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ARTICLE

Anthropic action affects the cuticular chemical profile of social wasps

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Abstract. As a result of environmental change by anthropic action, animal species that inhabit these areas may suffer the effects of it on their phenotypes as a consequence of adapting to these conditions. In the case of social wasps, cuticular chemical compounds may be influenced, since these vary depending on genetic and environmental factors. However, few studies have investigated the synanthropic effects over the cuticular surface of social wasps. Therefore, the aim of this study was to investigate how cuticular compounds vary according to the different degrees of human activity and test the hypothesis that cuticular compounds of social wasps are affected by the level of anthropic activity in which their nests are found. Data on the cuticular chemical compounds composition of colonies of 3 species of social wasps were used along with the level of anthropization of their nesting sites in four municipalities in the state of Mato Grosso do Sul, Brazil. From the geographical coordinates of the sampling sites, the percentages of urban construction areas, agriculture, water body, vegetation and exposed land were calculated, and the nesting sites of the colonies were classified as more or less anthropized areas. The chemical profile was determined by extraction of cuticular compounds and analyzed by Gas Chromatography coupled to Mass Spectrometer (GC-MS). The results show that the cuticular chemical composition of the individuals of these species is affected by the level of anthropization in their nesting sites, with a qualitative and quantitative variation that must be tied not only to genetic differences, but, above all, to the local environmental conditions to which their colonies are subjected.

Keywords. *Polistes versicolor; Polybia paulista; Polybia occidentalis;* Anthropization; Chemical signature.

INTRODUCTION

Currently, ecosystems are facing unprecedented environmental changes, in which deforestation and the introduction of invasive species are the most common anthropic actions for land conversion, especially for agricultural cultivation (Tylianakis *et al.,* 2008; Sih *et al.,* 2011).

In Brazil, the Instituto Brasileiro de Geografia e Estatistica (IBGE, 2018) reported that between 2000 and 2016 there was an increase of 40% of the areas destined for agricultural production. In addition, intensive land use has commonly been associated with the decline in biodiversity (Huston, 2005), because with increased use for agricultural crops and urban cover, patches of suitable habitat tend to become smaller and increasingly isolated (Luck & Wu, 2002).

Social insects make up a significant part of the biomass and biodiversity of our environments, developing interactions with a wide range of organisms, thus influencing the ecology and evolution of other organisms (Wilson, 1990). On the other hand, they are also affected by other organisms,

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including humans, which should affect the evolution of several characteristics of their biology (Fisher *et al.,* 2018).

Social wasps are the group, among social insects, with the least amount of information regarding the consequences that environmental impacts cause in their colonies (Fisher *et al.,* 2018). One proof of that is that until 2020 no species were on the Red List of the International Union for Conservation of Nature and Natural Resources (IUCN, 2021). On the other hand, it is important to understand what anthropic actions can generate on social wasps' colonies, since they are important in the ecological maintenance of environments (Prezoto *et al.,* 2008, 2016), being important in the control of phytophagous insects in natural and agricultural environments (Prezoto & Machado, 1999; Southon *et al.,* 2019; Brock *et al.,* 2021) and as pollinators (Clemente *et al.,* 2012; Hallett *et al.,* 2017).

Among the few studies that have used social wasps as bioindicators are those of Souza *et al.* (2010) who evaluated the degree of forest conservation through the diversity of social wasps, Michelutti *et al.* (2013) who assessed how anthropic activities can affect the productivity of colonies of a wasp species and Graça & Somavilla (2019) who analyzed how forest fragmentation can affect the populations of these insects.

Fisher *et al.* (2018) assessed the resilience of social insects in face of drastic global changes such as climate change, deforestation, invasive species introduction and land conversion. The authors concluded that the same adaptations responsible for the diversity and ecological dominance of social insects (chemical coordination of cooperative behavior and nest architecture, for example) can also make them more vulnerable in the face of drastic environmental changes.

One of the most important factors that explain the evolutionary success of social insects is how they manage to maintain the cohesion of their colonies through efficient communication, exchanging different types of signals, such as visual, tactile, sound and especially chemical. (Billen, 2006; Leonhardt *et al.,* 2016). Chemical signals are called semiochemicals (Abd El-Ghany, 2019), which can be called pheromones when they are compounds involved in intraspecific communication. Among the most important compounds to maintain the cohesion of the colonies, therefore acting as pheromones, are the cuticular hydrocarbons (CHCs) which have been received greater attention in recent decades (Blomquist & Bagnères, 2010a).

In social insects, CHCs are compounds used in the recognition of conspecifics signaling their caste, age, physiological status, among others (Bagneres *et al.,* 1996; Provost *et al.,* 2008). Studies show that these compounds may vary according to genetic factors (Ratnieks, 1991; Page *et al.,* 1991), but also due to environmental factors (Ratnieks, 1991; Singer *et al.,* 1998; Etges & Ahrens, 2001).

Indeed, adaptations to local environmental conditions can lead to significant variation of cuticular chemical compounds in social wasps and ants (Dapporto *et al.,* 2004a, b; Dapporto *et al.,* 2009; Menzel *et al.,* 2017). As a result, variations in the CHC profiles of social wasps may be important as a biogeographic tool, since significant differences are found between the CHCs profiles of different social wasp populations (Dapporto *et al.,* 2004b; Bonelli *et al.,* 2015; Ferreira *et al.,* 2017).

Although there is currently growing concerned about the effects of human activity on several biological aspects of biodiversity, few studies have already evaluated this issue in social wasp colonies (Michelutti *et al.,* 2013; Oliveira *et al.,* 2017; Torres *et al.,* 2014; Graça & Somavilla, 2019). Moreover, none to date has evaluated the effects of anthropic activity on the cuticular chemical compounds of social wasps. Thus, the aim of this study was to investigate how cuticular compounds vary according to the different degrees of human activity and test the hypothesis that cuticular compounds of social wasps are affected by the level of anthropic activity in which their nests are found.

MATERIAL AND METHODS

Sample collection

Colonies of three species of social wasps nested in different areas of four municipalities in the State of Mato Grosso do Sul, Brazil, were collected from 2014 to 2017. Species, number of colonies sampled, collection sites and their respective geographic coordinates are detailed in Table 1. Colonies were collected with their nests using plastic bags containing a cotton wetted with ether. The nests were wrapped and after a few minutes the wasps were anesthetized, and the nests were detached from the substrate where they were fixed. The cotton was then removed to prevent the degradation of the chemical compounds. In the laboratory, the wasps were stored individually in

Table 1. Species, number of colonies, collection sites with the respective sampled points in the different municipalities of Mato Grosso do Sul state.

