal, 1817)	0	0	1	0	1
Xylop	*Oxymerus aculeatus* Dupont, 1838	36	28	41	11	116
Xylop	*Oxymerus basalis* (Dalman, 1823)	4	8	17	2	31
Xylop	*Paromoeocerus barbicornis* (Fabricius, 1792)	32	35	31	20	118
Xylop	*Pentheochaetes turbida* Melzer, 1934	0	1	1	0	2
Xylop	*Peritrox nigromaculatus* Aurivillius, 1920	0	1	0	0	1
Xylop	*Polymitoleiopus nutrix* (Nascimento, Santos-Silva & Flechtmann, 2021)	3	2	0	0	5
Xylop	*Polymitoleiopus ovalis* (Bates, 1866)	0	0	1	0	1
Xylop	*Polymitoleiopus prolixus* (Melzer, 1931)	1	0	0	0	1
Xylop	*Psapharochrus brunnescens* (Zajciw, 1963)	0	1	2	0	3
Xylop	*Rhopalessa clavicornis* (Bates, 1873)	0	1	0	0	1
Xylop	*Rhopalophora collaris* (Germar, 1824)	0	0	1	0	1
Xylop	*Sphaerion inerme* White, 1853	0	0	1	0	1
Xylop	*Sphallotrichus sericeotomentosus* Fragoso, 1995	1	0	0	0	1
Xylop	*Stenoidion corallinum chapadence* (Gounelle, 1909)	2	1	1	0	4
Xylop	*Stizocera lissonota* (Bates, 1870)	0	0	1	0	1
Xylop	*Terpnissa litrospterina* Bates, 1867	0	0	0	1	1
Xylop	*Thoracibidion flavopictum* (Perty, 1832)	0	1	0	0	1
Xylop	*Trachelissa maculicollis* (Audinet-Serville, 1834)	16	13	15	10	54
Xylop	*Trachyderes succinctus succinctus* (Linnaeus, 1758)	18	30	22	9	79
Xylop	*Tropidion epaphum* (Berg, 1889)	1	0	0	0	1
Xylop	*Tropidion flechtmanni* Santos-Silva, Nascimento & Biffi, 2019	0	0	1	0	1
Xylop	*Tropidion personatum* (Gounelle, 1909)	0	1	0	0	1
	Σ Cerambycidae specimens	609	639	665	336	2248
	Σ Cerambycidae species	**53**	**58**	**52**	**40**	**87**

Supplementary Table S2. List of guilds (myelo: myelophagous, phloe: phloeophagous, sperm: spermophagous, xylom: xylomycetophagous and xylop: xylophagous), species and total specimens of Curculionidae (Scolytinae and Platypodinae) trapped in ethanol-baited flight-intercept traps in African mahogany (*Khaya grandifoliola*) stands planted in November of 2013 (S1), 2014 (S2), and 2015 (S3), and in adjacent riparian forest fragment (RF). Capinópolis, state of Minas Gerais, Brazil. Collections in the plantation stands were conducted from April 2017 to March 2024, and in the riparian forest from August 2021 to March 2024

Guild	Family/Species	Study areas				
		S1	S2	S3	RF	Total
	Scolytinae					
Xylom	*Ambrosiodmus hagedorni* (Iglesias, 1914)	22	16	16	4	58
Xylom	*Ambrosiodmus obliquus* (LeConte, 1878)	127	132	103	38	400
Xylom	*Amphicranus* sp. 01	0	0	1	0	1
Xylom	*Amphicranus* sp. 02	4	4	7	9	24
Phloe	*Araptus* sp. 01	0	1	3	2	6
Phloe	*Araptus* sp. 02	0	1	0	0	1
Phloe	*Araptus* sp. 03	0	0	1	0	1
Phloe	*Araptus* sp. 04	0	1	0	0	1
Phloe	*Araptus* sp. 05	0	0	1	1	2
Phloe	*Bothrosternus rudis* Wood, 2007	1	0	0	0	1
Phloe	*Chramesus cylindricus* Schedl, 1952	0	1	0	0	1
Phloe	*Cnemonyx brevisetosus*Schedl, 1939	0	0	1	0	1
Myelo	*Cnesinus advena* Schedl, 1973	2	0	0	0	2
Myelo	*Cnesinus dividuus* Schedl, 1938	48	40	46	12	146
Xylom	*Cnestus laticeps* (Wood, 1977)	24	35	31	25	115
Xylom	*Cnestus retusus* (Eichhoff, 1868)	11	23	25	11	70
Sperm	*Coccotrypes aciculatus* Schedl, 1952	0	0	0	1	1
Sperm	*Coccotrypes cyperi* (Beeson, 1929)	0	1	0	1	2
Sperm	*Coccotrypes distinctus* (Motschulsky, 1866)	5	0	0	3	8
Sperm	*Coccotrypes* sp. 01	0	1	1	0	2
Sperm	*Coccotrypes* sp. 02	0	1	0	0	1
Xylom	*Coptoborus ricini* (Eggers, 1932)	0	1	0	0	1
Xylom	*Coptoborus tolimanus* (Eggers, 1928)	0	1	1	0	2
Xylom	*Coptoborus vespatorius* (Schedl, 1931)	0	1	2	1	4
Xylom	*Coptoborus villosus* (Blandford, 1898)	1	0	0	0	1
Xylom	*Corthylocurus* sp.	0	0	0	1	1
Xylom	*Corthylus convexicauda* Eggers, 1931	1	0	0	0	1
Xylom	*Corthylus parvicirrus* Wood, 2007	5	2	8	5	20
Phloe	*Cryphalus mangiferae* Stebbing, 1914	1	0	3	2	6
Myelo	*Cryptocarenus brevicollis* Eggers, 1937	1	1	0	0	2
Myelo	*Cryptocarenus diadematus* Eggers, 1937	726	781	986	140	2633
Myelo	*Cryptocarenus heveae* (Hagedorn, 1912)	1043	1157	1607	140	3947

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Myelo	*Cryptocarenus seriatus* Eggers, 1933	385	447	657	142	1631
Xylom	*Dryocoetoides cristatus* (Fabricius, 1801)	7	3	18	6	34
Xylom	*Dryocoetoides flavus* (Fabricius, 1801)	0	1	1	1	3
Phloe	*Eidophelus jalappae* (Letzner, 1849)	2	0	0	0	2
Xylom	*Euwallacea fornicatus* (Eichhoff, 1868)	15	26	14	8	63
Xylom	*Euwallacea posticus* (Eichhoff, 1869)	0	1	0	1	2
Xylop	*Hylocurus plaumanni* Wood, 2007	1	2	0	0	3
Phloe	*Hypothenemus areccae* (Hornung, 1842)	198	183	185	6	572
Phloe	*Hypothenemus bolivianus* (Eggers, 1931)	1	0	3	2	6
Phloe	*Hypothenemus brunneus* (Hopkins, 1915)	53	46	26	0	125
Phloe	*Hypothenemus crudiae* (Panzer, 1791)	7	7	4	2	20
Phloe	*Hypothenemus eruditus* Westwood, 1836	1692	1700	1808	168	5368
Phloe	*Hypothenemus gossypii* (Hopkins, 1915)	6	3	1	1	11
Phloe	*Hypothenemus javanus* (Eggers, 1908)	4	3	5	0	12
Phloe	*Hypothenemus lunzi* Atkinson & Flechtmann, 2021	0	1	0	0	1
Phloe	*Hypothenemus meridensis* Wood, 2007	0	3	1	0	4
Sperm	*Hypothenemus obscurus* (Fabricius, 1801)	2025	1541	1430	387	5383
Phloe	*Hypothenemus opacus* (Eichhoff, 1872)	0	5	4	2	11
Phloe	*Hypothenemus plumeriae* (Nordlinger, 1856)	62	69	62	2	195
Phloe	*Hypothenemus rugosipes* Wood, 2007	0	0	1	0	1
Phloe	*Hypothenemus setosus* (Eichhoff, 1868)	170	61	48	6	285
Phloe	*Hypothenemus subsulcatus* Atkinson & Flechtmann, 2021	3	7	13	0	23
Phloe	*Hypothenemus suspectus* Wood, 1974	229	183	195	19	626
Phloe	*Hypothenemus wilsoni* Atkinson & Flechtmann, 2021	2	1	2	0	5
Xylom	*Microcorthylus minimus* Schedl, 1950	5	6	12	5	28
Xylom	*Microcorthylus* sp.	1	0	0	0	1
Xylom	*Monarthrum gracilior* (Schedl, 1959)	2	1	2	4	9
xylom	*Monarthrum* sp.	4	6	2	4	16
Sperm	*Pagiocerus frontalis* (Fabricius, 1801)	5	0	1	0	6
Xylop	*Phloeoborus rudis* Erichson, 1836	2	2	1	0	5
Phloe	*Phloeotribus* sp.	1	2	0	0	3
Phloe	*Phloeotribus pilula* (Erichson, 1847)	1	0	0	0	1
Phloe	*Pityophthorus* sp.	0	1	0	0	1
Xylom	*Premnobius ambitiosus* (Schaufuss, 1897)	1	1	3	1	6
Xylom	*Premnobius cavipennis* Eichhoff, 1878	719	1053	1301	679	3752
Xylom	*Premnobius perezdelacrucei* Petrov & Atkinson, 2017	0	0	4	0	4
Xylom	*Sampsonius dampfi* Schedl, 1940	262	411	619	106	1398
Xylom	*Sampsonius pedrosai* Schönherr, 1994	3	0	0	0	3
Phloe	*Stegomerus* sp.	1	0	0	0	1
Myelo	*Sternobothrus ater* (Schedl, 1952)	0	7	2	2	11
Myelo	*Sternobothrus paraguayensis* (Schedl, 1936)	1	0	0	0	1
Xylom	*Taurodemus varulus* (Wood, 1974)	1	2	2	0	5

