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Wasps Beyond Bees: Crop Species of *Spondias* (Anacardiaceae) Vary in Floral Scent and Attract Different Pollinator Taxa

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ABSTRACT

Spondias species are increasingly valued for their fruit production, which relies heavily on insect pollination. The flowers of these species are generalised, attracting a diverse array of insect visitors, including bees, beetles, flies, wasps and butterflies. This study provides the first comprehensive analysis of floral scents emitted by three *Spondias* crop species—*Spondias mombin* (cajá), *S. purpurea* (siriguela) and *S. tuberosa* (umbu) and explores the potential relationships between floral cues and pollinator spectra. We examine the spectrum of floral visitors across these species from both literature and original field observations. Our results reveal significant interspecific differences in both the number and quantity of volatile compounds released, as well as in the relative composition of these scents. Cajá flowers were dominated by (*E*)-β-ocimene, α- and β-pinene, methyl benzoate and benzyl alcohol, whereas siriguela flowers primarily emitted (*E*)-β-caryophyllene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, α-pinene, hexyl butyrate, methoxybenzene and 4-methylanisol. Umbu flowers predominantly emitted linalool and its derivatives, and (*Z*)-3-hexenyl butyrate. The floral visitor composition varied between species. Bees, particularly from the Meliponini tribe, were the main visitors of cajá (70%), whereas siriguela attracted primarily wasps (80%), especially from the Epiponini tribe. Umbu flowers attracted in similar proportions both wasps (38%) and bees (32%). These findings highlight the importance of a broad range of insect pollinators in *Spondias* species, particularly the role of non-bee pollinators like social wasps in the pollination of siriguela and umbu. We propose that variations in floral scent profiles and visual cues among these species are key factors in shaping their specific pollinator communities. This underscores the critical role of diverse insect pollinators in maintaining ecosystem services, reinforcing the need to preserve and support their populations.

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1 | Introduction

Generalised pollination systems have been considered an important driver of robustness and resilience for plant–pollinator natural communities (Waser et al. 1996; Ollerton et al. 2009; Bascompte and Jordano 2014) and crop landscapes (Garibaldi et al. 2013, 2021). Most plant species are suitable for attracting a diversity of pollinating insect taxa. Although floral traits are expected to relate to the most effective pollinators (Rosas-Guerrero et al. 2014) and repel opportunistic interactors (Camargo et al. 2019), floral cues of generalised plants may maintain pollination complementarity. Pollinators rely on a combination of flower cues, such as morphology, colours and scent, to locate host plants, although the relative importance of these cues can vary across different pollination systems (Raguso and Willis 2005; Dötterl et al. 2011; Milet-Pinheiro et al. 2012; Rachersberger et al. 2019). Floral scents, for example, are key in constraining or broadening the array of flower visitors (Dötterl and Gershenzon 2023). Generalised plants therefore might produce scent compounds that are perceived by different pollinators (Tollsten et al. 1994; Theis 2006). Hence, assessing the temporal and among-species variation in the floral scents, as well as floral morphology, colour and rewards of generalised pollination systems is crucial for understanding how these plants can attract not only bees but also other pollinator groups such as wasps, flies and beetles. Despite being understudied, these diverse pollinators play a significant role in providing pollination services. Since each group of pollinators has different scent preferences (Dobson 2006; Dötterl and Gershenzon 2023), understanding these preferences can provide valuable insights into how plants communicate with these neglected pollinators.

Tropical trees that produce small flowers clustered into large inflorescences available to pollinators over extended flowering seasons and massive floral displays, such as those belonging to the Anacardiaceae family, are good examples of generalised pollination systems. Anacardiaceae is a plant family known for its fruit crop tree species, including cashew (*Anacardium occidentale* L.), mango (*Mangifera indica* L.), pistachio (*Pistacia vera* L.) and various *Spondias* L. species. With approximately 20 described tree species distributed across Pantropical regions, prevalent in South America and Asia, *Spondias* species have gained attention for their cultivation as fruit crops, such as *Spondias mombin* L., *S. purpurea* (L.) and *S. tuberosa* Arruda (Airy-Shaw and Forman 1967; Mitchell and Daly 2015). Notably, regions like North and Northeastern Brazil have emerged as centres for the production of *Spondias* fruits with socio-economic importance, providing vital income for smallholder farmers, enhancing food security and nutrition, supporting cultural practices and contributing to sustainable agricultural systems (Cavalcanti et al. 2000; Araújo et al. 2007; Lins Neto et al. 2010).

Flowering and fruiting of *Spondias* mainly occur during the dry season (Adler and Kielpinski 2000; Nadia et al. 2007; Almeida et al. 2011; Kill et al. 2013). This period is when many plant species lose their leaves prior to blooming (Araújo et al. 2007). This underscores the ecological significance of *Spondias* as a critical food source for flower-visiting insects in semiarid environments, where flowering during the dry season provides a crucial resource in periods of scarcity (Nadia et al. 2007; Almeida et al. 2011). Furthermore, the fruits of *Spondias* play a vital role in facilitating zoochorous seed dispersal, serving as essential food sources for many animals (Griz and Machado 2001).

The flowers of *Spondias* species are generalised, attracting a diverse array of insect species such as bees, beetles, flies, wasps and butterflies (Nadia et al. 2007; Carneiro and Martins 2012; Mitchell and Daly 2015; Tavares et al. 2020). Their open floral morphology allows floral rewards to be readily accessible to a wide variety of flower visitors (Faegri and Van Der Pijl 1971; Nadia et al. 2007; Carneiro and Martins 2012; Tavares et al. 2020). *Spondias* species strongly depend on insect pollinators for reproduction since they are all self-incompatible (Nadia et al. 2007; Carneiro and Martins 2012; Tavares et al. 2020). Therefore, pollinator generalisation may explain the success of *Spondias* across the tropics (Mitchell and Daly 2015).

While the floral biology of *Spondias* is relatively well understood (Nadia et al. 2007; Carneiro and Martins 2012; Tavares et al. 2020), their floral scent chemistry and its connection with the wide range of associated pollinators remain unknown. Hence, this study aims to fill this gap by presenting the first comprehensive description of floral scents emitted by *Spondias* crop species. Specifically, we determined the floral scent composition and the amount of each compound emitted by three *Spondias* species over different times during the day. Furthermore, we discuss the potential associations between patterns of floral cues and the various taxa of pollinators these generalised trees attract.