Species	Colonies (n)	Area feature	Collection municipalities	Geographic coordinate	Sampling
Polistes versicolor	3	Less anthropized	Dourados point 1	22°11′51.0″S; 54°55′48.8″W	DDS1
	1	More anthropized	Dourados point 2	22°12′35.8″S; 54°47′13.9″W	DDS2
	2	More anthropized	Mundo Novo point 1	23°56′08.3″S; 54°17′04.1″W	MN1
	1	More anthropized	Mundo Novo point 2	23°55′20.1″S; 54°17′08.0″W	MN2
Polybia paulista	1	More anthropized	Dourados point 2	22°12′35.8″S; 54°47′13.9″W	DDS2
	1	Less anthropized	Ivinhema	22°21′16.6″S; 53°45′31.9″W	IVIN
	2	More anthropized	Mundo Novo point 2	23°55′20.1″S; 54°17′08.0″W	MN2
Polybia occidentalis	2	Less anthropized	Dourados point 1	22°11′51.0″S; 54°55′48.8″W	DDS1
	2	Less anthropized	Ivinhema	22°21′16.6″S; 53°45′31.9″W	IVIN
	1	More anthropized	Ponta Porã	22°33′51.1″S; 55°41′24.7″W	PP

Eppendorf, frozen, and stored in a freezer (-20°, Brand: METALFRIO, Model: VF55DB) until the chemical analysis.

Analysis of the degree of anthropic activity of nesting environments based on land use and occupation

From the geographical coordinates of the collection points of the three wasp species, the land use and occupation were quantified and qualified. The variables were determined through an unsupervised classification, performed with Geographic Information System (GIS), using SENTINEL 2 images with a resolution of 10 meters. To limit the study areas, buffers of 1 km radius were generated around each sampling point. This measure was based on the foraging range of the social wasps already studied, which is approximately 900 m (Gobbi, 1978; Santos *et al.,* 2001). The forms of land use and occupation were classified as: Urban constructions; Agriculture; Water body; Vegetation and Exposed land (adapted from the IBGE, 2013 definition).

For interpretation of the images, the unsupervised classification was performed using the classification tools provided by the software and calculating the areas and percentages for each class of buffers. All data were processed using the ArCgis®, version 10.3.

Extraction of cuticular compounds and Gas Chromatography Coupled to Mass Spectrometer (CG-MS) Analysis

For the extraction of chemical compounds from the wasps' cuticle, the whole individual was used, being immersed in 2 mL hexane (HPLC Grade, TEDIA) for 2 minutes. The cuticular compounds were extracted from 15 wasps from each colony, categorized as older according to the methodology described by Richards (1971), in which wasps with relatively darker apodeme would be older in the colony. All extracts were dried under fume hood and later solubilized in 200 µL hexane (HPLC Grade, TEDIA) for analysis by Gas Chromatography coupled to Mass Spectrometer (GC-MS).

All samples were analyzed using a gas chromatograph (GC-2010 Plus, Shimadzu, Kyoto, Japan) coupled to a mass spectrometer (GC-MS Ultra 2010, Shimadzu, Kyoto, Japan) using a DB-5 fused silica capillary (J and W, Folsom, California, USA) with 5% of phenyl dimethylpolysiloxane on capillary fused silica (30 m long × 0.25 mm internal diameter × 0.25 µm film thickness). For analysis using gas chromatography coupled to mass spectrometry (GC-MS), the dried samples were solubilized by vortexing in 200 µL of hexane and then transferred to vials. The conditions of analysis were heating ramp with initial temperature of 150°C, reaching 280°C at 3°C/min and remaining at the final temperature for 10 min. Helium (99.999%) was used as drag gas (1 mL/min), and injections were 1 µL in splitless mode. The injector, detector and transfer line temperatures were 250°C, 250°C and 290°C, respectively. Scanning parameters of the mass spectrometer included electron beam ionization voltage of 70 eV, with m/z 40-600 and scanning range of 0.3 s (Duarte *et al.,* 2019). The identification of the compounds was performed using the calculated retention index (van Den Dool & Dec. Kratz, 1963), employing a mixture of linear alkanes (C_7-C_{40}, Sigma Aldrich with purity ≥ 90%) as an external reference in relation to the retention index of the literature (Jackson, 1983; Bonavita-Cougourdan *et al.,* 1991; Brown *et al.,* 1991; Meskali *et al.,* 1995; Lorenzi *et al.,* 1997; Sevala *et al.,* 2000; Howard, 2006; Howard *et al.,* 2006; Kaib *et al.,* 2004; Zhu *et al.,* 2006; Yusuf *et al.,* 2010; Ruther *et al.,* 2011; Tokoro & Makino, 2011; Weiss *et al.,* 2014; Bonelli *et al.,* 2015; Silva *et al.,* 2016; Michelutti *et al.,* 2017, 2018; Soares *et al.,* 2017) and associated with the interpretation of the mass spectra obtained from the samples and compared with the databases (NIST21 and WILEY229).

After the identification of the compounds, a table was made with the respective means of the relative percentage areas of each compound present in the samples. These data were used for statistical analysis. Compounds that represented at least 5% of the mean relative percentage area were considered major compounds.

Statistical analyses

A cluster analysis was applied using the percentage values of land use and occupation types in order to classify the environments, using the Euclidean distance and the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) method for the construction of a dendrogram. To evaluate whether this dendrogram reflects the similarity matrix between environments, the cophenetic correlation coefficient was used, defining the minimum value of 0.75 as a measure of the quality of the dendrogram adjustment (McGarigal *et al.,* 2000). Based on the grouping formed and the analysis of the percentage of urban construction areas, the environments were classified as: "more anthropized" when it presented a percentage above 50% of constructions and "less anthropized" with a percentage below 50%.

A multivariate analysis of permutational variance (PERMANOVA) was applied using the values of the relative percentage areas of all peaks to test whether there are significant differences between the colonies nested in the more or less anthropized environments. The Bray-Curtis index was used to generate the similarity matrix and the significance of the commutations was calculated from the randomization of the original matrix (999 permutations). Then, a cluster analysis was applied following the parameters mentioned above using the species/environmental categories as a predictor variable and the relative percentage areas of the compounds that had relative percentage > 1% as response variable, in order to identify the similarity and/or differences between the groups.