continues…

continuation…

Xylom	*Tricolus minutissimus* Schedl, 1976	6	5	3	1	15
Xylom	*Xyleborinus gracilis* (Eichhoff, 1868)	15	12	8	7	42
Xylom	*Xyleborinus linearicollis* (Schedl,1937)	1	1	2	1	5
Xylom	*Xyleborinus reconditus* (Schedl, 1963)	66	46	30	4	146
Xylom	*Xyleborinus saginatus* Wood, 2007	1	0	0	0	1
Xylom	*Xyleborinus tribulosus* Wood, 1974	10	4	5	0	19
Xylom	*Xyleborus affinis* Eichhoff, 1868	311	774	444	156	1685
Xylom	*Xyleborus biconicus* Eggers, 1928	8	5	13	4	30
Xylom	*Xyleborus bispinatus* Eichhoff, 1868	117	165	129	33	444
Xylom	*Xyleborus bolivianus* Eggers, 1943	2	2	4	3	11
Xylom	*Xyleborus confluens* Schedl, 1966	0	0	1	0	1
Xylom	*Xyleborus ferrugineus* (Fabricius, 1801)	10	21	10	4	45
Xylom	*Xyleborus foederatus* Schedl, 1963	3	0	0	0	3
Xylom	*Xyleborus latipennis* Schedl, 1976	7	6	7	1	21
Xylom	*Xyleborus pusio* Eggers, 1941	0	1	0	0	1
Xylom	*Xyleborus spinulosus* Blandford, 1898	1438	1058	916	453	3865
Xylom	*Xyleborus volvulus* (Fabricius, 1775)	35	48	48	4	135
Xylom	*Xylosandrus compactus* (Eichhoff, 1875)	1	0	1	0	2
Xylom	*Xylosandrus curtulus* (Eichhoff, 1869)	8	8	6	4	26
	Σ Scolytinae specimens	9932	10142	10897	2625	33596
	Σ Scolytinae species	66	67	65	52	93
	Platypodinae					
Xylom	*Euplatypus parallelus* (Fabricius, 1801)	67	136	249	35	487
Xylom	*Euplatypus segnis* (Chapuis, 1865)	0	1	0	0	1
Xylom	*Megaplatypus asperatus* (Schedl, 1976)	0	0	1	0	1
Xylom	*Megaplatypus brevicaudatus* (Nunberg, 1939)	1	1	0	0	2
Xylom	*Myoplatypus* sp.	0	1	0	0	1
Xylom	*Teloplatypus ratzeburgi* (Chapuis, 1865)	1	1	1	0	3
Xylom	*Tesserocerus dewalquei* Chapuis, 1865	0	0	1	0	1
	Σ Platypodinae specimens	69	140	252	35	496
	Σ Platypodinae species	3	5	4	1	7

Supplementary Table S3. Number of species, abundance and ranking of ten most abundant species over the years of studies in each area African mahogany stands (1, 2 and 3) and riparian forest fragment (RF) by guild in Capinópolis, state of Minas Gerais, Brazil. Collections in the plantation stands were conducted from April 2017 to March 2024, and in the riparian forest from August 2021 to March 2024

“Ch2_suplemmentary_Table_S3-ranking_species.xls”

Supplementary Table S4. Forestry operations (pruning, thinning or both) carried out in African mahogany stands (1, 2 and 3). Capinópolis, state of Minas Gerais, Brazil from January 2017 to April 2024

year	stand	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	1												
2017	2												
	3												
	1												
2018	2												
	3												
	1												
2019	2												
	3												
	1												
2020	2												
	3												
	1												
2021	2												
	3												
	1												
2022	2												
	3												
	1												
2023	2												
	3												
	1												
2024	2												
	3												

pruning
thinning
both

Supplementary Table S5. Sum of rainfall (mm) and means of temperatures: medium (Tmed), minimum (Tmin) and maximum (Tmax) in Celsius degrees (°C) by study years. Capinópolis, state of Minas Gerais, Brazil, from April 2017 to March 2024

	study year	**rainfall[1]**	**Tmed[2]**	**Tmin[2]**	**Tmax[2]**
1	(abr 17 - mar 18)	1452	24.2	15.0	33.0
2	(abr 18 - mar 19)	1863	24.1	15.0	33.6
3	(abr 19 - mar 20)	1557	24.7	15.5	33.8
4	(abr 20 - mar 21)	918	24.9	15.6	35.9
5	(abr 21 - mar 22)	1495	24.5	14.6	34.3
6	(abr 22 - mar 23)	1912	24.0	14.2	33.4
7	(abr 23 - mar 24)	1159	26.0	16.2	36.6

[1] rainfall recorded using an on-site rain gauge installed at the farm

[2] temperatures obtained from NASA POWER (Prediction of Worldwide Energy Resources)

CHAPTER III

SPATIOTEMPORAL PATTERNS OF *Euplatypus parallelus* (FABRICIUS) (CURCULIONIDAE: PLATYPODINAE) ATTACKS ON *Khaya grandifoliola* C.DC.: INSIGHTS FOR PEST MANAGEMENT

"Only when the last tree has been cut down,
the last fish caught, and the last river poisoned,
will we realize that we cannot eat money."
American Indian Proverb

Spatiotemporal patterns of *Euplatypus parallelus* (Fabricius) attacks *on Khaya grandifoliola* C.DC.: insights for pest management

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Abstract

Understanding the spatial distribution and temporal dynamics of woodboring beetle attacks is essential for developing effective pest management strategies in commercial forestry. African mahogany (*Khaya grandifoliola* C.DC.) is a valuable hardwood species widely planted in Brazil, yet its productivity can be compromised by infestations of platypodine beetles. This study investigated the spatial and temporal patterns of *Euplatypus parallelus* (Fabricius) attacks in three *K. grandifoliola* stands planted in 2013, 2014, and 2015 in Capinópolis, Minas Gerais, Brazil, with a particular focus on the role of host defense, forestry operations, and environmental factors. Monthly inspections recorded georeferenced attacks, distinguishing entry holes with gum exudation (indicative of active host defense) from frass-expelling holes (failed defense), and assessed crown health. Generalized linear mixed models evaluated the effects of tree age, pruning, thinning, and rainfall on attack probability, while kernel density estimation characterized spatial clustering. Results indicated that gum exudation was the primary defense, effectively immobilizing beetles and preventing gallery establishment, whereas frass-expelling holes were infrequent and transient. Forestry operations increased attack likelihood, with pruning and thinning raising odds by 2.1 and 3.0 times, respectively. In contrast, older trees and higher rainfall reduced attack probability by 54% and 39% per standard deviation. Spatial analyses revealed clumped distributions, concentrated along stand edges near native forests, suggesting resource concentration and spillover effects. Attack intensity peaked between June and September and varied with forestry practices and tree age. These findings demonstrate that *K. grandifoliola* possesses effective endogenous defenses against *E. parallelus*, but forestry practices can create localized hotspots by increasing host susceptibility. Micro-scale environmental factors, particularly rainfall, further modulate attack patterns. Integrating these insights into management strategies highlights the importance of carefully planning forestry operations, promptly removing residues, and targeting monitoring efforts to mitigate beetle impacts, thereby supporting sustainable African mahogany production.