2 | Materials and Methods

2.1 | Studied Species

In this study, we investigated three *Spondias* crops of Northern and Northeastern Brazil: *Spondias mombin* (cajá, hog plum, taperebá, yellow mombin [thereafter: cajá]), *Spondias purpurea* (hog plum, jocote, red mombin, siriguela [thereafter: siriguela]) and *Spondias tuberosa* (Brazil plum, umbu, [thereafter: umbu]) (Figure 1). The fruit set in these species is pollinator-mediated (Nadia et al. 2007; Ramos 2009; Almeida et al. 2011; Santos et al. 2011; Carneiro and Martins 2012; Oliveira et al. 2012; Tavares et al. 2020). These three species play an important socioeconomic role in Northern and Northeastern Brazil, where they are eaten fresh or as jellies and juices with a well-established market (Lorenzi et al. 2006).

All three species exhibit an arboreal habit. Cajá and umbu are andromonoecious, whereas siriguela is a dioecious species. Their flowers are small (2–3.5 mm), pentamerous and actinomorphic, which are clustered in terminal inflorescences and offer both nectar and pollen. *Spondias* flowers have 10 conspicuous stamens with longitudinally dehiscent anthers and up to five unilocular carpels, each containing a single ovule (Mitchell and Daly 2015). Anthesis begins at 4–5 a.m., preceding sunrise, with flowers lasting 2–3 days. The flowers emit a sweet scent perceptible to the human nose. Cajá and umbu flowers display white petals, whereas those of siriguela can range from red to purple (Hernández-Martínez et al. 1999; Nadia et al. 2007; Vargas-Simón et al. 2011; Carneiro and Martins 2012; Mitchell and Daly 2015).

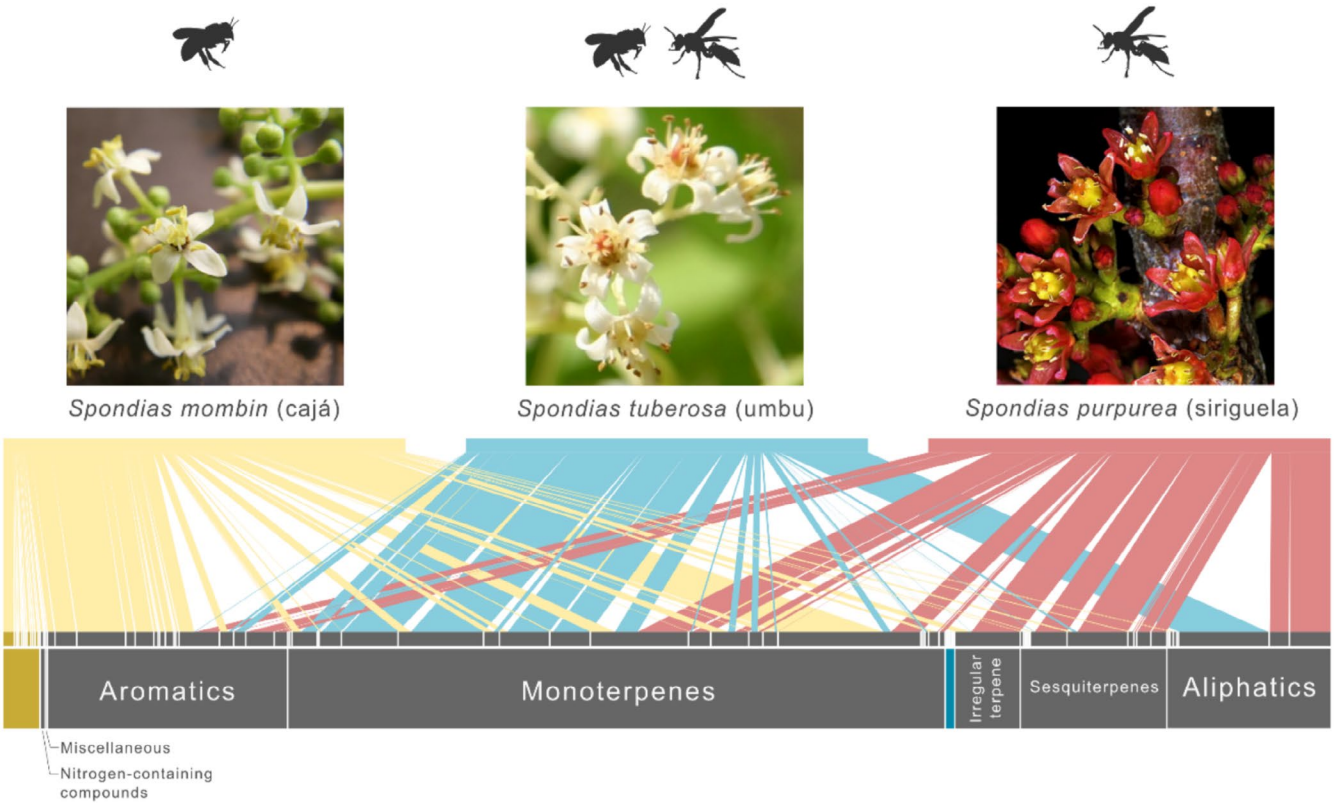


FIGURE 1 | The *Spondias* species—floral scent compounds network. The compounds are grouped by chemical classes (bars). The dark yellow and dark blue bars are unknown compounds of cajá and umbu, respectively. Bar widths correspond to relative amount (%) of the different compounds. Flower picture sources: Cajá, umbu—Discover of Life (discoveroflife.org); siriguela—Field Museum of Natural History (fieldmuseum.org). [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Sampling of Floral Scents

Floral volatiles were extracted from inflorescences of the three *Spondias* species during field collections using standard dynamic headspace methods (Dötterl et al. 2005), for two different purposes: (1) to characterise the chemical composition of the flower scent bouquet of each species and (2) to evaluate the variation in scent emission over the day. To obtain floral scent samples for thermodesorption (TD), intact inflorescences (one per sample) were enclosed within a polyester oven bag (8 × 5 cm; Toppits) for 1 min, after which scented air was drawn for 5 min by a membrane pump (Rietschle Thomas, Puchheim, Germany) at a constant flow rate of 200 mL min^{-1}. The air enriched with volatile organic compounds (VOCs) inside the bags was trapped in a thermal desorption filter (length: 30 mm; inner diameter: 2.5 mm) containing a 1:1 mixture of Tenax TA (80/100 mesh, Supelco, USA) and Carbopack X (20/40 mesh, Supelco, USA) as adsorbent polymers (3 mg). The filters consisted of ChromatoProbe quartz microvials (Agilent Inc., length: 30 mm; inner diameter: 2.5 mm), cut at the closed end and filled with 3 mg of a 1:1 mixture of Tenax-TA (mesh 60–80, Supelco) and Carbotrap (mesh 20–40, Supelco). The mixture was fixed in the tubes using glass wool.