Finally, Detrended Correspondence Analyses (DCA) were performed using the values of each wasp species, with the environmental categories as a predictor variable and the cuticular hydrocarbons (only compounds that had relative percentage > 1%) as a response variable, in order to identify which compounds are most characteristic of the cuticle of wasps whose colonies were nested in environments with different degrees of anthropic activity. All analyses were performed in the statistical software Past version 3.22 (Hammer *et al.,* 2001).

RESULTS

As results, our analysis of the degree of anthropic activity of nesting environments showed that areas around the collected points represent many different land use and occupation soil, that correspond: agriculture, exposed soil, urban construction, vegetation or water body (Fig. 1). At six of the collection points, four of them (66,66%) have soil with more than 50% of urban constructions which were categorized as "more anthropized" while two points (IVIN, DDS1) had larger areas with vegetation and less urban constructions categorized as "less anthropized" (Fig. 1). The type of land cover most common in all areas were urban construction and the smallest were water bodies.

According to the cluster analysis, based on the degree of anthropic activity, we can observe two main clusters. The first encompassing MN1, PP, DDS2 and MN2, whose areas correspond to "more anthropized" and the second group encompasses IVIN and DDS1, whose areas are "less anthropized" environments (Fig. 2).

The peaks detected in all samples with concentration greater than 1% are described in Table 2. In the samples of *P. versicolor,* in more anthropized environments, a total of 167 peaks were detected, of these 120 were identified, with 70.83% of branched alkanes, 15% of linear alkanes and 14.17% of alkenes. Two peaks were exclusive to this environment, 4-methylheneicosane and 3,13-dimethylheptacosane. In the samples collected in less anthropized environments, 131 peaks were detected, of these 109 were identified, with 66.97% of branched alkanes, 17.43% of linear alkanes, 14.68% of alkenes and 0.92% of alkadienes. Seven compounds (heptadecane, octadecane, 9-methylnonadecane, x-eicosene, 5-methylheneicosane, 11-methyltricosane and x-pentacosene) were exclusive to the samples of this environment. Forty-three peaks are shared by samples of both types of environments (Fig. 3a and Table 2).

For the samples of the species *P. paulista* collected in more anthropized environments, 135 peaks were detected and of these, 82 were identified, 68.29% of them being branched alkanes, 19.51% linear alkanes and 12.20% alkenes. Eight peaks are exclusive to these samples: octadecane, nonadecane, eicosane, heneicosane, x-methylheneicosane, 9,13-dimethylnonacosane, 11,15-di-

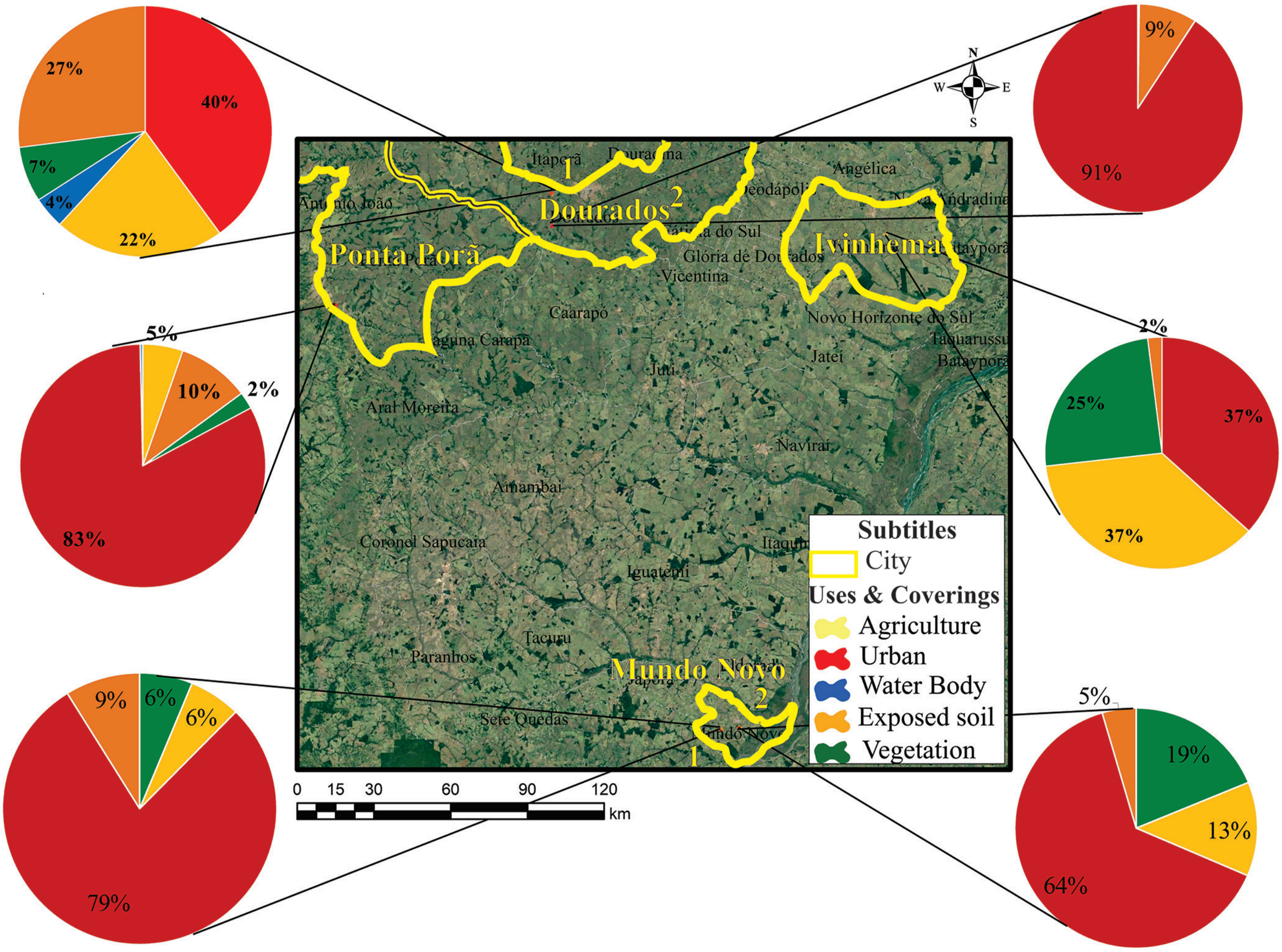

Figure 1. Satellite image showing the places in the municipalities where the colonies of the 3 social wasp species were nesting and, the percentages (pie charts) of the different types of land use and occupation (adapted from the IBGE, 2013 definition). Number 1 and 2 indicates the two collection points in the same city.