Resumo

Compreender a distribuição espacial e a dinâmica temporal dos ataques de besouros broqueadores de madeira é essencial para o desenvolvimento de estratégias eficazes de manejo de pragas na silvicultura comercial. O mogno-africano (*Khaya grandifoliola* C.DC.) é uma espécie de madeira nobre amplamente plantada no Brasil, cuja produtividade pode ser comprometida por infestações de besouros da subfamília Platypodinae. Este estudo investigou os padrões espaciais e temporais dos ataques de *Euplatypus parallelus* (Fabricius) em três povoamentos de *K. grandifoliola* plantados em 2013, 2014 e 2015 em Capinópolis, Minas Gerais, Brasil, com foco especial no papel da defesa do hospedeiro, das operações silviculturais e de fatores ambientais. Inspeções mensais registraram ataques georreferenciados, distinguindo orifícios de entrada com exsudação de goma (indicativos de defesa ativa do hospedeiro) de orifícios com expulsão de serragem (defesa malsucedida), além de avaliar a sanidade da copa. Modelos lineares generalizados mistos avaliaram os efeitos da idade das árvores, poda, desbaste e precipitação sobre a probabilidade de ataque, enquanto a estimativa de densidade de kernel caracterizou o agrupamento espacial. Os resultados indicaram que a exsudação de goma foi a principal defesa, imobilizando eficazmente os besouros e impedindo o estabelecimento de galerias, enquanto os orifícios com expulsão de serragem foram pouco frequentes e transitórios. As operações silviculturais aumentaram a probabilidade de ataque, sendo que a poda e o desbaste elevaram as chances em 2,1 e 3,0 vezes, respectivamente. Em contraste, árvores mais velhas e maior precipitação reduziram a probabilidade de ataque em 54% e 39% por desvio-padrão, respectivamente. As análises espaciais revelaram distribuições agregadas, concentradas nas bordas dos povoamentos próximos a florestas nativas, sugerindo efeitos de concentração de recursos e transbordamento. A intensidade dos ataques

atingiu o pico entre junho e setembro e variou conforme as práticas silviculturais e a idade das árvores. Esses achados demonstram que *K. grandifoliola* possui defesas endógenas eficazes contra *E. parallelus,* mas que práticas silviculturais podem criar pontos críticos localizados ao aumentar a suscetibilidade do hospedeiro. Fatores ambientais em microescala, particularmente a precipitação, modulam ainda mais os padrões de ataque. A integração desses insights nas estratégias de manejo destaca a importância de planejar cuidadosamente as operações silviculturais, remover prontamente os resíduos e direcionar os esforços de monitoramento para mitigar os impactos dos besouros, apoiando, assim, a produção sustentável de mogno-africano.

1 INTRODUCTION

The spatial distribution and temporal variation of insect pest attacks are fundamental to understanding pest behavior and developing effective management strategies (Liebhold et al. 1993; Wiegand et al. 2006). Among forest species, African mahogany (*Khaya grandifoliola* C.DC.) stands out as a valuable hardwood widely used in forestry and timber production (Ferraz Filho et al. 2021). However, its economic potential can be threatened by woodboring beetles, which may compromise tree growth and wood quality, thereby jeopardizing the viability of commercial plantations (Wylie & Speight 2012; Covre et al. 2025).

Particularly concerning are woodboring beetles from the subfamily Platypodinae, which have been reported attacking living *K. grandifoliola* trees in apparently healthy stands (Covre et al. 2025). In some cases, infestations appear to be associated with specific silvicultural practices, such as pruning (Covre et al. 2018; Pelozato et al. 2018; Covre et al. 2025) or thinning operations (Cristovam et al. 2018). However, in all these cases, African mahogany trees exhibited a defensive response to insect attacks through gum exudation — a notable natural defense mechanism of *Khaya* species, known as gummosis, characterized by the secretion of a viscous gum from the trunk or branches, and it likely involves the production of toxic secondary compounds as well (Covre et al. 2025).

While gummosis is more commonly documented in conifers (Franceschi et al. 2005), it also occurs in angiosperms, including members of the Meliaceae family (Pennington & Styles 1975). The gum is produced and stored in specialized ducts located within the xylem or bark, and upon injury or infestation, it is exuded to form a physical and chemical barrier capable of trapping or repelling woodborers and limiting pathogen development (Phillips & Croteau 1999; Trapp & Croteau 2001; Franceschi et al. 2005).

This endogenous defense plays a crucial role in plant protection and may reduce or even eliminate the need for chemical treatments (Covre et al. 2025). However, the effectiveness of gummosis is not uniform and can vary according to the tree's age, physiological condition, and prevailing environmental conditions (Lombardero et al. 2000; Langenheim 2003). Understanding this variability is essential for evaluating the natural resistance of trees and incorporating it into broader integrated pest management strategies.

Despite the limited number of studies assessing the full impact of woodboring beetles on *live K. grandifoliola* trees (see chapter 1), continuous monitoring of pest activity remains essential, particularly in the context of increasing demand for sustainable forestry practices. Mapping the spatial distribution of infested trees and analyzing the temporal variation in attack intensity provide critical data for integrated pest management (IPM) (Kogan 1998; Kehlenbeck et al. 2012). Such data enable forest managers to detect spatial clustering and seasonal trends, thereby enhancing monitoring efficiency, anticipating outbreaks, optimizing the scheduling of forestry operations, and implementing more targeted control measures (Paine et al. 1997).

Recent advances in geospatial analysis tools and statistical modeling have greatly enhanced our ability to detect and interpret complex patterns, thereby providing a solid foundation for data-driven decision-making in pest management (Radeloff et al. 2000; Perry & Enright 2006).

Therefore, this study aims to characterize the spatial distribution and temporal variation of woodboring beetle attacks in *K. grandifoliola* stands. By integrating geospatial analysis and statistical modeling, the research seeks to generate insights that support the development of more sustainable and effective monitoring and pest management strategies in African mahogany.

2 MATERIAL AND METHODS

2.1 Study sites

The study sites consisted of three *K. grandifoliola* stands (18°46'6.18"S 49°28'51.59"W), planted in November 2013 (S1), 2014 (S2), and 2015 (S3) in Capinópolis, state of Minas Gerais, Brazil (Figure 1). Stands S1 and S2 each cover 25 ha, while S3 measures 30 ha. Silvicultural practices, such as pruning and thinning, were carried out as needed in each stand, and the month of each practice was recorded (Supplementary Table S1).

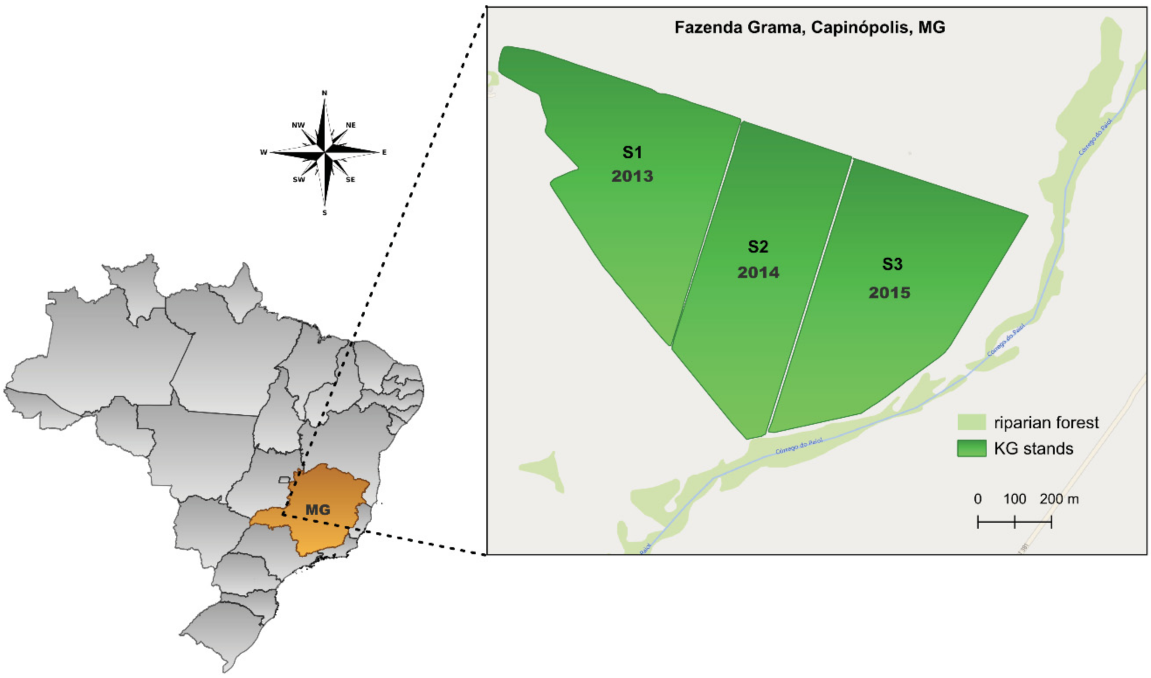

Figure 1. Study sites. *Khaya grandifoliola* (KG) stands planted in November of 2013 (S1), 2014 (S2) and 2015 (S3). Fazenda Grama, Capinópolis, Minas Gerais, Brazil.

2.2 Inspection of attacked trees

During the period from May 2017 to December 2024, monthly inspections were conducted on all trees within the plots, except during June and December 2017, February and May 2018, April 2019, August 2021, and February 2022, when inspections were not conducted, resulting in a total of 85 inspections.

Every tree in all three stands was georeferenced, and attacked trees were marked with paint to distinguish between new infestations and re-infestations. During each inspection, all trees exhibiting signs of woodboring beetles attack were recorded, including the number of entry holes associated with points of gum exudation (which indicates active and successful tree defense) and sawdust/frass (which indicates failed tree defense). Additionally, the crown health status of attacked trees was classified as follows: intact (healthy green, apparently vigorous, no mechanical damage), broken (entire crown broken by wind), and branch broken (one or more branches broken by wind) (Figure 2).