The floral scents of cajá were collected at EMPAER (Empresa Paraibana de Pesquisa, Extensão Rural e Regularização Fundiária) (07°11′52″S; 34°48′42″W) in the municipality of João Pessoa, located in the state of Paraíba. Siriguela floral scent samples were obtained in the municipality of Sertania (8°00′68″ S; 37°21′15″), and umbu samples were collected in the municipality of Chã Grande (8°11′19″ S; 35°28′13″ W), both situated in the state of Pernambuco. For each species, inflorescence volatiles of different individuals ($N = 8$ for cajá, $N = 8$ for siriguela, $N = 7$ for umbu) were each collected at four times across the day: (1) 04:30–05:30 h, (2) 08:30–09:30 h, (3) 12:30–13:30 h and (4) 16:30–17:30 h. The number of sampled flowers per inflorescence varied within and among species (cajá: 20–196, siriguela: 7–35, umbu: 15–57), representing the natural variation in daily flower density of species. To detect ambient contaminants and scents emitted by vegetative parts, we collected samples of the surrounding air ($N = 2$, empty bags) and leaves ($N = 2$ for each species), respectively, using the same methods described above. All TD-samples were stored in 2 mL screw cap vials at −24°C until the conduction of chemical analysis.

2.3 | Chemical Analysis

The samples were analysed on a gas chromatograph coupled to a mass spectrometer (GC–MS; Agilent 7890A gas chromatograph, Agilent 5975C Series MSD mass spectrometer, Palo Alto, USA), equipped with a non-polar HP-5 ms column (Agilent J&W; 30 m × 0.25 mm i.d., 0.25 μm film thickness) and a thermal separation probe (TSP, Agilent, Palo Alto, USA). Configuration of the GC–MS system was the same as in Milet-Pinheiro et al. (2018). The data were acquired and stored in the .D format during the analysis on the Agilent GC–MS system. In the MassHunter software, the data were exported in NetCDF format and then imported into

the GCMSsolution software, which converted the data into its proprietary .qgd format. The GC/MS data were processed using GCMSsolution (Version 4.41, Shimadzu Corporation). The identification of compounds was carried out using the mass spectral and retention index libraries Wiley 9, Nist 2011, FFNSC 2 and Adams 2007 as well as the database available in MassFinder 3. The identity of most of the compounds was confirmed by comparison of mass spectra and retention times with authentic standard compounds available at the Chemical Ecology Lab of the Federal University of Pernambuco and the Plant Ecology lab of the Paris-Lodron University of Salzburg (Table 1). In order to do a qualitative comparison between samples, we used the peak areas of the total ion chromatograms. It is important to state that what is referred to as main compound, and the percentages reported in the results are the compound with the strongest signal, and the relative abundance in the TIC for each sample, not necessarily the compound of highest abundance or the reported percentage in the sample. Due to that, the selectivity of the extraction method and the GC/MS has been taken into account in our calculations; no quantitative analysis can be performed. Compounds detected in the ambient and leave samples were excluded from the list of floral scent compounds.

2.4 | Floral Visitors

We aimed to integrate both existing literature (Nadia et al. 2007; Ramos 2009; Venturieri and Venturieri 2010; Almeida et al. 2011; Carneiro and Martins 2012; Oliveira et al. 2012) and original field observations to provide a comprehensive overview of floral visitors across the target *Spondias* species. While previous studies provided data on floral visitors for cajá and umbu, information regarding siriguela was absent. Consequently, field observations were conducted to fill this gap. Field sampling for floral visitors of siriguela was conducted over two consecutive days in November 2020 at the Agua Fria Farm (8°11′19″S, 35°28′13″W) in the municipality of Chã Grande, Pernambuco state, Northeastern Brazil. The location is situated in a transition zone between Atlantic Rainforest and Caatinga, a seasonally tropical dry forest typical to NE-Brazil. The samplings occurred from 04:00 to 20:00 h, with intervals of 30 min. During each interval, we observed six siriguela plants for 5 min each.

Floral visitors were captured using entomological nets and killed in glass vials containing ethyl acetate for preservation. Notably, all captured insects were observed exhibiting behaviour indicative of potential pollination roles, as they touched the reproductive parts of siriguela flowers. We considered the main floral visitors to be the insect taxa with the highest number of species visiting the *Spondias* species, according to literature data and our sampling. The captured insects were deposited in the CEPANN collection (Coleção Entomológica Paulo Nogueira Neto) at the Institute of Biosciences, University of São Paulo, Brazil.

2.5 | Data Analysis

To test for differences in the number of scent compounds, total absolute scent amounts (calculated as the TIC of all compounds in each sample) and relative scent patterns (based on percentage amounts of the single compounds) among species and sampling times, we performed PERMANOVA analyses (10,000 permutations) in Primer 7 (Clarke and Gorley 2015). This non-parametric approach is appropriate for the analyses of uni- and multivariate data. The global analyses considered *species* and *time* as fixed factors, *individual nested in species* as a random factor, and the interaction between *species* and *time*. Depending on the outcome of the global analyses, post hoc analyses were performed. The PERMANOVA analyses were based on pairwise Euclidean distances (number of scent compounds, total absolute scent amounts) and pairwise Bray-Curtis similarities (relative scent patterns) among the samples.

PERMANOVA was also used to test for qualitative differences in the composition of floral visitors (presence/absence) among the three *Spondias* species (fixed factor: plant species; 10,000 permutations). This analysis was based on pairwise Sørensen similarities (floral visitors species recorded per *Spondias* species).