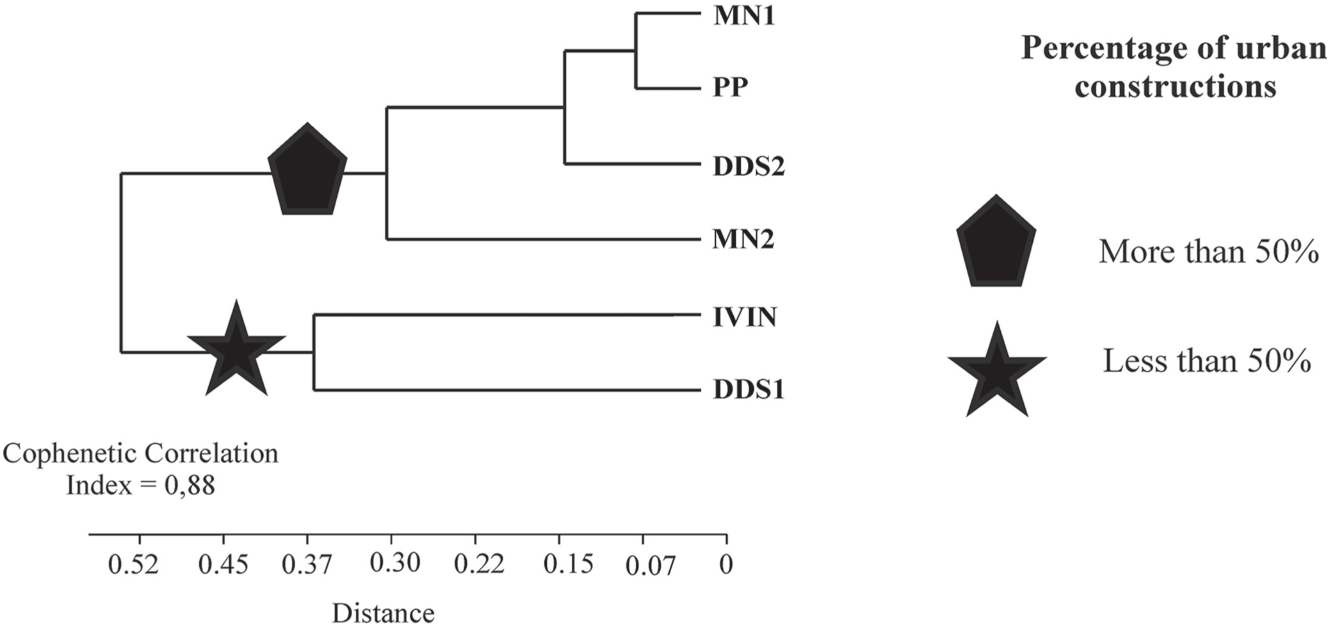

Figure 2. Similarity dendrogram generated based on the percentages of different types of land use in the municipalities where the colonies of the 3 species of social wasps were sampled. Pentagon: more anthropized areas. Star: less anthropized areas. DDS1: Dourados point 1; DDS2: Dourados point 2; IVIN: Ivinhema; MN1: Mundo Novo point 1; MN2: Mundo Novo point 2; PP: Ponta Porã.

methylnonacosane and 11-methylhentriacontane. In the samples collected in less anthropized environments, 94 peaks were detected and of these, 60 were identified, 68.33% of them branched alkanes, 18.33% linear alkanes and 13.33% alkenes. The compound 11-methyltricosane is exclusive to these samples. Thirty-seven peaks are shared between the samples of the two types of environments (Fig. 3b and Table 2).

As for the *P. occidentalis* samples from the most anthropized environments, 145 peaks were detected, of these 102 were identified, 69.61% being branched alkanes, 17.65% linear alkanes, 11.76% alkenes and 0.98% alkadienes. Only 11,15-dimethylnonacosane is exclusive to these samples. In the samples of this species collected in less anthropized environments, 44 peaks were detected and identified, 63.64% of which were branched alkanes, 29.54% linear alkanes and 6.82% alkenes. Twenty-one compounds are exclusive to the samples of this environment: 16 branched alkanes, three linear alkanes, one alkene and one unidentified compound. Twenty-eight compounds are shared by samples of both types of environments (Fig. 3c and Table 2).

In general, the relative abundance of the classes of compounds varies little in the 3 species in both types of

