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CAN THE ANATOMICAL STRUCTURE OF HISTORICAL WOODS PREDICT BEE NESTING IN THE CULTURAL LANDSCAPE OF THE ATLANTIC FOREST?

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Resumo
Poderia a estrutura anatômica de madeiras históricas prever a nidificação de abelhas na paisagem cultural da Mata Atlântica? Objetivou-se analisar quais atributos anatômicos da madeira influenciam na nidificação das abelhas em antigas construções rurais de madeira em Santa Catarina, na Mata Atlântica, para testar a hipótese de que há relação entre a estrutura da madeira e a preferência das abelhas em termos de nidificação. Amostras de madeira foram coletadas de ninhos ativos de abelhas, preparadas, identificadas e seus atributos anatômicos verificados. Aplicou-se análise de componentes principais (PCA) para determinar qual atributo da madeira melhor influenciou a seleção do táxon de árvore pelas espécies de abelhas. Duas espécies de abelhas foram identificadas: *Eufriesea violacea* (Euglossini) e *Xylocopa frontalis* (Xylocopini). *E. violacea* totalizou 43 ninhos, nas espécies lenhosas*:* *Calophyllum brasiliense* (Calophyllaceae), *Maprounea guianensis* (Euphorbiaceae), *Heisteria silvianii* (Olacaceae), *Hyeronima alchorneoides* (Phyllanthaceae), *Casearia sylvestris* (Salicaceae), *Nectandra/Ocotea* sp.4 (Lauraceae). *E. violacea* foi encontrada escavando seus ninhos. *X. frontalis* totalizou seis ninhos, no morfotipo lenhoso *Nectandra/Ocotea* sp. 2. e *Nectandra/Ocotea* sp. 3. A análise de componentes principais (PCA) mostrou que, para os atributos da madeira, os componentes 1 e 2 explicaram 50,12% da variância do conjunto de dados, sendo que o componente principal 1 explicou 29,11% (diâmetro do elemento de vaso, frequência de vasos, diâmetro do lúmen da fibra e diâmetro da fibra) e o componente principal 2 explicou 21,0% (comprimento do elemento de vaso e altura do raio). Os atributos dos elementos do vaso foram os mais influentes na nidificação das abelhas na madeira.
Palavras-chave: anatomia da madeira, *Eufriesea, Xylocopa*, patrimônio em madeira, ninhos.

Abstract
This study aimed to analyze which anatomical attributes of wood influence bee nesting in old rural wooden buildings in the state of Santa Catarina, in the Atlantic Forest, to test the hypothesis that there is a relationship between wood structure and bee nesting preferences. Wood samples were collected from active bee nests. The wood was prepared, identified, and its anatomical attributes verified. Principal component analysis (PCA) was used to determine which wood attribute best influenced bee species' selection of tree taxon. Two species of bees were identified: *Eufriesea violacea* (Euglossini) and *Xylocopa frontalis* (Xylocopini). *E. violacea* totalized 43 nests, in the woody taxa: *Calophyllum brasiliense* (Calophyllaceae), *Maprounea guianensis* (Euphorbiaceae), *Heisteria silvianii* (Olacaceae), *Hyeronima alchorneoides* (Phyllanthaceae), *Casearia sylvestris* (Salicaceae), *Nectandra/Ocotea* sp.4 (Lauraceae). *E. violacea* was found excavating its nests. *X. frontalis* totalized six nests, in the woody morphotype *Nectandra/Ocotea* sp. 2. and *Nectandra/Ocotea* sp. 3. The PCA showed, for wood attributes, that components 1 and 2 explained 50.12% of the variance of the data set, with principal component 1 explaining 29.11% (vessel element diameter, vessel frequency, fiber lumen diameter and fiber diameter), and principal component 2 21.0% (vessel element length and ray height). Attributes of vessel elements were the most influential on bee nesting in wood.
Keywords: wood anatomy, *Eufriesea, Xylocopa*, wood heritage, nests.

INTRODUCTION

The maintenance of fauna in ecosystems depends on the balance of their ecological needs, such as food, shelter, and nest-building materials, which need to be available within their home range. Among the various factors that reduce natural forest areas is the use of wood by humans as fuel and as a construction material in most societies (MELO JÚNIOR, 2024), thereby reducing the availability of this resource for several animal species. Various taxa of wasps, bees, and other invertebrates use pre-existing cavities in tree wood or excavate them for nesting. Most of the bees use wood, living or dead, as a substrate for nest construction, and it is estimated that around 300 to 350 species of bees live in tree hollows, and most bee species nest in pre-existing cavities or excavate their nests in dead wood (HOPFENMÜLLER *et al.*, 2014).

Most bees nest inside forests, in living or dead trees, with wood that varies from low to high density, and some species of bees use pre-existing cavities in dry wood or even in living plants as a substrate for their nests (RUBENE *et al.*, 2015). Nevertheless, the reasons these species choose specific wood for nesting remain unclear. Data on nesting and behavior are needed for many native Brazilian bee species, as nesting patterns are quite varied and characteristic at the family or genus level, including knowledge of bionomy, and are of descriptive importance in legal provisions for the protection of bees and in the assessment of the conservation status of species. Bees that use trees have had their nest-construction resources and habitat reduced by logging and deforestation; however, several species are capable of nesting in human-made structures when suitable nesting substrates are available (FORTEL *et al.*, 2016).