Floral visitor data were sourced from previous studies for cajá and umbu, where either the raw number of individuals sampled on flowers was recorded (Ramos 2009; Oliveira et al. 2012; Carneiro and Martins 2012) or only visitation records were documented (Nadia et al. 2007; Venturieri and Venturieri 2010; Almeida et al. 2011). Additionally, for siriguela, we obtained the raw number of individual floral visitors during field sampling. Given these differences in our data set, we applied PERMANOVA to test for qualitative differences in floral visitor composition among the three *Spondias* species, transforming all records of floral visitors into presence/absence data (fixed factor: plant species; 10,000 permutations). This analysis was conducted using pairwise Sørensen similarity indices, which compare floral visitor species between the different *Spondias* species.

To visually represent similarities in scent profiles and floral visitors among species (and time for scent data), non-metric multidimensional scaling (NMDS) based on the Bray-Curtis and Sørensen similarity matrices, respectively, were employed. We also created a floral scent–plant network using the function *plotweb* from the R package *bipartite* (Dormann et al. 2008).

3 | Results

3.1 | Floral Scent Traits

3.1.1 | Number of Compounds

A total of 76 compounds were identified in the three *Spondias* species. These included 22 monoterpenes, 16 aromatics, 10 sesquiterpenes, eight aliphatics, one irregular terpene, one nitrogen-containing compound and 18 unknown compounds (Table 1, Figure 1). The number of compounds differed among species (pseudo-$F_{2,60}=92.11$, $p<0.001$) and sampling times (pseudo-$F_{3,60}=4.59$, $p=0.007$), with a non-significant interaction effect (pseudo-$F_{6,60}=0.54$, $p=0.79$). Post hoc analyses revealed that all species differed among each other in the number of compounds detected ($p<0.001$), with cajá releasing 30 (median) compounds (57 in total), umbu 12 (median) compounds (35 in total) and siriguela 5 (median) compounds (20 in total).

TABLE 1 | Total absolute amount (mean ± SE) of scent and relative amount (%) of the different compounds detected at different times of the day for the three studied species of *Spondias* (cajá—*S. mombin*, siriguela—*S. purpurea*, umbu—*S. tuberosa*).

		Cajá				*Siriguela*				*Umbu*			
Time		**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**
Mean of number of compounds		32 (±3)	34 (±2)	31 (±3)	24 (±3)	6 (±1)	8 (±2)	7 (±1)	6 (±1)	14 (±3)	17 (±2)	13 (±1)	11 (±2)
Total absolute amount of scent (ng/flower/h)		142 (±56)	147 (±31)	72 (±32)	42 (±12)	35 (±12)	81 (±33)	96 (±53)	80 (±48)	175 (±56)	699 (±365)	163 (±24)	36 (±4)
Compounds	**RI**												
Aliphatics													
2-nonanone[a]	1094									tr	tr		
methyl octanoate[a]	1124	tr	tr	tr									
(*Z*)-3-hexenyl butyrate[a]	1186									**7.7**	**20.6**	**28.0**	**32.0**
(*E*)-2-hexenyl butyrate[a]	1215					7.1	6.7	1.5	3.4				
butyl butyrate[a]	1280					**13.8**	**13.8**	3.3	**9.3**				
(*Z*)-3-hexenyl hexanoate	1363	tr	tr	tr	tr								
methyl dodecanoate	1593	tr	tr	tr	tr								
methyl hexadecanoate	1594	tr	tr	tr	tr								
Aromatics													
methoxybenzene[a]	920					**16.5**	tr	3.4	5.9				
benzaldehyde[a]	963	1.0	1.0	1.2	2.8								
p-methylanisol[a]	1024	2.2	4.0	2.9	5.1	5.8	3.2	**7.3**	**7.1**	tr			
benzyl alcohol[a]	1035	**5.6**	**7.0**	**4.5**	3.0								
methyl benzoate[a]	1100	**8.3**	**11.9**	**11.8**	**15.1**								
phenylacetonitrile[a]	1145	3.1	2.5	tr	1.9								
1,2-dimethoxybenzene[a]	1146	3.0	**5.4**	**5.3**	3.2								
benzyl acetate[a]	1167	tr	1.0	tr	tr								
1,4-dimethoxybenzene[a]	1168					4.6	1.4	1.3	4.6				
methyl salicylate[a]	1202	tr	1.4	2.1	3.7	tr	tr	tr	tr	1.2	tr	tr	1.1

(Continues)

TABLE 1 | (Continued)

		Cajá				*Siriguela*				*Umbu*			
Time		**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**
p-anisaldehyde[a]	1262						tr	tr		tr	2.9	2.8	3.5
benzyl butyrate[a]	1351	tr	tr	tr	tr								
methyl *p*-anisate[a]	1383	tr	tr	1.7	tr								
methyleugenol[a]	1407	tr	2.0	3.0	1.4								
elemicine	1561	tr	tr	tr	tr								
benzyl benzoate[a]	1781	tr	tr	tr	tr								
Monoterpenes													
α-pinene[a]	938	**11.3**		4.2	**8.5**	**8.9**	**10.0**	**14.2**	**16.9**	2.1	5.6	7.3	**7.1**
camphene[a]	956	tr	tr	tr	tr	**7.2**	1.0	4.6	4.8	tr	tr		tr
verbenene	969	3.8	2.4	1.0	tr		1.3						
β-pinene[a]	982	**5.8**	tr	3.2	**7.7**	tr	2.5	5.4	4.3	tr	2.7	1.7	1.9
β-myrcene[a]	993	tr	tr	tr	1.0	tr		3.6		1.3	3.2	1.0	tr
α-terpinene[a]	1022									tr	tr		tr
limonene[a]	1033	1.4		2.3	4.8					4.3	5.1	1.7	3.6
(*Z*)-β-ocimene[a]	1039	2.8	**4.3**	3.2	1.1	tr			tr	tr	tr	tr	tr
(*E*)-β-ocimene[a]	1050	**30.4**	**31.4**	**24.7**	**17.4**	5.6	**13.7**	5.3	4.4	3.8	2.0	tr	tr
ɣ-terpinene[a]	1064	tr								tr	tr		
(*Z*)-linalool oxide furanoid[a]	1076	tr	tr	tr	tr					**7.7**	**5.7**	2.6	tr
(*E*)-linalool oxide furanoid[a]	1093		tr	tr	tr					**10.1**	**16.3**	**18.3**	**8.3**
2,2,6-trimethy-6-vinyldihydro-2H-pyran-3(4H)-one[a]	1113	tr	tr	tr									
allo-ocimene[a]	1132	tr	tr	tr	tr								
(*Z*)-linalool oxide pyranoid[a]	1176	3.0	1.8	1.5	1.2					**9.5**	**7.4**	**9.7**	**14.3**
(*E*)-linalool oxide pyranoid[a]	1180	1.2	tr	tr	tr					4.9	5.6	**10.9**	**14.7**
α-terpineol[a]	1200									tr	tr	tr	tr
dihydrocarvone[a]	1204									tr	tr	0.7	1.0