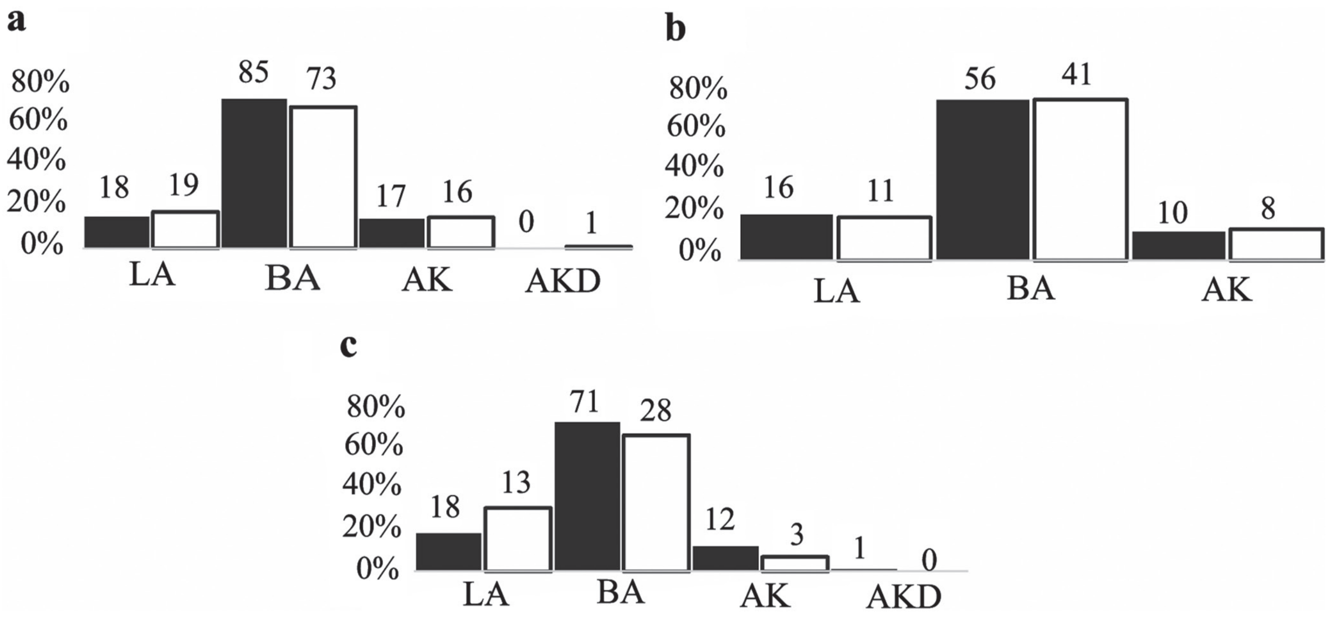

Figure 3. Bar charts showing the relative abundance and number of compounds belonging to the different classes of cuticular hydrocarbons present in the samples of *Polistes versicolor* (A), *Polybia paulista* (B) and *Polybia occidentalis* (C) whose colonies were nesting in more anthropized environments (black box) and less anthropized (white box). LA = Linear Alkanes, BA = Branched Alkanes, AK = Alkenes, ALD = Alkadienes.

Table 2. Average percentage and standard deviation (M ± SD) of peaks (> than 0.1%) for the species of social wasps *Polistes versicolor, Polybia paulista* and *Polybia occidentalis* collected in more anthropized and less anthropized environments. Abundances in bold = major peaks that have a relative abundance above 5%; TR = Relative abundance < 1%; NI = Not identified.

Index calculated	Peak identification	*Polistes versicolor*		*Polybia paulista*		*Polybia occidentalis*	
		More anthropized	Less anthropized	More anthropized	Less anthropized	More anthropized	Less anthropized
1500	Pentadecane	TR	0.16 ± 0.40	—	—	5.20 ± 5.83	2.44 ± 3.07
1613	x-Methylhexadecane	TR	0.30 ± 0.65	—	—	**9.38 ± 4.85**	2.72 ± 4.06
1700	Heptadecane	—	0.45 ± 0.85	—	—	—	2.72 ± 5.09
1715	x-Methyheptadecane	—	—	—	—	2.40 ± 0.97	0.39 ± 0.78
1800	Octadecane	—	1.78 ± 3.26	TR	—	**24.03 ± 7.90**	**19.03 ± 24.17**
1900	Nonadecane	TR	TR	0.16 ± 0.86	—	1.16 ± 0.36	0.28 ± 0.52
1932	9-Methylnonadecane	—	0.30 ± 0.59	—	—	0.11 ± 0.20	1.02 ± 2.08
1965	4-Methylnonadecane	0.67 ± 2.03	TR	0.18 ± 0.29	2.77 ± 3.86	—	0.11 ± 0.12
1990	x-Eicoseno	—	TR	0.13 ± 0.31	TR	—	1.23 ± 1.97
2000	Eicosane	TR	TR	TR	—	1.55 ± 0.54	0.61 ± 0.82
2100	Heneicosane	0.15 ± 0.37	TR	0.64 ± 2.78	—	1.37 ± 1.32	TR
2139	9-Methylheneicosane	1.39 ± 2.35	0.23 ± 0.53	—	—	—	—
2150	5-Methylheneicosane	—	0.16 ± 0.34	1.09 ± 1.83	0.56 ± 1.75	—	0.13 ± 0.41
2156	4-Methylheneicosane	1.47 ± 5.27	—	—	—	—	0.33 ± 1.11
2160	2-Methylheneicosane	0.64 ± 0.67	0.12 ± 0.26	1.12 ± 1.44	1.40 ± 1.49	—	0.69 ± 1.70
2170	3-Methylheneicosane	—	—	2.74 ± 2.79	**7.08 ± 4.24**	—	3.90 ± 6.25
2174	x-Methylheneicosane	TR	0.21 ± 0.64	**10.25 ± 23.82**	—	—	—
2182	x-Docosene	—	—	TR	TR	1.29 ± 0.43	0.44 ± 0.95
2274	Tricosadiene	**5.93 ± 4.27**	1.68 ± 2.18	—	—	0.11 ± 0.12	TR
2300	Tricosane	0.72 ± 1.04	0.48 ± 0.92	2.49 ± 6.00	0.71 ± 1.56	2.77 ± 2.70	0.41 ± 1.03
2323	11-Methyltricosane	—	1.29 ± 2.59	—	TR	0.20 ± 0.23	0.11 ± 0.18
2400	Tetracosane	TR	1.98 ± 3.85	TR	TR	0.76 ± 0.31	0.11 ± 0.14
2496	x-Pentacosene	—	1.87 ± 3.79	TR	TR	—	—
2500	Pentacosane	0.24 ± 0.25	0.18 ± 0.26	2.81 ± 6.83	0.43 ± 0.30	0.95 ± 0.30	0.95 ± 1.81
2552	5-Methylpentacosane	0.46 ± 0.57	0.38 ± 0.68	1.36 ± 0.66	0.76 ± 0.61	1.74 ± 0.49	1.72 ± 3.07
2573	3-Methylpentacosane	0.16 ± 0.23	1.78 ± 3.23	0.53 ± 0.77	0.40 ± 0.19	0.44 ± 0.51	1.15 ± 1.73
2700	Heptacosane	0.62 ± 0.58	1.04 ± 0.77	**7.09 ± 3.62**	4.34 ± 1.19	4.87 ± 1.05	**11.8 ± 8.01**
2732	13-Methylheptacosane	—	—	2.71 ± 3.22	2.36 ± 1.64	—	—
2735	11-Methylheptacosane	0.12 ± 0.15	0.31 ± 0.51	1.10 ± 1.01	4.05 ± 3.18	2.99 ± 2.97	2.89 ± 2.57
2749	5-Methylheptacosane	TR	TR	0.62 ± 0.51	1.51 ± 0.75	0.68 ± 0.82	0.45 ± 0.39
2772	3-Methylheptacosane	1.12 ± 0.56	1.33 ± 1.02	4.00 ± 2.26	**5.33 ± 1.48**	3.47 ± 1.64	2.32 ± 1.59
2800	Octacosane	0.79 ± 1.48	2.34 ± 3.73	0.91 ± 0.54	0.56 ± 0.24	0.26 ± 0.38	2.10 ± 1.17
2807	3.13-Dimethylheptacosane	—	—	0.69 ± 0.70	2.09 ± 1.94	—	—
2811	3.11-Dimethylheptacosane	0.38 ± 1.03	—	—	—	1.13 ± 1.62	1.63 ± 3.08
2835	12-Methyloctacosane	0.90 ± 0.80	0.67 ± 1.41	1.86 ± 1.18	1.69 ± 0.87	1.10 ± 1.06	1.39 ± 1.48
2860	2-Methyloctacosane	1.55 ± 4.20	3.62 ± 7.81	—	—	—	TR
2900	Nonacosane	4.76 ± 2.64	**6.11 ± 4.50**	**7.81 ± 4.00**	**6.06 ± 2.18**	4.78 ± 1.83	4.48 ± 3.39
2931	15-Methylnonacosane	0.66 ± 0.96	1.57 ± 1.89	—	—	**14.72 ± 4.53**	2.70 ± 5.08
2935	9-Methylnonacosane	2.37 ± 2.48	2.97 ± 3.15	**16.45 ± 8.97**	**19.8 ± 4.65**	—	**6.13 ± 6.57**
2958	13.17-Dimethylnonacosane	0.26 ± 0.16	0.36 ± 0.22	0.76 ± 0.68	0.83 ± 0.17	0.22 ± 0.49	1.16 ± 1.26
2962	9.13-Dimethylnonacosane	2.36 ± 5.59	3.36 ± 6.67	1.03 ± 2.19	—	—	—
2964	11.15-Dimethylnonacosane	0.23 ± 0.68	**5.09 ± 5.72**	0.15 ± 0.31	—	2.14 ± 0.75	—
2975	3-Methylnonacosane	**9.64 ± 5.23**	3.17 ± 4.49	2.39 ± 2.28	2.90 ± 0.87	—	0.91 ± 0.98
2980	5.15-Dimethylnonacosane	—	—	0.40 ± 0.34	1.43 ± 0.69	—	—
3000	Triacontane	0.46 ± 0.17	0.39 ± 0.43	2.85 ± 1.35	4.73 ± 1.64	2.46 ± 1.14	0.22 ± 0.31
3034	10-. 11-. 12-. 13- and 14-Methyltriacontane	0.34 ± 0.22	0.71 ± 0.46	0.87 ± 0.80	1.51 ± 0.46	—	0.14 ± 0.26
3074	3-Methyltriacontane	2.73 ± 2.41	0.86 ± 1.29	TR	TR	—	0.14 ± 0.79
3097	NI	—	—	0.35 ± 0.54	3.10 ± 2.97	—	1.67 ± 3.06
3100	Hentriacontane	3.31 ± 2.96	3.38 ± 3.92	2.56 ± 2.56	1.50 ± 1.98	—	0.80 ± 1.69
3119	11-Methylhentriacontane	TR	TR	2.63 ± 5.00	—	—	—
3132	15-Methylhentriacontane	**12.37 ± 6.22**	**19.06 ± 11.39**	**5.90 ± 5.31**	**9.13 ± 2.01**	3.58 ± 1.61	0.89 ± 1.30
3148	5-Methylhentriacontane	2.88 ± 9.47	1.60 ± 1.52	—	—	—	0.16 ± 0.47
3162	11.19-Dimethylhentriacontane	1.28 ± 6.65	0.31 ± 0.45	0.15 ± 0.26	0.12 ± 0.12	—	0.10 ± 0.32
3172	3-Methylhentriacontane	3.32 ± 2.16	1.14 ± 1.96	0.15 ± 0.18	0.12 ± 0.13	—	TR
3200	Dotriacontane	0.51 ± 0.52	0.92 ± 0.87	0.74 ± 0.52	1.08 ± 0.28	—	TR
3228	14- and 16-Methyldotriacontane	1.48 ± 1.26	1.01 ± 0.77	0.16 ± 0.18	0.16 ± 0.10	—	0.10 ± 0.29
3338	7-Methyltritriacontane	**18.58 ± 10.89**	**12.76 ± 10.08**	0.48 ± 0.74	0.52 ± 0.32	—	—
3365	11.15-Dimethyltritriacontane	1.27 ± 1.35	0.84 ± 0.97	0.18 ± 0.32	TR	—	0.30 ± 0.53
3530	11- 13- 15- and 17-Methylpentatriacontane	1.12 ± 1.11	0.30 ± 0.38	—	—	—	TR