There are no studies that verify the anatomical characteristics of the wood of tree species used by bees to construct their nests, nor that relate such structural attributes to nesting in wood present in human buildings. In Santa Catarina, there are no records of surveys or bionomic studies that identify the tree species used by wood-nesting bees for nesting, either in natural environments or in wood from human constructions, leaving this a gap in information regarding their bionomy. Trees go beyond being a foraging resource, as wood also serves as a substrate for nest construction for several bee species (COSTA; GONÇALVES, 2019). On the other hand, with the advance of civilizations, forests have been reduced by selective logging, and consequently, this substrate has become increasingly scarce, intensifying competition for habitat among various bee species.

The municipality of Joinville, Santa Catarina state, holds a valuable architectural heritage represented by its half-timbered-technique historical buildings, dating from the 19th century (MELO JÚNIOR, 2017; ANDRADE & MELO JÚNIOR, 2026). Part of this historical colonial architectural complex is constituted of wooden rural ranches (MELO JÚNIOR *et al.*, 2025a). Historical Anatomy is an interdisciplinary theoretical and methodological field that can be applied to expand knowledge of the interactions among trees, humans, and other species (MELO JÚNIOR, 2024), strengthening the idea of building multispecies landscapes. The precise list of wood species of great cultural interest in Brazilian regions is known (MELO JÚNIOR *et al.*, 2025b), but there remains a gap in the scientific literature regarding how these woods interact with other species in forest areas that have given rise to cultural landscapes.

The objective of this study was to verify the presence of bee nests in human historic constructions in rural landscapes of the Atlantic rain Forest, aiming to identify the species of wood used and analyze which of its anatomical attributes influence bee nesting, hoping that the information would further enhance the protection of bee species, this topic being pertinent especially within a conservation context, as well as the preservation of historical buildings as traces of old human settlements and reproductive havens for bee fauna.

In this context, this work intends to test the hypothesis that there is a link between wood structure and bee nesting preference in the Atlantic rain forest. The main objective was to analyze which anatomical attributes of wood influence bee nesting in old rural wooden buildings in the state of Santa Catarina, in the Atlantic Forest. This study is believed to contribute to integrated strategies for the conservation of biodiversity and cultural heritage in wood, showing interdependent connections and processes within the context of possible cultural landscapes.

MATERIAL AND METHODS

Study area

The study site was conducted in southern Brazil, in the northeast region of the State of Santa Catarina, a rural area in the municipality of Joinville (Figure 1), within the domain of the Atlantic Forest, a vegetation cover of low land rain forest, with climate, according to Koeppen, Cfa Subtropical (humid mesothermal, with hot summer), with an average annual temperature of 21.35ºC, average annual precipitation of 2,200 mm and average relative humidity of 83 to 84%.

In this work, three colonial buildings were studied, chosen by the fact that they still preserve their original parts, located on three rural properties (Figure 1): Property A (26°10'57"S 48°55'27" W), altitude of 38 m, was built in 1949, with the aim of housing tools and animals; Property B (26°10'33"S 48°55'09"W), altitude of 37m, was built in 1889, with the aim of housing animals, tools and *cachaça* (distilled spirit made from fermented sugarcane juice); Property C (26°10'33"S 48°54'36"W), altitude of 24 m, was built in 1879 with the aim of housing animals and tools. The three sheds were built with wood taken from the surrounding forest, according to their owners, and are still owned by the original family. Properties A and B still maintain agricultural activity. The distances between the property areas: A - B 917m, A - C 978m, and B – C 1648m. These structures, built throughout the 19th and 20th centuries by predominantly German European immigrants, testify not only to the richness of local history but also to the importance of the timber industry in the region and bear witness to the local timber biodiversity.

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Figure 1 - Rural buildings used for collecting historical wood and observing bee behavior. Legend: 1= Property A, 2= Property B, 3= Property C. Source: primary.

Figura 1 - Construções rurais utilizadas para a coleta de madeira históricas e as observações do comportamento das abelhas. Legenda: 1= Propriedade A, 2= Propriedade B, 3= Propriedade C. Fonte: primária.

Historic wood: collection, processing, anatomical identification, and anatomical attributes of wood

Wood samples were collected from architectural structures (arm, rafter, ceiling, board, truss, beam) where active bee nests were observed. The sample collection points in the construction structures were selected to guarantee the structural integrity of the buildings.

The samples were collected using a saw, chisel, and hammer from architectural structures, with the samples reduced in size to ensure the structural and aesthetic stability of the architectural elements. The samples were collected in accordance with the unified protocol for collecting historical wood samples (MELO JÚNIOR, 2025). The specimens were prepared following the usual protocol for wood anatomy studies (KRAUS & ARDUIN, 1997). The anatomical description of the wood was done by the recommendations and terminology of IAWA (1989), employing only those considered important in taxonomic diagnosis. Quantitative attributes of wood, such as length of vessel elements, tangential diameter and frequency of vessels, length and diameter of fibers, fiber wall thickness, and ray height, were measured, and the microphotographs were obtained using an Olympus CX31 optical photomicroscope with N=30 and with an attached Dino-Eye camera and DinoCapture 2.0 software.

Taxonomic identification was carried out using a comparative method, with reference to the Xiloteca Joinvillea (JOIw) (MELO-JÚNIOR *et al.*, 2014), the Inside Wood database (WHEELER, 2011), and specialized literature. Validation of species names and geographic distributions was carried out by consulting the REFLORA database (2020).