(Continues)

TABLE 1 | (Continued)

		Cajá				*Siriguela*				*Umbu*			
Time		**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**
α-terpinolene[a]	1205					tr	tr	tr	3.4				
(*Z*)-citral[a]	1246	tr	tr	tr									
linalool[a]	1295	3.1	3.0	2.1	3.7					**33.4**	**17.3**	**11.1**	6.5
1,5,8-p menthatriene	1298	2.4	3.8	2.1	1.0					tr	1.5	2.3	tr
Sesquiterpenes													
α-copaene[a]	1392	tr	tr	tr	1.4	**12.8**	**9.6**	3.3	5.7	tr	tr		
isocaryophyllene	1400									tr	tr	tr	tr
(*E*)-β-caryophyllene[a]	1439	tr	2.6	2.0	tr	5.6	4.9	**23.4**	**15.4**	2.5	tr	tr	tr
β-bisabolene[a]	1512		tr	1.6									
(*Z*,*Z*)-α-farnesene[a]	1498	tr	1.0	1.6	tr	tr	tr	tr				tr	
(*Z*,*E*)-α-farnesene	1499					tr	tr	tr	tr				
α-caryophyllene[a]	1473					4.8	tr	**5.6**	1.6	tr			
(*E*)-β-farnesene[a]	1461	tr	tr	tr									
curcumene	1480					tr	1.0	tr	**12.3**				
(*E*,*E*)-α-farnesene[a]	1513									tr			
Irregular terpenes													
(*E*)-4,8-dimethyl-1,3,7-nonatriene[a]	1118	1.0	3.0	**5.9**	**5.4**	3.7	**27.6**	**16.6**		tr	tr	tr	
Nitrogen-containing compounds													
methyl pyrrole-2-carboxylate	929	tr		tr									
Unknowns[b]													
m/*z*: 91.105.134	1094	2.7	3.8	2.6	1.1								
m/*z*: 67.93.79	1104	tr	tr	tr	tr								
m/*z*: 109.152.89	1231	tr	tr	tr									
m/*z*: 69.93.121	1290	tr	tr	tr	tr								
m/*z*: 91.69.120	1439									tr	tr		

(Continues)

TABLE 1 | (Continued)

		Cajá				*Siriguela*				*Umbu*			
Time		**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**	**5:00**	**9:00**	**13:00**	**17:00**
m/z: 124.166.151	1459	tr	tr	tr	tr								
m/z: 79.93.135	1490	tr	tr	tr	tr								
m/z: 93.119.69	1498	tr	tr	tr	tr								
m/z: 93.119.204	1594	tr	tr	tr	tr								
m/z: 135.164.149	1671	tr	tr	tr	tr								
m/z: 91.105.119	1742									tr			
m/z: 69.81.94	1774	tr	tr	tr	tr								
m/z: 69.81.95	1775	tr	tr	tr	tr								
m/z: 59.68.111	1782									tr			
m/z: 79.108.95	1874	tr	tr	tr	tr								
m/z: 91.105.79	1898									tr			
m/z: 93.107.189	1984									tr	tr		
m/z: 161.119.134	2038									tr	tr		

Note: The number of compounds is also given. Compounds are listed according to chemical class.
Abbreviation: tr, Trace amount <1%.
[a]Compounds were identified based on mass spectra and retention indices (RI—Linear Retention Index) of authentic standards; the other compounds (without 'a') were tentatively identified based on mass spectrum and retention index libraries.
[b]The unknown compounds were listed along with the most abundant *m/z* ion fragments, arranged in order of increasing abundance. The five most abundant compounds per species are in bold.

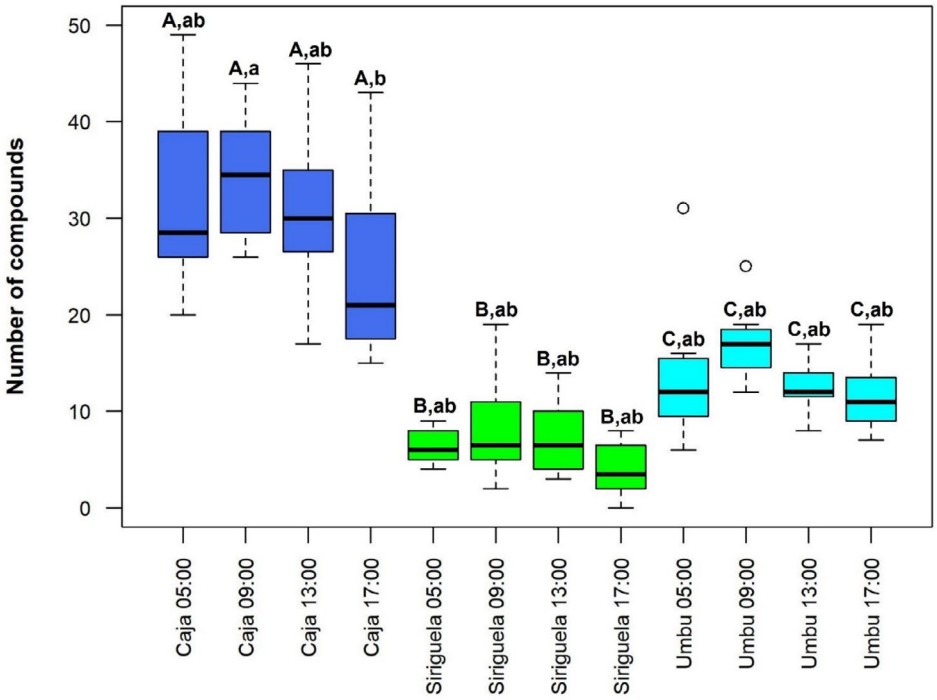


FIGURE 2 | Number of compounds detected throughout the day from the three studied species of *Spondias*. Different letters indicate significant differences among species at each time of a day (capital letters) and among different times of a day within species (case letters; PERMANOVA followed by post hoc tests). [Colour figure can be viewed at wileyonlinelibrary.com]

Post hoc analyses also revealed that the species emitted a higher number of compounds at 09:00 h than at 17:00 h ($p < 0.001$), with all other pairwise time comparisons being non-significant ($p > 0.053$) (Figure 2).