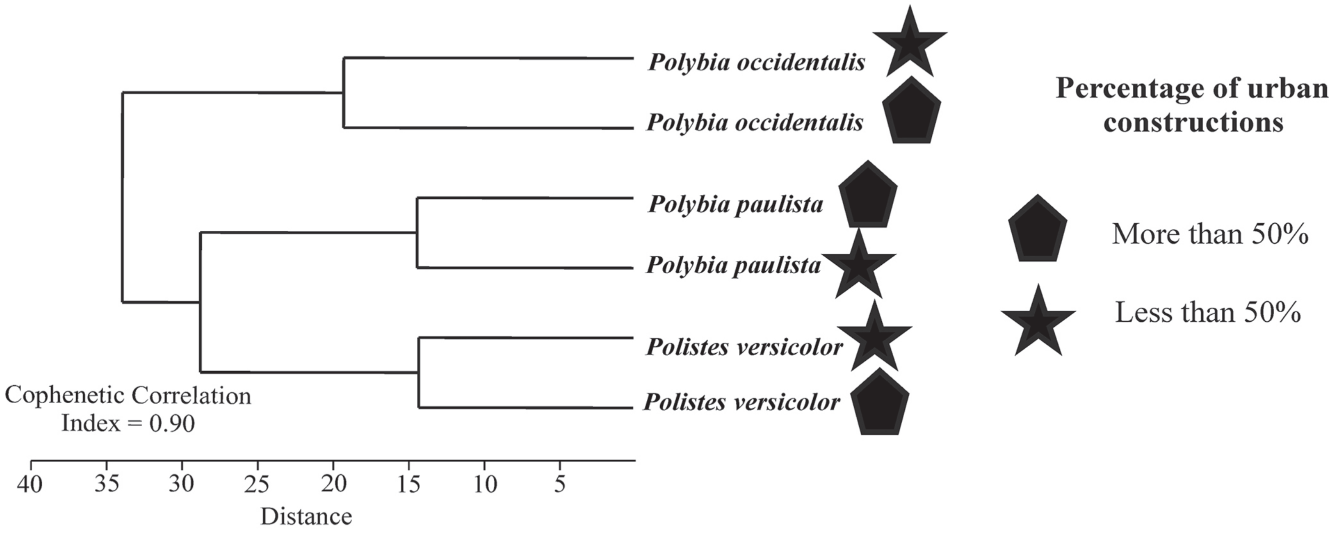

Figure 4. Similarity dendrogram based on the cuticular hydrocarbon profile of the samples of the 3 species whose colonies were nested in two types of environments. Pentagon: more anthropized areas. Star: less anthropized areas.