Bees: nests, behavior, and identification

Bee nests were searched for in the different architectural structures of the three studied buildings and identified by the activity of bees entering and leaving the wooden entrance. Only active nests were considered. For the external characterization of the nest, measurements of the diameter of the entrance and height of the entrance in relation to the floor were taken. Descriptive visual observations and photographic records/filming were made of the bees' nesting behavior regarding excavations and nest occupations. Material from the excavation of one of the species was collected to investigate the presence of wood fragments. The material was stored in an Eppendorf, frozen, and analyzed using an optical microscope (400x magnification). The bees were collected using an entomological net, taxonomically identified, and listed in the CRABEU - Reference Collection of the *Universidade da Região de Joinville*. The sampling effort took place in December 2022 and January 2023, totaling 27 hours, distributed equally across the properties, between 9 am and 4 pm on sunny days.

Statistical analysis of data

The influence of the anatomical attributes of the wood on the choice of nest location was determined by crossing the quantitative structural attributes of the wood and the occurrence/frequency of nests of the identified bee species. To this end, the anatomical attribute of wood that most influenced bee nesting was determined using principal component analysis (PCA). Statistical analysis was performed in the R environment (ANUNCIAÇÃO, 2021).

RESULTS

Woods: taxonomy and anatomical characteristics

The results indicate that attributes of vessel elements influence nesting, as described further. As only two bee species were found in the three studied buildings, the data analysis has limitations regarding the potential to generalize the findings to other species or ecosystems. However, as these data are related to the bionomy of bee species, the information is judged relevant and reported below from a perspective of contribution to the knowledge about these species.

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Wood samples totaling 29 units were collected from the various architectural elements in the three rural buildings. Five taxa of wood were identified, all angiosperms: *Calophyllum brasiliense* Cambess (Calophyllaceae), *Maprounea guianensis* Aubl. (Euphorbiaceae), *Heisteria silvianii* Schwacke (Olacaceae), *Hyeronima alchorneoides* Allemão (Phyllanthaceae), *Casearia sylvestris* Sw (Salicaceae), and four morphotypes belonging to the botanical family Lauraceae (table 1). All taxa occur in the Atlantic rainforest of Santa Catarina (REFLORA, 2020).

From the analysis of the wood anatomy, it was observed whether the growth layer is present or not and whether the type of porosity is diffuse-porous (figure 2). It was verified that groupings of solitary vessels are predominant, that the thickness of the fiber wall varies from thin to very thick, that the perforation plates are simple or scalariform, and that there are crystals in all species. However, peculiar characteristics were observed in each sample, allowing diagnosis according to supplementary material (see doi.org/10.5281/zenodo.20547035). The distribution of *Eufriesea violacea* and *Xylocopa frontalis* nests by historical wood species is in Table 1. The quantitative anatomical attributes of the wood used by the bee species are tabulated in Table 2.

Table 1 – Taxonomic identification and distribution of *Eufriesea* violacea and *Xilocopa frontalis* nests in historic wood in a rural landscape in Santa Catarina.
Tabela 1 – Identificação taxonômica e distribuição dos ninhos de *Eufriesea violacea* e *Xilocopa frontalis* em madeiras históricas numa paisagem rural em Santa Catarina.

Familly	**Taxon**	**Architectural structure**	**Bee species**	**NN**	**HN (m)**	**DNE (cm)**	**Record (JOIhw)**
Calophyllaceae	*Calophyllum brasiliense*	right arm	*Eufriesea violacea*	4	2.2	1.03	247,248
Euphorbiaceae	*Maprounea guianensis*	beam	*Eufriesea violacea*	5	2.2	1.13	240, 249, 263
Lauraceae	*Nectandra/Ocotea* sp.1	beam	*Eufriesea violacea*	6	2.25	1.11	244, 245, 259
	Nectandra/Ocotea sp.2	right foot	*Xylocopa frontalis*	3	1.2	2.41	360, 361, 365, 366
	Nectandra/Ocotea sp.3	right foot	*Xylocopa frontalis*	3	0.58	2.11	362, 363
	Nectandra/Ocotea sp.4	beam	*Eufriesea violacea*	9	2.1	1	236, 242, 246, 258, 359, 364
Olacaceae	*Heisteria silvianii*	rafter, beam	*Eufriesea violacea*	10	1.72	1.2	238, 239
Phyllanthaceae	*Hyeronima alchorneoides*	right foot, truss	*Eufriesea violacea*	3	3.12	1.1	241,243, 260
Salicaceae	*Casearia sylvestris*	rafter, board	*Eufriesea violacea*	6	1.5	1.12	237, 261,262,264

Legend: NN = number of nests; HN = average height of the nest in relation to the ground (m); DNE: average diameter of the nest entrance.

Table 2 - Means, and standard deviations of the anatomical quantitative attributes of the wood of the species used for nesting of *Eufriesea violacea* and *Xylocopa frontalis*.
Tabela 2 - Médias e desvios-padrão dos atributos anatômicos quantitativos da madeira das espécies utilizadas para a nidificação de *Eufriesea violacea* e *Xylocopa frontalis*.