3.1.2 | Total Amount of Scent

There were also differences in the total amount of scent detected among species (pseudo-$F_{2,60} = 2.77$, $p = 0.017$) and sampling times (pseudo-$F_{3,60} = 3.44$, $p = 0.001$). In contrast to the number of compounds, the interaction between species and time was also significant for this scent trait (pseudo-$F_{6,60} = 2.32$, $p = 0.012$). As determined by post hoc analyses, the total amount of scent differed among species only for samples collected at 09:00 h ($p < 0.001$), but not for samples collected at other times ($p \geq 0.09$) (Figure 3). At 09:00 h, umbu (median of 9.7×10^6 total ion current/flower/6 min) released higher amounts of scent than both cajá (5.2×10^6 TIC/flower/6 min) and siriguela (1.1×10^6 TIC/flower/6 min) ($p < 0.01$), whereas the latter two released statistically similar amounts ($p = 0.18$). At the other times of the day, the species released in the median between 8.5×10^5 TIC of scent per flower and 6 min (siriguela at 17:00 h) and 6.8×10^6 TIC of scent per flower and 6 min (umbu at 13:00 h).

Time effects were found for umbu and cajá ($p < 0.04$ each), but not for siriguela ($p = 0.75$). In umbu, the time of higher floral scent emission was at 09:00 h (median of 9.7×10^6 TIC/flower/6 min), followed by 05:00 h (5.3×10^6 TIC/flower/6 min) and 13:00 h (6.8×10^6 TIC/flower/6 min), which were similar to each other, and 17:00 h (1.4×10^6 TIC/flower/6 min). In cajá, the total amount of scent was higher at 05:00 h (3.4×10^6 TIC/flower/6 min) and 09:00 h (5.2×10^6 TIC/flower/6 min) than at 13:00 h (1.7×10^6 TIC/flower/6 min) and at 17:00 h (1.2×10^6 TIC/flower/6 min) (Figure 3).

3.1.3 | Relative Scent Composition

The relative scent composition differed among species (pseudo-$F_{2,58} = 20.75$, $p < 0.001$) and times (pseudo-$F_{3,58} = 2.83$, $p < 0.001$), and there was also a significant interaction between species and time (pseudo-$F_{6,58} = 2.83$, $p < 0.001$) (Figure 4). Post hoc analyses revealed that at each time all species differ from one another ($p < 0.002$ each). Also, the relative scent composition differed among times for all three species ($p < 0.02$ each). In umbu the composition differed among all sampling times ($p < 0.032$ each), whereas in siriguela it only differed between 05:00 h and 09:00 h ($p = 0.022$). In cajá, it differed between 05:00 h and 13:00 h ($p = 0.006$), and between 05:00 h as well as 09:00 h and 17:00 h ($p < 0.03$ each).

In umbu, we detected mainly terpenoids, especially linalool and some of its derivatives as well as (*Z*)-3-hexenyl butyrate (Figure 1). Linalool was the main compound detected at 05:00 h (33.4%), whereas for the rest of the day (*Z*)-3-hexenyl butyrate was predominant, with an increasing relative amount of this ester throughout the day (20.6% at 09:00 h, 28.0% at 13:00 h, 32.0% at 17:00 h). From the flowers of siriguela were mainly terpenoids (e.g., (*E*)-β-caryophyllene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, α-pinene), fatty acid derivatives (e.g., hexyl butyrate) and aromatics (e.g., methoxybenzene, 4-methylanisol) detected (Figure 1). Most prominent differences between 05:00 h and 09:00 h, where the scents differed significantly, were that the detected relative amount of methoxybenzene was much higher at 05:00 h (16.5%) than 09:00 h

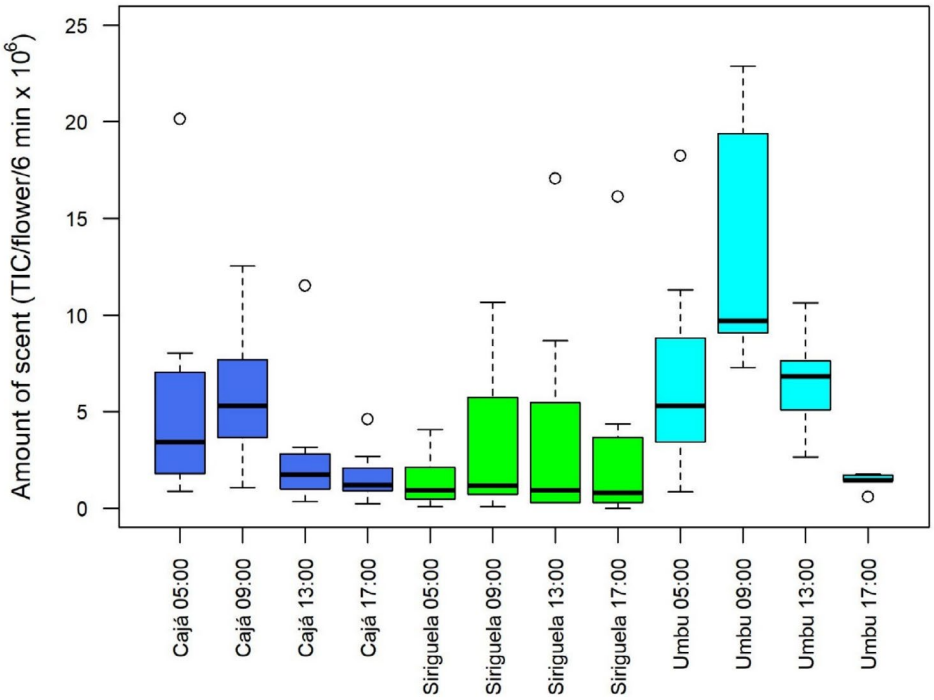


FIGURE 3 | Total amount of scent detected throughout the day from the three studied species of *Spondias*. Different letters indicate significant differences among species at each time of a day (capital letters) and among different times of a day within species (case letters; PERMANOVA followed by post hoc tests). [Colour figure can be viewed at wileyonlinelibrary.com]

(trace amount), whereas (*E*)-4,8-dimethyl-1,3,7-nonatriene was a main compound at 09:00 h (27.6%), but only a minor compound at 05:00 h (3.7%) (Table 1). The flower scent detected from cajá was dominated by monoterpenes (e.g., (*E*)-β-ocimene, α- and β-pinene) and aromatic compounds (methyl benzoate, benzyl alcohol), with (*E*)-β-ocimene being the most abundant compound throughout the day (Figure 1). At 05:00 h and 09:00 h, its relative contribution to the total detected scent was on average more than 30%, whereas it was less than 25% at 13:00 h and 17:00 h.