environments, except for the linear alkanes of *Polybia occidentalis,* which in the less anthropized environment have almost twice as many linear alkanes compared to the more anthropized environments. However, by comparing the number of compounds of the samples, branched alkanes, linear alkanes and alkenes presented higher number in more anthropized environments than in less anthropized environments, except in *P. versicolor* samples which have the number of linear alkanes similar in more anthropized environments and which presents 1 alkadiene in samples from a less anthropized environment (Fig. 3).

The non-parametric permutation analysis shows that there are significant differences between the composition of CHCs of the 3 species from the two types of environment: *P. versicolor* (Pseudo-$F_{(5\cdot 34358)} = 6.54$; $p < 0.01$), *P. paulista* (Pseudo-$F_{(5\cdot 34358)} = 3.29$; $p < 0.01$) and *P. occidentalis* (Pseudo-$F_{(5\cdot 34358)} = 5.96$; $p < 0.01$). The cluster analysis (Fig. 4) shows that the cuticular composition of the different samples of the 3 species is grouped, primarily according to the species itself, but separate according to the type of environment.

The DCA analysis shows that, indeed, there are compounds that are more characteristic of a certain environment in relation to the other in the samples of the 3 species (Fig. 5).

DISCUSSION

According to our results, the cuticular composition of the samples from the 3 species vary significantly depending on the type of environment where the colonies are nested. Indeed, several studies show that there are variations of different phenotypic characteristics between different populations of a species, as a function of genetic differences, but also due to adaptations to the local environment (Miyanaga *et al.,* 1999; Weeks *et al.,* 2002). In particular, cuticular compounds may also vary depending on these two factors (Page *et al.,* 1991; Gamboa *et al.,* 1996).

Our results show that, there is a qualitative and quantitative variation in the composition of CHCs between the samples of the two types of environments in the three species (Table 2; Fig. 4), and in general a higher number of cuticular compounds in colonies belonging to more anthropized environments. Previous studies have shown that the composition of CHCs in colonies of social hymenopterans may vary specifically due to environmental factors (Dapporto *et al.,* 2004b; Blomquist & Bagnères, 2010b). Among the environmental variables that can influence chemical composition in different populations of a species are the types of food resources available (Liang & Silverman, 2000; Buczkowski *et al.,* 2005), climatic factors (Menzel *et al.,* 2017), the use of pollutants (Müller *et al.,* 2017; Sessa *et al.,* 2021; Hamida *et al.,* 2021; Schuehly *et al.,* 2021) and even the rate of parasitism (Lorenzi *et al.,* 2014).

This variation is more noticeable, for example in the samples of *P. paulista* and *P. occidentalis* that have higher number of linear and branched alkanes in more anthropized environments. The variation found between the chemical composition of the species and more anthropized environments can be explained, in part, by the fact that less anthropized environments have a more complex vegetation structure, which provides more stable microclimatic conditions, such as temperature and humidity (Lawton, 1983).

A higher number of linear alkanes in environments with less stable microclimatic conditions might be advantageous, as these compounds are known to play a primary role in protecting against insect desiccation by having a higher melting point compared to the other classes, such as branched alkanes. The highest melting point of linear alkanes is important because it influences the semi-fluid characteristic of the cuticle, the less fluid, the greater the protection against water loss (Gibbs, 2002; Gibbs & Rajpurohit, 2010). The higher content of linear alkanes in the cuticle of these wasps may influence the melting range (Menzel *et al.,* 2019) and viscosity of their cuticle (Sprenger *et al.,* 2018), providing adaptive