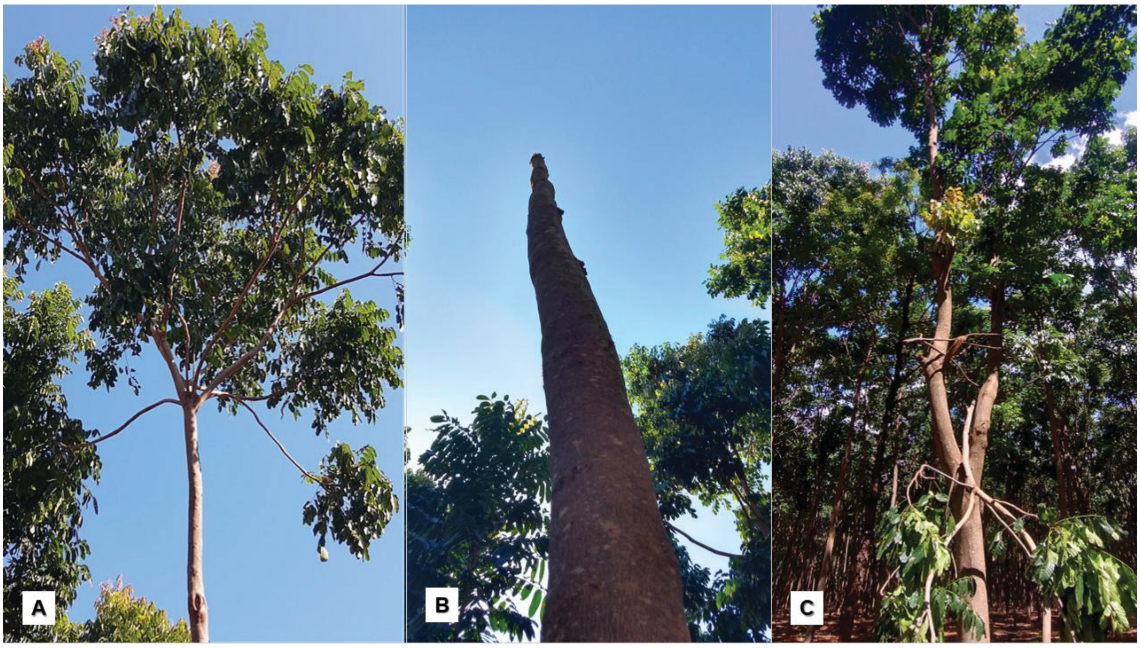

Figure 2. African mahogany (*Khaya grandifoliola*) crown health classified as: (A) intact, (B) broken, and (C) branch broken. Fazenda Grama, Capinópolis, Minas Gerais, Brazil. Source: L.S. Covre).

During some inspections, exuded gum adhering to the tree trunks, with attached woodboring beetles, was collected. Additionally, we removed bark to capture specimens for producing the expelling-frass holes. These woodborers were determined at the Entomology Laboratory of the São Paulo State University, Ilha Solteira campus (FEIS/UNESP).

Using data obtained from the forest inventory on tree density (number of trees per hectare), we were able to calculate the proportion of trees attacked relative to the total number of trees within each stand.

Additionally, monthly climatic data were obtained from NASA POWER (Prediction of Worldwide Energy Resources), including mean, minimum, and maximum air temperature (°C) and relative humidity (%) (NASA POWER, 2024), while precipitation (mm) was recorded using an on-site rain gauge installed at the farm.

2.3 Data Analysis

2.3.1 Influence of tree age, forestry operations and climatic variables on beetle attacks

The influence of pruning and thinning on the number of trees attacked by woodboring beetles were evaluated using generalized linear mixed models (GLMMs) with a binomial distribution and logit link function (lme4 package; Bates et al. 2015). Fixed effects included pruning, thinning, tree age (yearly) and monthly climatic variables (minimum, mean, and maximum temperatures, rainfall and relative humidity). Due to strong multicollinearity among the climatic variables, their effects were tested separately, with only rainfall retained in the final model. Monthly inspections were included as random effects. Additionally, we tested the presence/absence of woodboring beetles trapped in the monitoring program conducted throughout the experiment (for trapping methodology, see Chapter 2) as a fixed effect, based on the hypothesis that seasonal activity of these beetles could influence the incidence of tree attacks. We checked for overdispersion by calculating the ratio of the Pearson chi-squared statistic to the residual degrees of freedom, with a ratio greater than 1 indicating overdispersion (Ganio & Schafer 1992). To account for this, we included an observation-level random effect (OLRE) to absorb unexplained variability.

To facilitate interpretation, odds ratios (OR) were calculated by exponentiating the model coefficients (OR = e estimate), and the percentage change in the odds of attack was computed as (OR−1) × 100 (Kleinbaum & Klein 2010). Positive percentages indicated an increased probability of attack, whereas negative percentages indicated a decreased probability, holding all other variables constant.

All statistical analyses were conducted in R version 4.3.1 (R Core Team 2024), while all graphs were created and customized using the ggplot2 package (Wickham 2016).

2.4 Spatial data processing and heat maps of attack intensity

The geographic boundaries and tree grids of each stand were digitized in shapefile format using the Universal Transverse Mercator (UTM) coordinate system, with the reference coordinate system set to EPSG:31982 (SIRGAS 2000 / UTM zone 22S), in QGIS software version 3.40.6 (QGIS Development Team 2024). These shapefiles were subsequently imported into R and converted into spatial objects using the sf package (Pebesma 2018) for further spatial analysis.

The spatial distribution of gum-exudation holes was analyzed using a kernel density estimation (KDE) approach (Silverman 1986), a method used to estimate the intensity of spatial events based on the distribution of point occurrences in a defined area. In this study, KDE was applied to identify regions with higher densities of gum-exudation holes, thereby enabling the visualization of hotspots of insect-induced tree defense responses. The two-dimensional kernel density surface was computed using the stat_density_2d_filled() function from the ggplot2 package (Wickham 2016), with density values normalized (contour_var = ‘ndensity’) and divided into five bins. These bins were classified into five density categories: ‘very low’, ‘low’, ‘medium’, ‘high’, and ‘very high’. The resulting iso-density contours were converted into polygonal spatial features using “sf”, and geometries were validated to ensure topological integrity. These polygons were then clipped to the boundaries of each stand to ensure that heat maps represented only the actual study area.

Additionally, trees exhibiting gum-exudation holes were classified into six intensity categories based on the total number of holes per tree: ‘<50’, ‘51–100’, ‘101–150’, ‘151–200’, ‘201–250’, and ‘>250’.

All heat maps were exported as high-resolution PNG files (500 dpi) and subsequently compiled into an animated sequence with gganimate (Pedersen & Robinson 2025) to illustrate the temporal dynamics of gum exudation over the inspection period (Supplementary Video S1).

3 RESULTS

3.1 Identification of the beetle species responsible for tree attacks

All specimens collected from attacked trees were identified as belonging to a single species, *Euplatypus parallelus* (Fabricius) (Curculionidae: Platypodinae), and all of them were males.

3.2 Crown health and beetle attacks

Most of the attacked *K. grandifoliola* trees had intact crowns, while a much smaller proportion showed broken branches or damage caused by wind (Figure 3).