3.2 | Floral Visitors

The flowers of the three studied *Spondias* species attracted a diverse array of insect visitors, comprising 99 species of various taxa including bees, beetles, butterflies, flies and wasps (Table S1). Despite attracting a similar array of insect taxa, the floral visitor spectra of each species varied significantly from one another (pseudo-$F_{2,91} = 1409.9$; $p = 0.0001$; post hoc: $p < 0.001$) (Figure 4B).

Siriguela flowers attracted 25 insect species. The predominant visitors were wasps, with 20 species (80% of all recorded species), followed by three bee species (12%). Wasps from the Vespidae family, notably those of the eusocial Epiponini tribe, dominated with eight species.

Cajá flowers were visited by 50 insect species. Bees constituted 70% of the recorded species, followed by flies (22%). Apidae bees, particularly from the Meliponini tribe, were the main visitors, with 20 species. Cajá flowers were the only ones to attract chrysomelid beetles and nocturnal–crepuscular bees.

Umbu flowers attracted 28 insect species. Wasps and bees were the most frequent visitors, comprising 38% and 32% of the observed visitors, respectively. The most diverse visitors were wasps from the Epiponini tribe (six species) and bees from the Meliponini tribe (five species). Umbu flowers were unique in attracting butterflies (21%).

4 | Discussion

Despite their similar open morphology, which guarantees easy access to rewards to different pollinator groups, the flowers of the three studied *Spondias* species attract a diverse array of insects, with each species hosting distinct visitor communities: siriguela mainly attracts wasps, cajá mainly attracts bees and flies, and umbu attracts both wasps and bees. Our results revealed clear differences in the composition of floral scents among these *Spondias* species, which likely contribute to the variation in their floral visitors (Figure 1).

Siriguela predominantly attracted social wasps, particularly those from the *Polybia* genus. This genus is known for its populous hives and honey storage behaviour, a trait shared by few insect species beyond bees (Detoni and Prezoto 2021). *Polybia* has already been reported as the main floral visitor of various plant species, including some Anacardiaceae (Santos et al. 2006; Hermes and Köhler 2006; Sühs et al. 2009; Takehana et al. 2013). The floral traits exhibited by siriguela (Figure 1), such as petals with red to purple coloration, may play a role in wasp attraction (Lunau et al. 2011; Burger et al. 2017; Camargo et al. 2019), but it is likely that these colours along with other traits, such as strong floral scents, filter floral visitors. While wasps are known to visit flowers

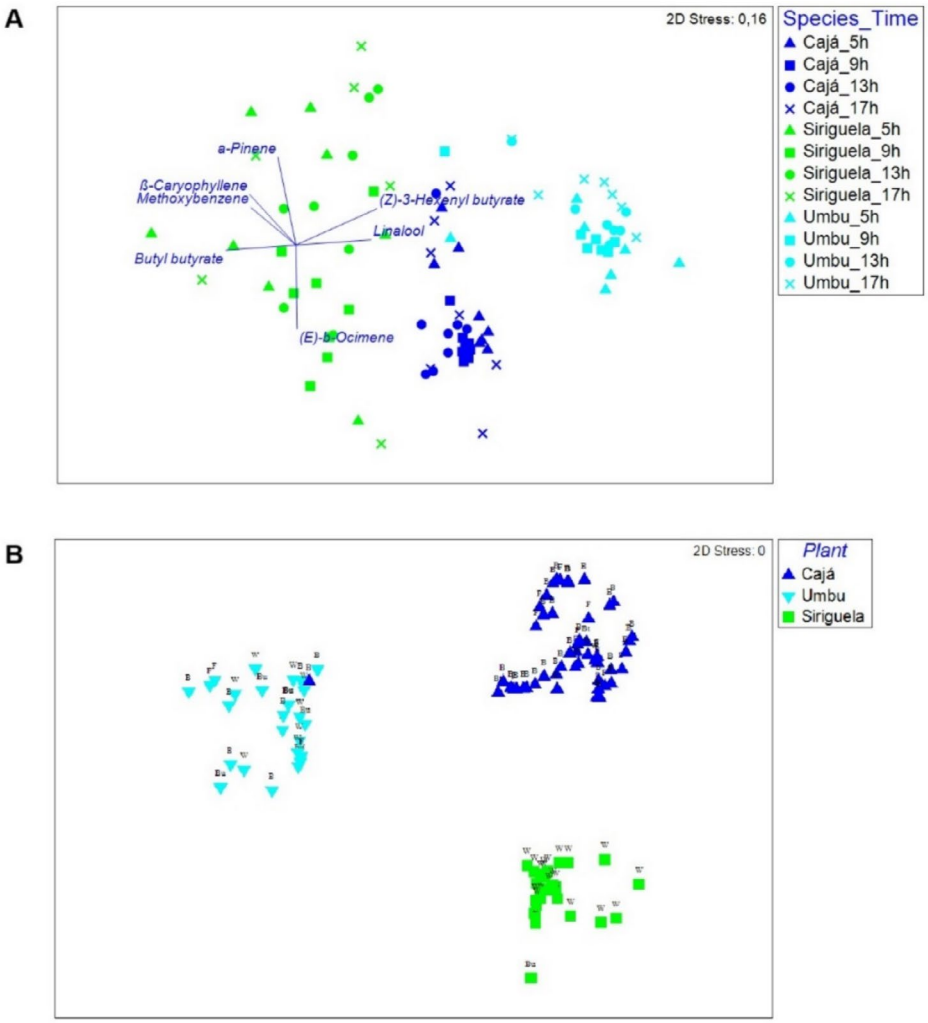


FIGURE 4 | Non-metric multidimensional scaling (NMDS) used to (A) display semi-quantitative differences in scent profiles among scent samples collected from the three studied species of *Spondias* and (B) display qualitative differences in the composition of floral visitors among three *Spondias* species. The main visitor groups are indicated: B, bee; Bt, beetle; Bu, butterfly; F, Fly; W, wasp. [Colour figure can be viewed at wileyonlinelibrary.com]