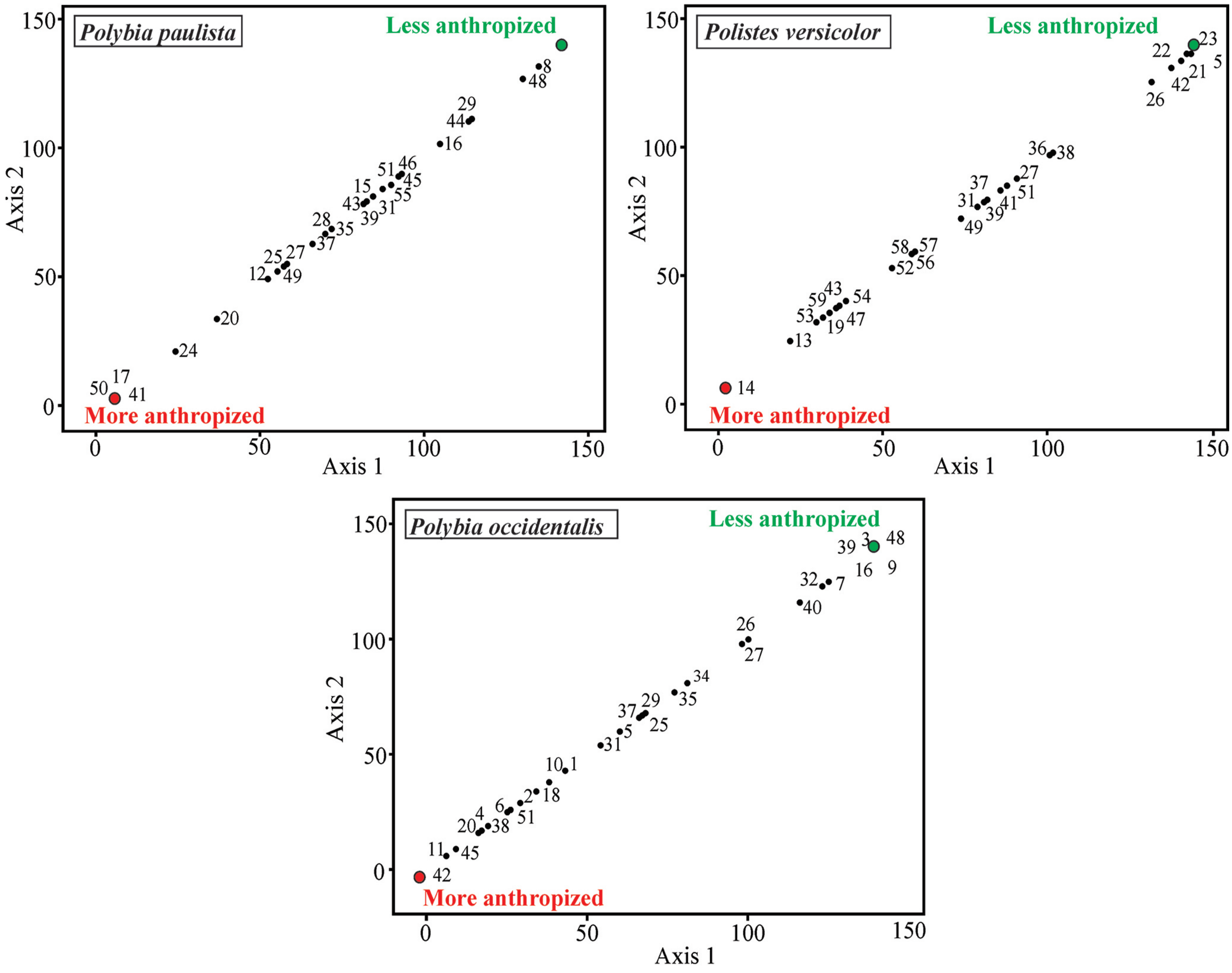

Figure 5. Ordering by Detrended Correspondence Analyses (Axes 1 and 2) based on the cuticular hydrocarbon profile of the samples of the 3 species whose colonies were nested in two types of environments. The points on Axis 1, between 0 and 50 on the left, represent compounds more characteristic of samples from more anthropized environments and between 100 and 150 on the right, from less anthropized environments.

value in response to the climatic variations in less stable environment (Sprenger & Menzel, 2020).

In this sense, even though these species could eventually nest in eaves of human constructions, they were more susceptible to the temperature variation imposed by the environment, different from the wasps nesting in less anthropized environments. In this type of environment, colonies were nested in plants, among the leaves and protected by the shading provided by the vegetation cover.

On the other hand, alkenes were found in the samples of all species regardless of the nesting environment. These compounds typically have a lower melting point compared to linear and branched alkanes (Gibbs & Pomonis, 1995), making the cuticle more fluid, even at room temperature (Menzel *et al.,* 2019). The presence of this class of compound is important because, together with the other classes that form the cuticle, they increase its melting range and also influence its viscosity, but also to ensure efficiency in the performance of other functions performed by cuticular composition (Gibbs, 2002; Menzel *et al.,* 2019), such as communication (Blomquist & Bagnères, 2010), cuticle lubrication (Cooper *et al.,* 2009) and protection against microorganisms (Howard & Blomquist, 2005; Turillazzi *et al.,* 2006).

We must also consider that the variation of compounds between one environment and another may also be tied to differences in the types and abundance of resources, both food and for the construction of their nests. For example, the diversity of plant species and potential prey in more anthropized environments is lower than in less anthropized environments (Oliveira *et al.,* 2017). In addition, as a direct consequence of the habitat degradation caused by humans, even in environments where buildings predominate, the foraging sites around the colony consist mainly of grasses, which can determine a lower supply of resources when compared to places where the original vegetation is preserved (Gould & Jeanne, 1984).

Another important factor to take in consideration is the variation of the compounds due to the differences in materials available for the construction of the nests, since they use material rich in cellulose from plants (Singer *et al.,* 1992). It is known that part of the cuticular composition of these insects is acquired by contact with the nest material (Pfennig *et al.,* 1983; Singer & Espelie, 1992).

Therefore, the differences in the material found for nest construction in less and more anthropized environments should account for this variation. Actually, although the nesting site chosen by social wasps is due to abiotic conditions (Dejean *et al.,* 1998; Klingner *et al.,* 2006) and also protection against predators and parasites (Gibo, 1978), it is also possible to be due to the compounds that can be part of the chemical signature of the colony (Sguarizi-Antonio *et al.,* 2021), but this hypothesis still needs more evidence.

Social wasps use plant resources available in the environment to build their nests (Wenzel, 1980). In this sense, the similarity of the chemical composition between nest and colony members is already well reported in the literature (Espelie *et al.,* 1990; Espelie & Hermann, 1990; Layton & Espelie, 1995; Gamboa *et al.,* 1996; Lorenzi *et al.,* 2004; Sumana *et al.,* 2005; Sguarizi-Antonio *et al.,* 2017). Social wasps also use the nectar and potential prey available in these environments as a resource for their colonies (Oliveira *et al.,* 2017), both factors that can directly influence the colonial profile (Espelie *et al.,* 1990; Liang & Silverman, 2000).

Pollution by heavy metals can also affect metabolic processes and indirectly the cuticular chemical composition. The presence of lead in larvae, pupae, adults and in the meconium of *Polistes dominulus* colonies has already been detected, this contaminant showed a significantly higher concentration in urban environments than in rural environments (Urbini *et al.,* 2006). However, effects from contamination by environmental pollutants on the CHC composition of social wasps are still rare.

Although, insect contact with pesticides can also indirectly influence the chemical composition of social wasps. In fact, changes in the cuticular chemical profile caused by these contaminants have been recently reported in some species of insects. (Müller *et al.,* 2017; Sessa *et al.,* 2021; Hamida *et al.,* 2021), including in *Apis mellifera* (Schuehly *et al.,* 2021) Pesticide contamination can increase the response of detoxification enzymes such as cytochrome P450, which is also involved in CHC synthesis (Nelson, 2018; Yan & Liebig, 2021). Therefore, the detoxification induced in response to pesticides can alter the synthesis of CHC and be another factor that helps to explain the differences found between the environments, however this hypothesis also needs to be properly investigated.

CONCLUSION

Our results allow us to confirm the hypothesis that cuticular compounds of social wasps are affected by the level of anthropic activity in which their colonies are nested and that wasps belonging to anthropic areas had a higher amount of CHC than wasps collected in more preserved areas. This effect on chemical composition can be mainly explained as a result of abiotic and biotic factors that wasp colonies face due to human occupation (such as unstable microclimatic conditions) and the decrease in forest areas caused by it.

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