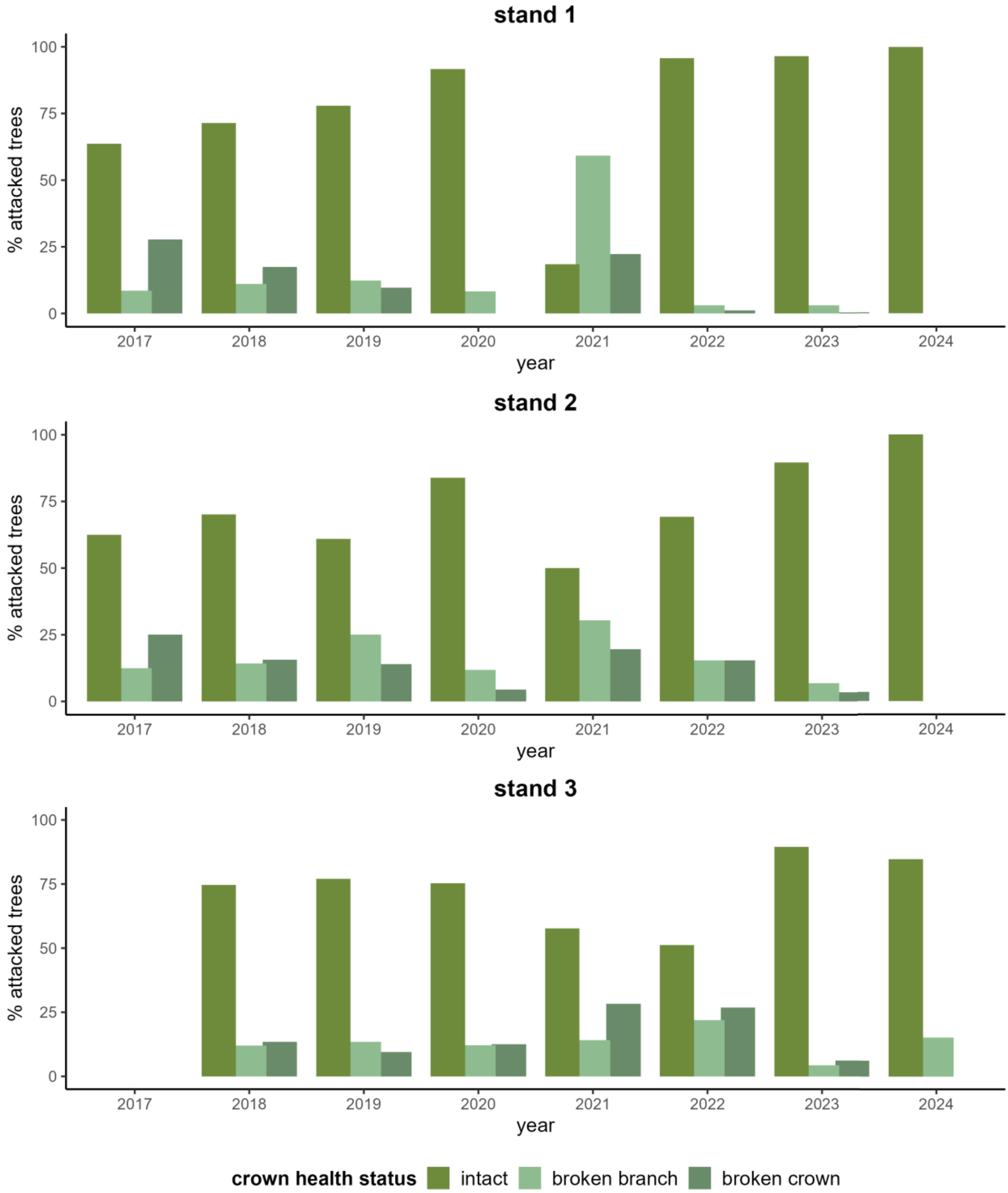

Figure 3. Percentage of trees attacked by *Euplatypus parallelus* according to their respective crown health status in all study years. Fazenda Grama, Capinópolis, Minas Gerais, Brazil.

3.3 Influence of tree age, forestry operations and climatic variables on beetle attacks

Visually, the highest percentage of attacked trees was observed in S3, followed by S2 and then S1. The greater intensity of attacks appeared to be related to the higher number of forestry operations conducted there, with an intermediate level in S2 and the lowest in S1. Overall, it appeared to be evident that pruning operations, especially during earlier years, led to increases in both the percentage of attacked trees and the number of gum-exudating holes. Thinning operations produced similar effects, although these were less pronounced in S2 between October 2022 to January 2023. Notably, peaks in attacks consistently occurred between June and September (Figure 4).

Over the years, as pruning operations decreased, thinning operations increased correspondingly. The number of attacked trees, and thus the number of holes, followed this trend. During the months when both pruning and thinning were performed, trees were consistently attacked, and holes were present. However, in the absence of these operations, attacks and the number of holes often decreased. This was true for both S1 and S3, whereas for S2 the trend remained only until early 2020. After that period, the number of attacks and holes declined significantly, despite the continued pruning and thinning. There was also a surge in attacks/holes between May and October 2019 in all stands, which did not appear to be related to any forestry operations (Figure 4).

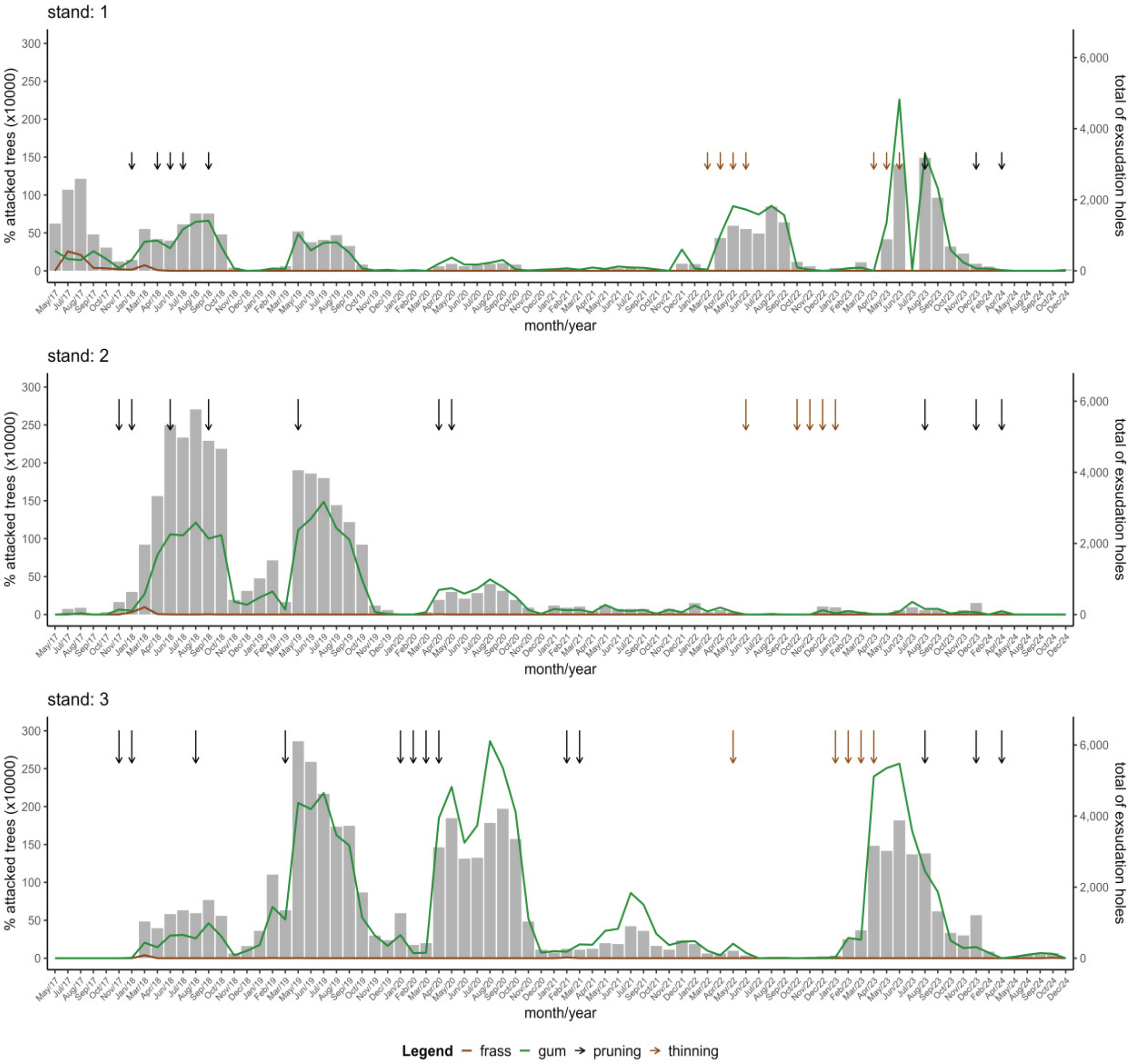

Figure 4. Percentage of trees attacked by *Euplatypus parallelus* (in bars) and total number of gum- and frass-expelling holes, in monthly inspections from May 2017 to December 2024 in African mahogany stands 1, 2 and 3, planted in November of 2013, 2014, and 2015, respectively. Fazenda Grama, Capinópolis, Minas Gerais, Brazil.

The number of gum-exuding holes varied among the three stands when compared at the same ages. Common patterns emerged: overall, there was a decrease in the number of gum-exuding holes from year 4 to year 7, except for an increase at S3 in year 7. In year 8, the numbers increased again in S1 and S2, while in S3 they continued to rise (Figure 5A).

When we analyze the number of holes expelling frass, this was only seen in the first year of observations, for all stands, independently of the age of the stand (Figure 5B and C). Overall, the percentage of number of gum-exuding holes was consistently and overwhelmingly greater than that of frass-exuding holes throughout all age classes and stands (Figure 5C).