	Anatomical attribute							
Wood	**FL**	**VL**	**FD**	**VD**	**FWT**	**VF**	**RH**	**FLD**
Hyeronima alchorneoides	1651.98 (±279.89)	1141.06 (±124.51)	40.57 (±12.29)	208.80 (±33.85)	13.40 (±2.71)	6.32 (±1.89)	16.72 (±3.66)	19.56 (±4.97)
Calophyllum brasiliense	1829.17 (±391.95)	831.16 (±154.93)	30.69 (±5.64)	139.06 (±38.34)	10.67 (±2.33)	11.70 (±3.33)	15.64 (±2.67)	6.73 (±2.11)
Casearia sylvestris	1651.96 (±383.69)	1078.90 (±437.30)	33.98 (±7.14)	90.20 (±13.22)	10.27 (±1.94)	20.66 (±7.91)	34.28 (±9.66)	9.73 (±2.84)
Heisteria silvianii	2313.46 (±375.43)	1373.39 (±422.15)	30.99 (±6.31)	84.04 (±16.47)	9.78 (±1.98)	20.13 (±3.64)	13.88 (±4.16)	7.83 (±2.66)
Maprounea guianensis	876.61 (±108.42)	486.15 (±294.11)	20.88 (±4.16)	98.17 (±14.42)	6.19 (±1.50)	12 (±2.54)	14.16 (±4.50)	9.83 (±2.31)
Nectandra/Ocotea sp.1	1665.57 (±350.93)	780.43 (±79.49)	24.28 (±4.95)	142.23 (±29.01)	7.81 (±2.24)	14.50 (±4,10)	31.16 (±13.31)	8.14 (±2.05)
Nectandra/Ocotea sp.2	1098.06 (±243.49)	353.66 (±87.47)	23.74 (±4.49)	114.20 (±18.41)	5.94 (±1.53)	15.56 (±3.90)	14.36 (±3.78)	8.75 (±2.82)
Nectandra/Ocotea sp.3	1366.44 (±354.67)	555.77 (±107.91)	24.61 (±4.27)	131.48 (±26.29)	8.13 (±2.27)	14.530 (±3.52)	13.68 (±3.22)	8.10 (±2.05)
Nectandra/Ocotea sp.4	2473.10 (±353.35)	576.81 (±217.28)	28.028 (±5.88)	109.13 (±15.56)	8.493 (±1.50)	20.800 (±367)	22.800 (±3.377)	12.82 (±4.74)

Legend: FL = fiber length (μm); VL = length of vessel elements (μm); FD = fiber diameter (μm); VD = diameter of vessel elements (μm) FWT = fiber wall thickness (μm); VF = frequency of vessel elements (n/mm²); RH = ray height (number of cells); FLD = fiber lumen diameter (μm).

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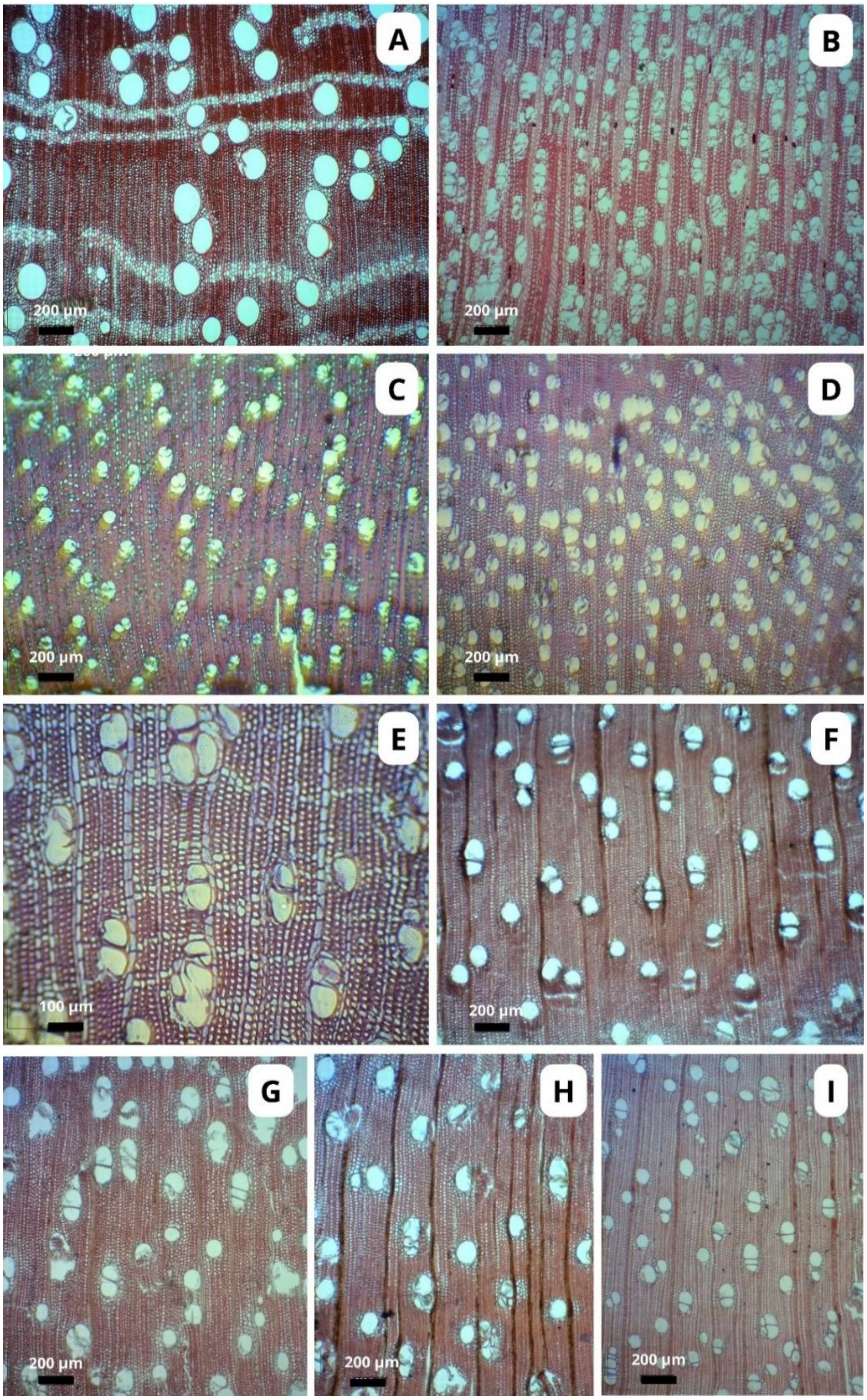