with dark colours, their attraction often depends on the presence of strong scents and accessible rewards. For instance, Shuttleworth and Johnson (2009a, 2009b) suggest that dark colours, in combination with strong scent emissions, can act as floral filters for open and accessible flowers. In the case of siriguela, the dominance of specific scent compounds such as (*E*)-β-caryophyllene and (*E*)-4,8-dimethyl-1,3,7-nonatriene likely plays an important role in attracting *Polybia* wasps more than visual cues alone. This aligns with findings from other wasp-pollinated plants, where scent and nectar composition are key drivers of pollinator selection (Brodmann et al. 2008, 2009; Burger et al. 2017, 2024; Kantsa et al. 2019). Additionally, butyl butyrate, another prominent compound detected from siriguela flowers in the morning, has been demonstrated to attract wasps (Landolt 1998). Furthermore, the presence of α-pinene in siriguela flowers may play a dual role, acting as an attractant for wasps while potentially repelling bee visitors, as high concentrations of this compound have been shown to deter honeybees (Fernandes et al. 2019). Such repellent compounds may contribute to the selective attraction of wasps over bees (Schiestl and Ayasse 2001). Another abundant compound in siriguela flowers is methoxybenzene, especially in the morning; however, its role in attracting floral visitors requires further investigation.

Cajá attracts mainly bee species and was intensely visited by the introduced honeybee *A. mellifera* and various species of stingless bees (Meliponini) (Ramos 2009; Carneiro and Martins 2012). The dominance of honeybees may disrupt the foraging dynamics of other floral visitors (Carneiro and Martins 2012), as observed in other Anacardiaceae species (Roubik and Villanueva-Gutierrez 2009). The floral characteristics of cajá are well suited to attract bees; for example, the white petals (Figure 1) (Faegri and Van Der Pijl 1971; Camargo et al. 2019), complemented by a strong, sweet scent emission. Our analysis revealed that the detected floral scent of cajá was dominated by (*E*)-β-ocimene throughout the day. (*E*)-β-ocimene, along with its *Z*-isomer, is a common and usually major compound across floral scents of many angiosperm species (Knudsen et al. 2006; Farré-Armengol et al. 2017) and plays a relevant function as a general pollinator attractant, including for bees (Gerlach and Schill 1991; Knudsen and Tollsten 1993; Borg-Karlson et al. 1994; Andersson

et al. 2002; Dufaÿ et al. 2003; Filella et al. 2013; Krug et al. 2018; Dötterl and Gershenzon 2023).

Umbu also features white petals (Figure 1) and we reported that umbu predominantly attracts Meliponini bees along with social wasps (Nadia et al. 2007; Almeida et al. 2011). The main scent compounds detected from umbu flowers include linalool and linalool oxides, along with (*Z*)-3-hexenyl butyrate. Linalool and linalool oxides are widely recognised as common and abundant components in the floral scent bouquets of various species, serving as general attractants for pollinators, including bees and social wasps (Dötterl et al. 2006; Knudsen et al. 2006; Steenhuisen et al. 2012; Raguso 2016; Krug et al. 2018; Lukas et al. 2020; Cordeiro and Dötterl 2023; Dötterl and Gershenzon 2023). In addition, (*Z*)-3-hexenyl butyrate has been proposed to play a prominent role in attracting social wasps (Brodmann et al. 2008). However, it is a minor compound in flowers visited by bees (Dötterl and Schäffler 2007; Rodriguez-Saona et al. 2011; Cordeiro et al. 2019).

It is important to recognise that other traits, such as nectar composition, may also contribute to the differences observed in floral visitors' communities among *Spondias* species. Various pollinator species are known to exhibit distinct preferences for the sugar composition and concentration of nectar (Galetto et al. 1998; Vaudo et al. 2015). For instance, flowers adapted to wasp pollination typically have sucrose-dominated nectar (Baker and Baker 1986), and some wasp-flowers have evolved nectar compositions that are unpalatable to certain flower-visiting insects, such as bees (Shuttleworth and Johnson 2009b; Burger et al. 2024). Although previous studies have shown that the flowers produce a very small amount of nectar unable to be quantified (Nadia et al. 2007; Carneiro and Martins 2012), future investigation of the nectar composition of *Spondias* should provide more insights into how open flowers can filter their pollinating insects.

Our findings highlight the broad spectrum of floral visitors in *Spondias* species, emphasising the importance of insects beyond bees in the pollination of these crops. We propose that differences in floral scents and visual cues among *Spondias* species are responsible for attracting specific visitor communities, that is, social wasps as the main floral visitors of siriguela and umbu. This underscores the need to recognise the role of various insect pollinators in providing essential ecosystem services and the importance of maintaining their populations. Social wasps, for instance, inhabit diverse ecosystems in Brazil (Souza et al. 2017), yet they are highly sensitive to environmental changes, making them valuable indicators of environmental quality (Richards 1971; Souza et al. 2010). Vegetation structure is a critical factor influencing social wasp communities, as it provides nesting and food resources, and indirectly affects temperature, air humidity, and shade in the environment (Santos and Gobbi 1998; Souza et al. 2017). Therefore, we highlight the role of these neglected pollinators in potentially providing pollination ecosystem services to tropical crops.

Author Contributions

Guaraci Duran Cordeiro: conceptualization, methodology, data curation, investigation, formal analysis, writing – original draft, writing – review and editing, validation, software. **Paulo Milet-Pinheiro:** conceptualization, methodology, data curation, investigation, validation, formal analysis, writing – original draft, writing – review and editing, software. **Liedson Tavares Carneiro:** data curation, investigation, writing – original draft, writing – review and editing, validation. **Daniela Maria do Amaral Ferraz Navarro:** writing – review and editing, resources. **Stefan Dötterl:** conceptualization, methodology, software, data curation, investigation, validation, formal analysis, supervision, funding acquisition, project administration, resources, writing – original draft, writing – review and editing. **Isabel Alves-dos-Santos:** conceptualization, methodology, data curation, investigation, validation, supervision, funding acquisition, project administration, resources, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15050665.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.