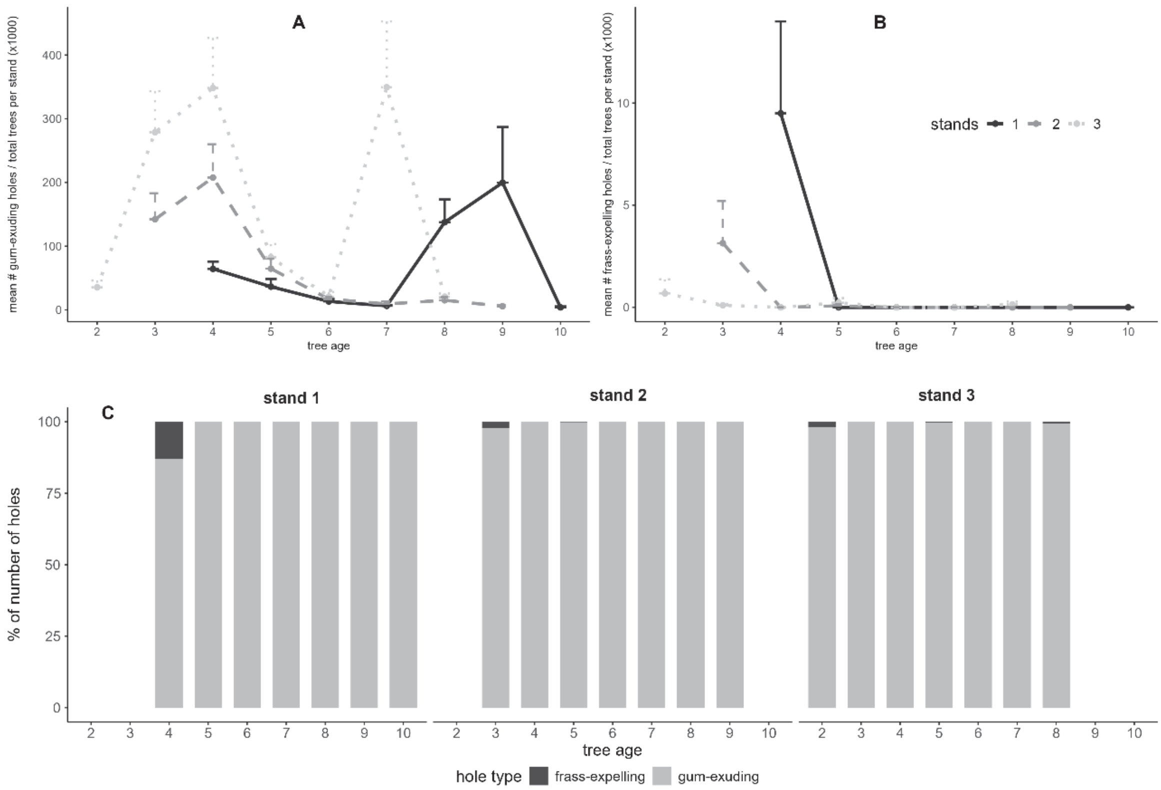

Figure 5. (A) Mean of number of gum-exuding and **(B)** frass-expelling holes by total number of trees in each stand, and **(C)** percentage of number of holes type (frass or gum) by tree age in African mahogany stand 1, 2 and 3, planted in November of 2013, 2014, and 2015, respectively. Fazenda Grama, Capinópolis, Minas Gerais, Brazil.

The GLMM analysis revealed significant effects of forest management operations, tree age, and rainfall on the probability of tree attacks (Table 1). Both pruning and thinning were positively associated with attack incidence. The odds of tree attack were approximately 2.1 times higher following pruning and 3.0 times higher following thinning compared to unmanaged conditions.

In contrast, tree age and rainfall were negatively associated with attack probability (Table 1). An increase of one standard deviation in stand age reduced the odds of attack by about 54%, whereas a one standard deviation increases in rainfall reduced the odds by 39%.

Random effects indicated substantial variability among individual observations, along with additional temporal variation among monthly inspections. Model fit statistics were AIC = 1899.0, BIC = 1923.1, and logLik = –942.5 (Table 1).

In addition, the presence/absence of *E. parallelus* was tested as a fixed effect but was not significant; therefore, this variable was disregarded in order to improve model performance.

Table 1. Generalized linear mixed model results for the proportion of attacked trees with pruning, thinning, tree age, and rainfall as fixed effects, monthly inspections and an observation-level random effect (OLRE) as random effects, showing odds ratios (OR) and 95% confidence intervals

fixed effect	estimate (β)	std. error	z value	p value		OR	OR (IC)
intercept	-6.986	0.133	-52.39	<0.001	***	0.001	0.001 – 0.001
pruning	0.754	0.315	2.39	0.017	*	2.13	1.15 – 3.95
thinning	1.103	0.406	2.72	0.007	**	3.01	1.33 – 6.83
tree age	-0.773	0.122	-6.36	<0.001	***	0.46	0.36 – 0.59
rainfall	-0.500	0.122	-4.09	<0.001	***	0.61	0.48 – 0.78

random effect	variance	std. dev.
observations (OLRE)	2.04	1.43
monthly inspections	0.32	0.57

3.4 Spatial data processing and heat maps of attack intensity

Based on the heat maps from monthly inspections (Supplementary Video S1), the distribution of attacked trees and the highest density of gum-exudating holes tended to shift sequentially from S1 to S2, and finally to S3. The attacks were overwhelmingly clustered rather than dispersed. When all inspections analyzed collectively, the spatial distribution of attacked trees and gum-exudating holes revealed clear clustering primarily along the edges of the stands, especially in the southeastern portion of stand 3 (Figure 6).

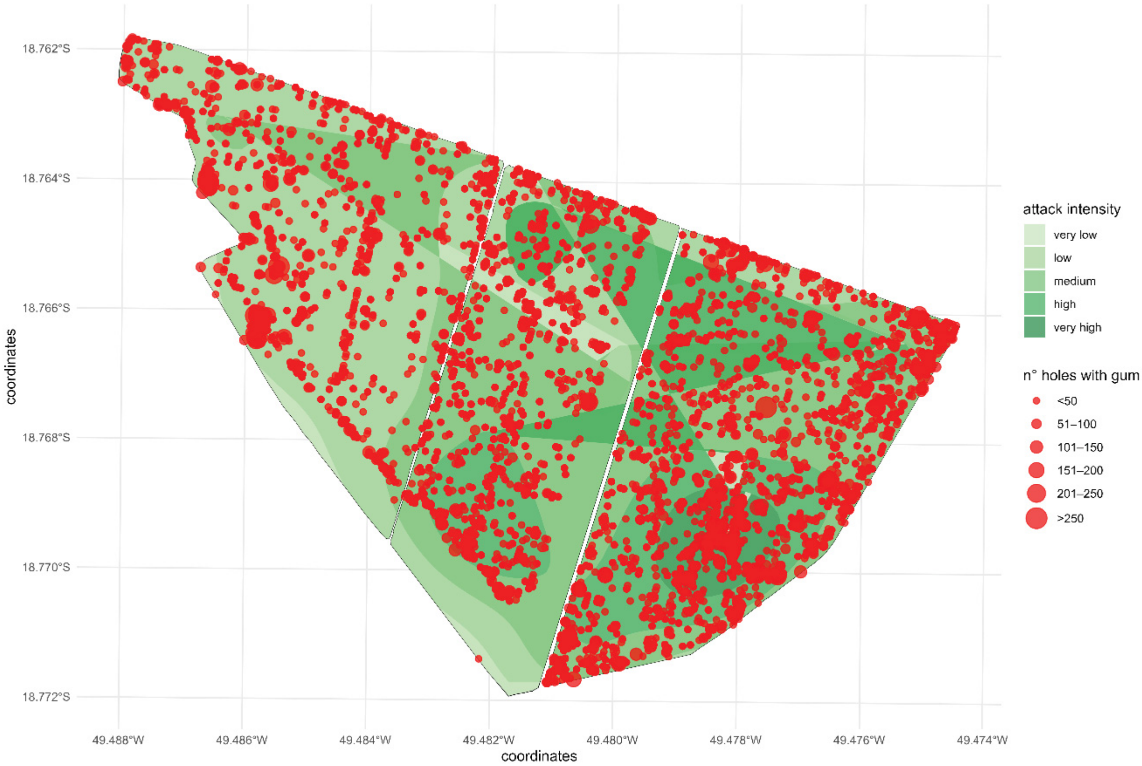

Figure 6. Spatial distribution of *Euplatypus parallelus* attack intensity and gum-exudating holes in *Khaya grandifoliola* plantation in Capinópolis, state of Minas Gerais, Brazil, from May 2017 to December 2024.

4 DISCUSSION

4.1 Host defense responses limiting *Euplatypus parallelus* establishment

The exclusive occurrence of *E. parallelus* in gum-exuding holes and bark dissections is noteworthy, as this species is frequently reported in association with various Khaya species in Brazil (see Chapter 1). Its detection in gum exudates, where only males were present, confirms that colonization attempts were still at an early stage. In Platypodinae, males are the pioneering sex, responsible for host selection and the release of sexual pheromones to attract females (Ytsma 1989; Beaver 2013). The observation of males trapped and killed in gum indicates that host defenses were effective in preventing brood establishment. This pattern highlights the capacity of *K. grandifoliola* to withstand colonization pressure, at least until defensive barriers are suppressed or environmental conditions become favorable to beetle establishment.