Figure 2 – Cross-sectional anatomy of the wood of historical species used by bees for nest construction. Legend: A – G - *Eufriesea violacea*. A - *Calophyllum brasiliense.* B - *Casearia sylvestris.* C - *Heisteria silvianii.* D - *Hyeronima alchorneoides.* E - *Maprounea guianensis*. F - *Nectandra/Ocotea* sp.1. G - *Nectandra/Ocotea* sp.4. H – I - *Xylocopa frontalis.* H - *Nectandra/Ocotea* sp.2. I - *Nectandra/Ocotea* sp.3. Source: primary.

Figura 2 – Anatomia transversal da madeira de espécies históricas utilizadas pelas abelhas na construção de ninhos. Legenda: A – G - *Eufriesea violacea*. A - *Calophyllum brasiliense.* B - *Casearia sylvestris.* C - *Heisteria silvianii.* D - *Hyeronima alchorneoides.* E - *Maprounea guianensis*. F - *Nectandra/Ocotea* sp.1. G - *Nectandra/Ocotea* sp.4. H – I - *Xylocopa frontalis.* H - *Nectandra/Ocotea* sp.2. I - *Nectandra/Ocotea* sp.3. Fonte: primária.

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Bees

Two species of nesting bees were identified in the wood species studied: *Eufriesea violacea* (Blanchard, 1840) (Euglossini) and *Xylocopa frontalis* (Olivier, 1789) (Xylocopini). The nesting patterns of these species clearly show distinct behaviors (figure 3). Components 1 and 2 of the PCA together explain 58.28% of the variance in the dataset. Axis 1 is influenced by the diameter and height of the nest entrance, while axis 2 is influenced by the number of nests of each species.

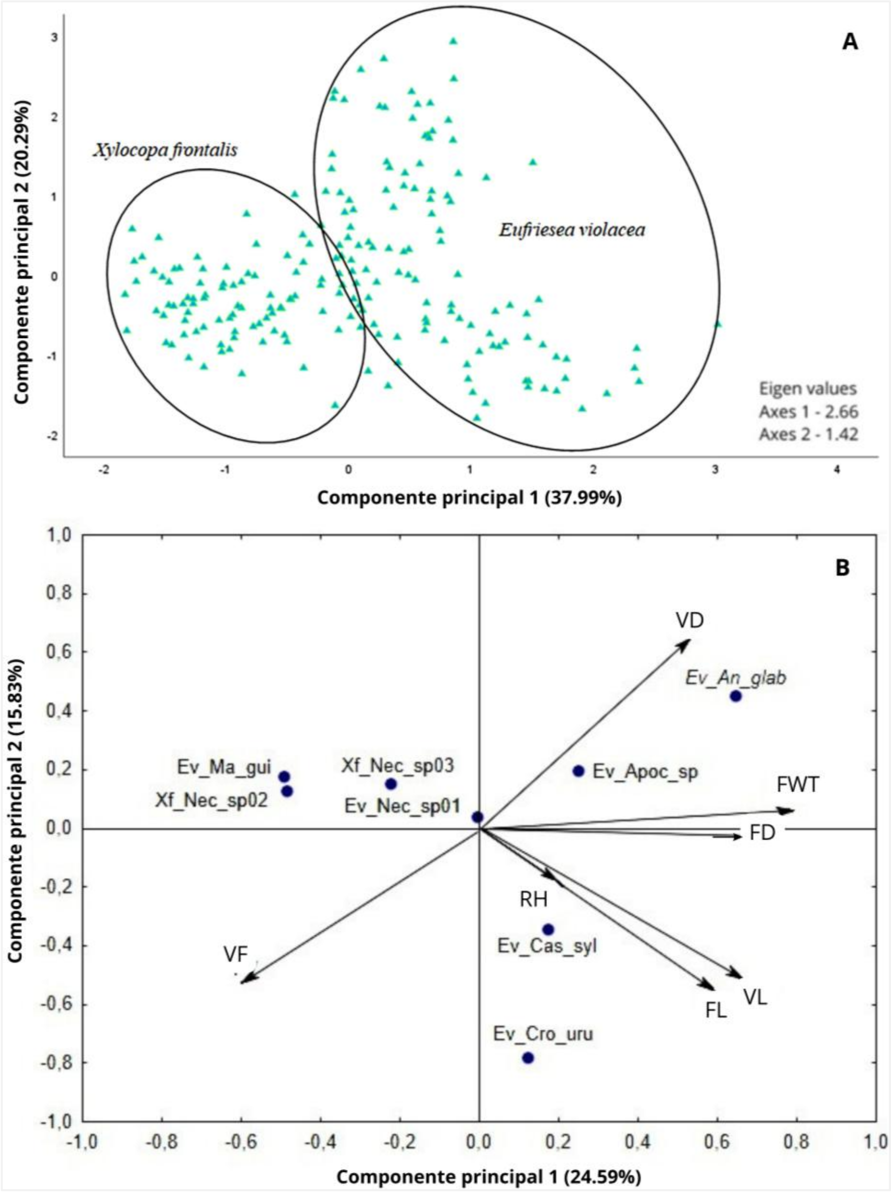

Figure 3 – Analysis of principal components. Legend: A - behavioral distinction in nesting between *Xylocopa frontalis* and *Eufriesea violacea* in the studied historical wooden structures. B - anatomical attributes of the wood used in the nesting of *Eufriesea violacea* and *Xylocopa frontalis*. Legend: FL = fiber length (µm); VL = length of vessel elements (µm); FD = fiber diameter (µm); VD = diameter of vessel (µm) FWT = fiber wall thickness (µm); VF = Frequency of vessel (n/mm²); RH = ray height (number of cells) Source: primary.

Figura 3 – Análise de componentes principais. Legenda: A - distinção comportamental na nidificação entre *Xylocopa frontalis* e *Eufriesea violacea* nas estruturas construtivas em madeira histórica estudadas. B - atributos anatômicos da madeira utilizada na nidificação de *Eufriesea violacea* e *Xylocopa frontalis.* Legenda: CF = comprimento da fibra (µm); CV = comprimento do elemento do vaso (µm); DF = diâmetro da fibra (µm); DV = diâmetro do vaso (µm); EPF = espessura da parede da fibra (µm); FV = frequência de vaso (n/mm²); RH = altura do raio (número de células). Fonte: primária.

E. violacea (figure 4E-H) was found in 43 nests, distributed in the following wood species: *C. sylvestris; H. silvianii, M. guianensis, H. alchorneoides, C. brasiliense, Nectandra/Ocotea* sp.1 and sp.4. It presented nests, with an average height in relation to the ground of 2.15 m and an average diameter of the nest entrance of 1.09 cm (table 2). *E. violacea* nests were unveiled, showing two distinct foundation patterns: nests installed in pre-existing holes and cracks, with horizontal cells (figure 4F); and nests settled by excavation in wood (figure 4E). Two excavation situations were observed: in the first, a bee initiating a hole, in which it gnawed on the surface of the wood, tearing off small chips with its jaws (figure 4F, G), and, in the second, a bee throwing moist, ocher-colored material, sticky, from the inside to the outside of the nest. This material was collected, and under a light microscope, wood fragments and various pollen types were observed, all of which were wrapped in a mass (figure 4H).

X. frontalis (figure 4A-D) was found exclusively in six nests in *Nectandra/Ocotea* sp.2 and sp.3. It presented nests with an average height in relation to the ground of 0.89 m and an average diameter of the nest entrance of 2.26 cm (table 3). Excavation was observed, in which the bees threw material resembling dry sawdust from inside the nest to the outside (figure 4B). In a broken piece of wood, it was possible to observe the internal part of the nest, with details of the brood cells (figure 4C). The nest entrances are clearly visible (figure 4D).