The failure of Platypodinae to establish galleries due to strong host defenses has been reported in several cases (Wright & Harris 1974; Roberts 1977a; Milligan

1979; Covre et al. 2025). In this study, the majority of *E. parallelus* individuals found on African mahogany (*K. grandifoliola*) were dead males, either expelled or embedded in gum at borehole entrances. This evidence clearly demonstrates the activation of a primary defense mechanism by the tree. One of the main defensive mechanisms in Khaya is gum exudation, a common strategy among several tree families, including Meliaceae (Pennington & Styles 1975). Mechanical injury, such as boring activity, can trigger gummosis, producing a physical barrier that immobilizes invaders (Jones 1959; Taylor 1960; Irvine 1961; Roberts 1969, 1977b; Nussinovitch 2010; Covre et al. 2025). Although some frass-expelling holes indicated initial successful penetration attempts, these signs were not detected in subsequent inspections, and no tree mortality was recorded. This outcome suggests that additional defense mechanisms, possibly chemical, also contributed to the failure of colonization attempts (Covre et al. 2025).

The repeated failure of pioneering males to establish galleries may have important behavioral implications for *E. parallelus*. The abortion of attacks by effective host defenses represents a critical constraint in the colonization process, as strong tree resistance can substantially reduce the reproductive success of local beetle populations. These dynamics likely contribute to the sporadic and patchy nature of *E. parallelus* outbreaks, which depend on the balance between host susceptibility and insect pressure. This aspect will be explored in greater detail below.

4.2 Forestry operations on host susceptibility

The higher incidence of *E. parallelus* attacks in stand S3, followed by S2 and S1, appears to reflect the intensity and type of forestry operations undertaken (Figure 4; Table 1). This pattern aligns with the known ecology of *E. parallelus*, which attacks living trees stressed by factores such as fire, drought, pathogens, or other causes (Bumrungsri et al. 2008; Beaver 2013). In Brazil, *E. parallelus* has been commonly associated with African mahogany, particularly on their fresh trunks or branches resulting from thinning or pruning activities (Covre et al. 2018; Cristovam et al. 2018; Pelozato et al. 2018). Although this relationship has often been observed, it had not been quantitatively demonstrated until now. The present findings reinforce the assumption that forest management practices, particularly thinning, create conditions that increase host susceptibility to colonization, with the odds of attack being three times higher (Table 1). Thinning leaves stumps and cut branches exposed for extended periods, which likely release volatile kairomones, which are well-known cues exploited by ambrosia beetles (Miller & Rabaglia 2009). In contrast, pruned branches were usually promptly removed from the study stands (personal information, A. Baduy), thereby reducing the release of attractive volatiles and limiting opportunities for beetle colonization. Nevertheless, pruning management still increased the odds of attack by 2.1 times (Table 1).

It is significant to highlight that the aggregation of beetles around freshly cut material likely influences the local population structure (see chapter 2). Thinning and pruning residues may serve as concentrated breeding sites, increasing local population density and reproductive success. High densities of colonizing individuals can intensify subsequent attack pressure on neighboring trees, potentially creating localized hotspots of infestation. This mechanism illustrates how forestry practices can indirectly influence population dynamics by concentrating resources both temporally and spatially. Markedly, *E. parallelus*, like other ambrosia beetle species, can reproduce and generate offspring from *K. grandifoliola* branches that are cut and left in the stand after pruning, further highlighting the role of slash as a source of population increase (Covre et al. 2018). This distinction between thinning and pruning emphasizes how subtle differences in management practices can shape pest dynamics.

The attraction of *E. parallelus* to thinning and pruning slash suggests that this species acts as a bioindicator of forest disturbance, responding to kairomones derived from mechanically injured or physiologically stressed trees (Elliott et al. 1983; Cavaletto et al. 2021). More broadly, this example illustrates how abiotic stressors, including forestry operations, can inadvertently promote pest outbreaks. Therefore, the recommendation to promptly remove residues from the field is thus reinforced, not only to prevent beetle breeding but also to minimize indirect impacts on surrounding apparently healthy trees. Our findings on the crown health status of attacked trees showed that the vast majority were intact (Figure 3). While broken branches or entire crowns would also release attractive volatiles similar to those from forestry operations, there is a notable difference: wounds created from pruning, or the branches themselves resulting from both pruning and thinning, are located closer to the ground, whereas the canopy is situated much higher (Supplementary Table

S2). Ambrosia beetles in the Neotropical region, such as *E. parallelus*, exhibit vertical flight stratification, and their preferred flight height is below 2 m (Igeta et al. 2004; Covre et al. 2021; Gerónimo-Torres et al. 2025). It is therefore reasonable to assume that kairomones released from the canopy are often too high to be detected by *E. parallelus*. Additionally, these volatiles would likely dissipate quickly due to wind exposure, reducing their concentration and making it more difficult for the beetles to detect them.

4.3 The role of climatic variables in *Euplatypus parallelus* attacks

Although *E. parallelus* is native to Central and South America, it has expanded significantly beyond its original range and is now considered pantropical, with established populations in several continents (Wood & Bright 1992; Beaver 2013; Maruthadurai et al. 2025). This widespread distribution is primarily associated with tropical environments, where the combination of warm temperatures and high humidity creates highly favorable conditions for its establishment and proliferation (Tang et al. 2019; Maruthadurai et al. 2025). Global-scale studies indicate that *E. parallelus* is primarily distributed in tropical and subtropical regions worldwide. Key climatic factors predicting its potential distribution include temperature seasonality, annual precipitation, and minimum temperature of the coldest month (Tang et al. 2019; Maruthadurai et al. 2025). The species shows higher probability of occurrence in regions where minimum temperatures exceed22 °C and annual precipitation exceeding 1000–1657 mm, highlighting its preference for warm, humid climates (Tang et al. 2019; Maruthadurai et al. 2025). In contrast, in our local-scale study, conducted in a tropical region with relatively stable temperatures (monthly temperature medium > 20 C°; supplementary Figure S1), we found no significant effect of temperature on attack probability, whereas precipitation negatively influenced attacks, reducing the odds by 39% per standard deviation increase (Table 1). This discrepancy reflects the difference between macroecological suitability and micro-scale activity: while climatic conditions define areas suitable for establishment, local rainfall may constrain beetle dispersal, wash away gum used as a cue in detecting fresh entry holes, and interfere with chemical communication essential for host location (Moser & Dell 1979; Nam & Choi 2014). These results underscore the importance of integrating large-scale climatic suitability with fine-scale environmental factors when assessing the risk and dynamics of *E. parallelus* infestation.

4.4 Clumped and edge-localized distribution of *Euplatypus parallelus* attacked trees

Platypodines are generally known to initiate infestations along stand edges unless their distribution is modified by forestry operations (Roberts 1977b). Our results corroborate this pattern, with most attacks concentrated along stand borders, particularly in stand S3 (Figure 6; Supplementary Video S1), which exhibited the highest intensity and is adjacent to a riparian native forest (Figure 1). The proximity to native vegetation suggests a spillover effect, where beetles dispersed from the native vegetation into the African mahogany plantations. Forestry practices such as thinning and pruning also influenced attack distribution, as discussed above. Within the plantation, conditions aligned with the resource concentration hypothesis, where a presence of a single host species (African mahogany) and the presence of physiologically stressed trees due to forestry operations or clusters of diseased individuals (as confirmed by field observations in the southern part of S3). The combination of source-sink dynamics (spillover from adjacent forest) and heightened host susceptibility (resource concentration) may thus account for the elevated attack intensity observed in the stands.

Spatially, Platypodinae species often exhibit clumped distributions within forests or plantations. Examples include *Platypus apicalis* White, *Platypus gracilis* Broun (Milligan 1979), and *Platypus quercivorus* (Murayama) (Yamasaki et al. 2014). Similarly, *Platypus subgranosus* Schedl also exhibits a clumped distribution, which appears to be associated with the aggregation of its diseased host trees (Elliott et al. 1987). Our findings reveal that trees attacked by *E. parallelus* also followed a clustered distribution (Figure 6; Supplementary Video S1).

This clustering likely results from ecological and behavioral factors. *Euplatypus parallelus* is classified as a 'B' species within the Platypodinae (Covre et al. 2025), which typically attacks stressed, dying, or recently felled trees, without strict preference for minimum diameter at breast height (DBH). Attacks occur on material ranging from small twigs to large trunks. The high number of entry holes per tree indicates extensive host colonization ability, potentially aided by aggregation pheromones, although it remains unclear whether *E. parallelus* employs such chemical cues. Such factors may explain variation in attack patterns while allowing high local population densities where suitable hosts are available.

5 CONCLUSIONS

This study characterized the spatial distribution and temporal variation of *E. parallelus* attacks in *K. grandifoliola* stands, demonstrating that African mahogany exhibited effective primary defense mechanisms, particularly gum exudation, which prevented the successful establishment of *E. parallelus* galleries and reduced its reproductive success. Forestry operations, including thinning and pruning, increased host susceptibility by creating slash material that attracted pioneering beetles, highlighting the influence of forestry management on local infestation dynamics. While broad climatic conditions define the species' potential distribution, fine-scale environmental factors, such as rainfall and host stress, strongly affected its attack probability and intensity. The clumped and edge-localized spatial pattern of attacked trees reflected both ecological processes, including spillover from adjacent native forests, and beetle behavior. Overall, these findings highlight the interplay between host defenses, management practices, environmental factors, and beetle behavior, providing a foundation for the development of more effective and sustainable monitoring and control strategies in African mahogany plantations.