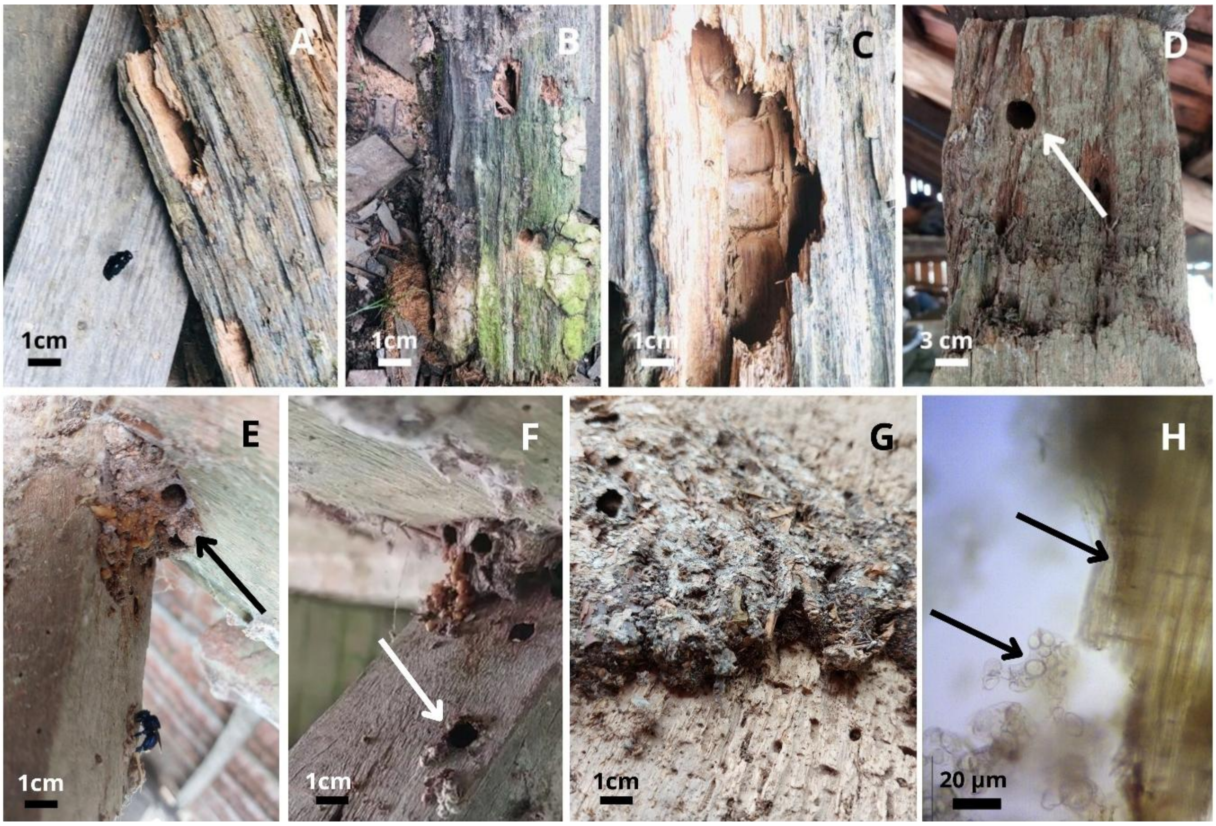

Figure 4 – Bee nests. Legend: A – D: records of *Xylocopa frontalis*, nest excavation material, and brood cells found in the historical wood studied. A: *Xylocopa frontalis* in front of the nest; B: sawdust resulting from nest excavation (arrow). C: internal cells of the nest. D: nest entrance (arrow). E – H: records *Eufriesea violacea*, nests, and nest excavation material found in the historic woods studied. E: *Eufriesea violacea* gnawing on wood and material thrown out of the nest (arrow). F: nest with the entrance excavated directly in the wood (arrow). G: nest entrance. H: wood fragment (right arrow), and pollen (left arrow). Source: primary.

Figura 4 – Ninhos das abelhas. Legenda: A – D: registos de *Xylocopa frontalis*, material de escavação de ninhos e células de cria encontradas na madeira histórica estudada. A: *Xylocopa frontalis* em frente ao ninho. B: serragem resultante da escavação do ninho (seta). C: células internas do ninho. D: entrada do ninho (seta). E – H: registros de *Eufriesea violacea*, ninhos e material de escavação de ninhos encontrados nas madeiras históricas estudadas. E: *Eufriesea violacea* roendo madeira e material atirado para fora do ninho (seta). F: ninho com entrada escavada diretamente na madeira (seta). G: entrada do ninho. H: fragmento de madeira (seta) e pólen (seta). Fonte: primária.

Wood and bee interactions

The PCA showed, for wood attributes, that components 1 and 2 explained 50.12% of the variance in the data set (figure 3B, supplementary material). Principal component 1 accounts for 29.11% of the variance, with vessel element diameter, vessel frequency, fiber lumen diameter, and fiber diameter being the most strongly related variables. *H. alchorneoides* is the species with the largest diameter of vessel elements (208.80 µm) and the lowest frequency of vessel elements (6.32 µm), *H. silvianii* with the smallest diameter of vessel elements (84.04 µm), *C. sylvestris, H. silvianii,* and *Nectandra/Ocotea* sp.4 have the frequency of vessel elements greater than 20 vessels/mm² and a total of 25 *E. violacea* nests (tables 1 and 2).

Principal component 2 accounts for 21.01% of the variance, with vessel element length and ray height being the most strongly related variables. *H. silvianii* has the greatest vessel element length (1373.39 µm) and *Nectandra/Ocotea* sp.2 has the lowest vessel element frequency (353.66 µm). *C. sylvestris* has the greatest radius height (34.28 µm) and *Nectandra/Ocotea* sp. 3, the smallest radius height (13.68 µm) (table 2).

DISCUSSION

In forest fragments lacking natural substrates, bees can use human-made structures built with wood removed from the forest. *Eufriesea* also named orchid bees, Neotropical, encompasses 72 species, nest in hollow trees, in bamboo stems, under tree bark, in wooden boxes made by humans, in ground cavities, under rocks, inside active nest of ants and termites, in abandoned carton nests of social wasps, and in nests of carpenter bees excavated in wood, in abandoned dens of small mammals and land crabs, in aerial nests made of resin and attached to the undersides of leaves or twigs, and in buildings (SOLANO-BRENES *et al.*, 2018). Nests of *Eufriesea* sp. were found to be constructed of wood chips and vegetable resins, with entrance diameters ranging from 1.5 to 2.5 cm (KAMKE *et al.*, 2008). We found an average diameter of 1.09 cm for *E. violacea*, which is therefore smaller.

Although studies on nest height relative to the ground were not found, Eberhard (1988) reported nests of the genus *Euglossa* in high parts of trees but without measurements. Nest architecture and brood-cell arrangement vary among cavity-nesting bee species, and several aspects of their nesting biology remain insufficiently documented (COSTA; GONÇALVES, 2019). Peruquetti and Campos (1997) described that females of *E. violacea* built their nests inside cracks and/or holes in the wood, but they did not mention excavation, nor the species of wood used. According to Solano-Brenes *et al.* (2018), orchid bees rarely excavate their nests, but rather transport construction materials, especially plant resins, to the nesting site, and several species build their nests in preexisting cavities in nature or even in human buildings.