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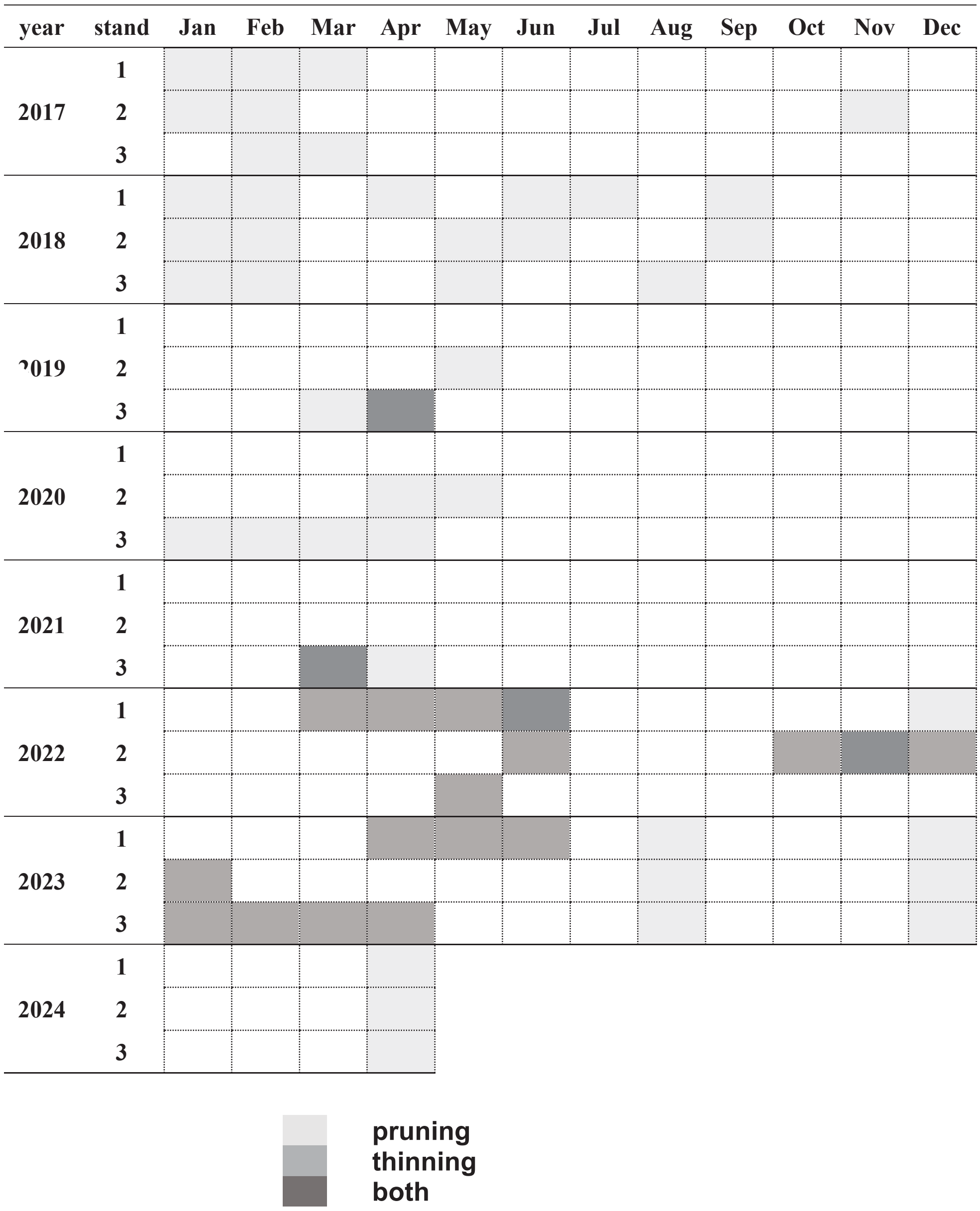
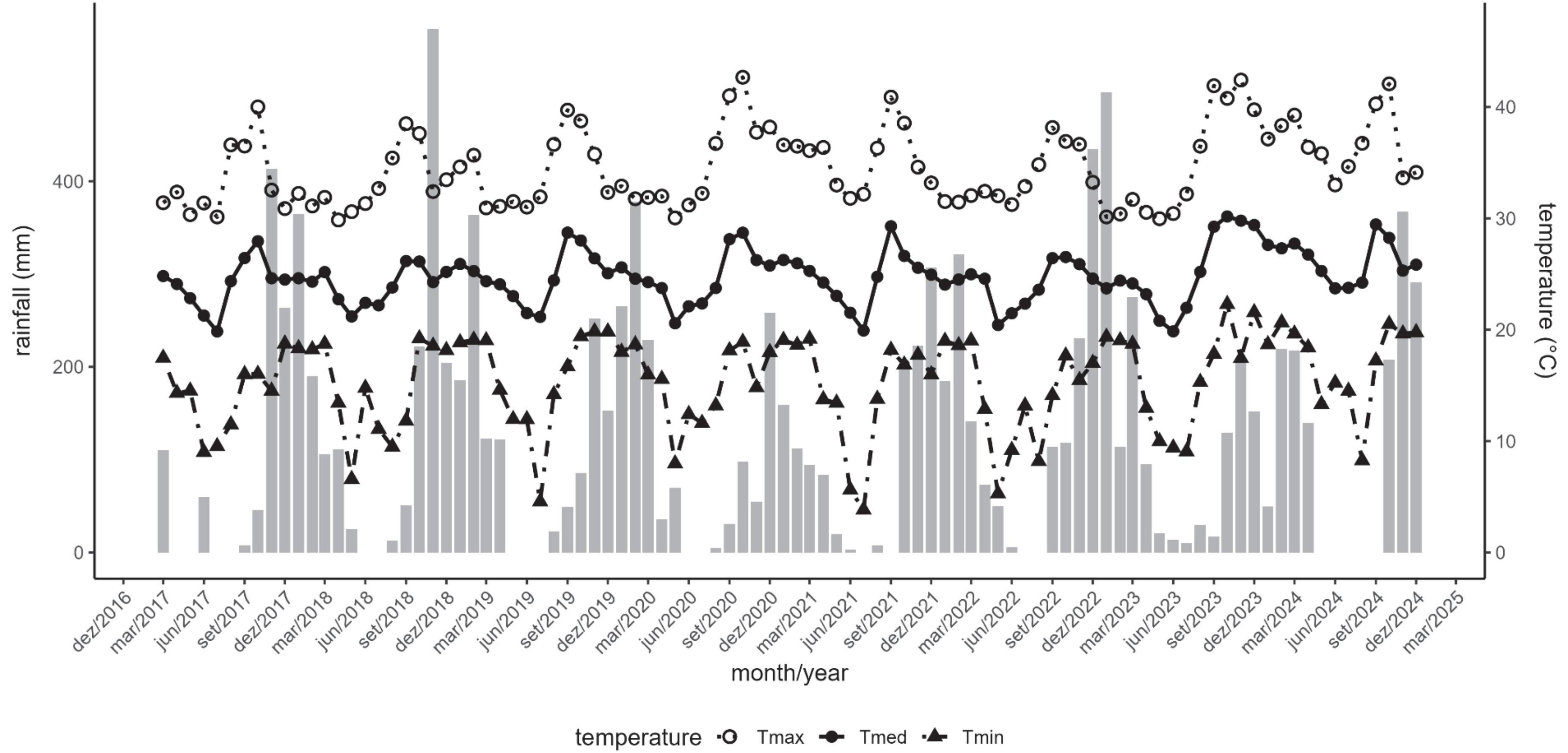
SUPPLEMENTARY MATERIAL

Supplementary Table S1. Forestry operations (pruning, thinning or both) carried out in African mahogany stands (1, 2 and 3). Capinópolis, state of Minas Gerais, Brazil from January 2017 to April 2024



Supplementary Table S2. The total height (meters) of the trees (*Khaya grandifoliola*) in each stand in the study years obtained from the forest inventory. Capinópolis, state of Minas Gerais, Brazil

stand	**study years**							
	2017	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**	**2024**
1	11.1	15.7	18.4	19.6	20.9	23.0	24.3	25.1
2	7.7	12.1	15.6	17.1	18.9	20.3	22.0	23.5
3	3.8	9.5	12.9	14.8	17.2	19.2	21.2	23.0



Supplementary Figure S1. Rainfall (mm), temperatures (C°; maximum, medium and minimum) monthly by each inspection of attacked *Khaya grandifoliola* trees by *Euplatypus parallelus* in Capinópolis, state of Minas Gerais, Brazil from March 2017 to December 2024

Supplementary Video S1. Monthly spatial distribution of *Euplatypus parallelus* attack intensity and gum-exudating holes in *Khaya grandifoliola* plantation in Capinópolis, state of Minas Gerais, Brazil, from May 2017 to December 2024.

‘Ch3_supplementary_Video_heat_maps_animated_MP4’