Here, *E. violacea* bees were recorded beginning to excavate their nest in the wood, using their own jaws and also carving the internal part of the nest, what was confirmed by the observations and the microscopic analysis of the scrapped material collected (small fragments of wood along with pollen and a sticky wet mass). *E. violacea* was, here, the bee that built the largest number of nests (43), distributed across six taxa of wood.

The choice of location for the nest's foundation was compared with the wood's anatomical attributes. The porosity of wood is linked to the distribution of elements of sap-conducting vessels, which represent holes/hollows in the wood (BEECKMAN, 2016). The attributes that refer to the vessel's conductors (diameter of vessel elements, vessel frequence, and length of vessel elements) were the most important for *E. violacea*'s nesting site choice. The woods of *C. sylvestris*, *H. silvianii*, and *Nectandra*/*Ocotea* sp.4 had the highest frequencies of vessel elements per mm², making them the most chosen species, totaling 25 nests (58%) of the 43 nests. The wood species *H. silvianii* had the largest nest record (10), the smallest vessel element diameter, the longest vessel lengths, and the highest vessel frequency. These anatomical characteristics may reflect a preference for wood with greater porosity, which makes excavation easier. The wood of *H. silvianii* is heavy (density 0.89 g/cm³), hard to cut, of medium texture, moderately resistant to rot (COSTA-LIMA; CHAGAS, 2024). This may be related to the protection of offspring and to the need of *E. violacea* to excavate its nests by wetting the wood, making it more malleable and reducing friction in the jaws.

The *Xylocopa* genus accounts for 730 species worldwide and 52 species for Brazil, known as carpenter bees, as they excavate their nests in the wood of dead or living trees. *X. frontalis* builds its nests in dead trees, trunks, branches, wooden posts and plant tissues that are relatively dry and in some degree of decomposition, excavating linear galleries, using pre-existing cavities such as bamboo buds, and wood used in human constructions, making the management of this group difficult (MARCHI; MELO, 2010). The presence of large heads is considered a pre-adaptation for large jaws, which *Xylocopa* species use to dig into dead wood and is in line with the coarse appearance (sawdust) of *X. frontalis* nests (SILVA *et al.*, 2024). *X. frontalis*, in this work, was present in six nests, equally distributed in two morphotypes of the Lauraceae family, excavated in wood with low and high degrees of deterioration, showing that it can excavate in both conservation situations. The presence of crystals, tylose, oil cells and great thickness of the fiber wall stand out. Wood with higher densities tends to have greater cell wall increments, making them more mechanically resistant (FAJARDO, 2022). Thus, seemingly, the wood excavated by *Xylocopa* is heavy and dense. The morphotype *Nectandra*/*Ocotea* sp.2 has the lowest frequency of vessel elements, and *Nectandra*/*Ocotea* sp.3 has the lowest radius height. The wood species of the rural buildings here studied are part of the Atlantic Forest remnants around and the nesting sites were built in these dead woods of anthropogenic origin.

E. violacea and *X. frontalis* are species capable of withstanding some degree of anthropogenic disturbance, adapting to the availability of substrates to establish their nests. *Xylocopa* typically digs nests in the type of substrate verified. *Eufriesea* can occupy old *Xylocopa* nests; thus, there is a probability that *Eufriesea* nests originated from *Xylocopa* ones. However, the PCA shows two distinct clusters of points: one for *Xylocopa* and another, more diffuse one, for *Eufriesea*, indicating that there are indeed different types of bee-wood associations, one for each bee species. For *E. violacea*, the anatomical attributes of the wood that had the greatest influence on the choice of nesting site were the characteristics of the vessel elements (hollow parts in the wood), which can be a facilitating factor to dig/gnaw through the wood, without depending on pre-existing cavities. This is evidenced by both the PCA components and the examination of residues found in *E. violacea* nests, which contain pollen and wood fragments (Figure 4D).

Bees that nest in dead wood are becoming scarce because dead trees are removed in urban areas, during reforestation, burned or treated. Physical attributes (density and secondary compounds associated with xylem) need to be investigated to assess their influence on the location chosen by the bees. Bees that nest in wood are considered harmful to wood structures from a human perspective. For prevention, the use of extractives is recommended, as they are related to heartwood quantity and composition, lignin composition in the cell wall, xylem anatomy, nutrient availability, and the presence of moisture-regulating components (MARTÍN & LÓPEZ, 2023). Wood extractives are important components of the natural defense system of wood and contribute to resistance against biological deterioration and wood-attacking organisms, factors that should be considered when evaluating substrates used by wood-nesting bees (KIRKER *et al.*, 2024).

CONCLUSIONS

Based on the data evaluated in this study, it can be concluded that:

- There is a link between wood structure and bee preference in terms of nesting.
- The anatomical attributes of wood influence bee nesting in old rural wooden buildings.
- For *E. violacea*, there is a greater diversity of woods exploited, showing a more generalist behavior.
- For *X. frontalis*, the reduced number of discovered nests hinders the understanding of the influences of anatomical attributes on the bee's choice of nest location.
- Individuals of *Eufriesea violacea* are able to excavate their nests.
- Historically used wood has proven to be an important niche for bee fauna in cultural landscapes, making the environmental approach to the historical anatomy of wood a field that contributes to biodiversity conservation.

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