UNIVERSIDADE FEDERAL DO MARANHÃO
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E BIOTECNOLOGIA – REDE BIONORTE

DISTRIBUIÇÃO, RECURSOS E EFEITOS DAS MUDANÇAS CLIMÁTICAS SOBRE AS ABELHAS CARPINTEIRAS (APIDAE: XYLOCOPINI) EM ÁREAS DE TRANSIÇÃO, MARANHÃO, BRASIL

LUCIANO ANDRÉ CHAVES FERREIRA

São Luís – MA

2024

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Tese de doutorado apresentada ao Curso de Doutorado do Programa de Pós-Graduação em Biodiversidade e Biotecnologia – Rede BIONORTE, na Universidade Federal do Maranhão, como requisito parcial para a obtenção do Título de Doutor em Biodiversidade e Biotecnologia.

Orientadora: Prof. Dra. Patrícia Maia Correia de Albuquerque

Coorientadores: Prof. Dra. Tereza Cristina Giannini e Prof. Dr. Fernando César Vieira Zanella

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Dedico esta tese à memória de meu pai, o melhor amigo que já tive. Que Deus o tenha, amo você!

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Moisset e Buchmann

“We can do what we want
We can live as we choose
You see there is no guarantee
We've got nothing to lose”

(Paul McCartney)

FERREIRA, Luciano André Chaves. **Distribuição, Recursos e Efeitos das Mudanças Climáticas sobre as abelhas carpinteiras (Apidae: Xylocopini) em áreas de transição, Maranhão, Brasil.** 2024. 210 f. Tese (Doutorado em Biodiversidade e Biotecnologia) – Universidade Federal do Maranhão, São Luís, 2024.

RESUMO

As abelhas carpinteiras de grande porte exercem um papel crucial, em diferentes tipos de ecossistemas, atuando como agentes polinizadores de uma ampla variedade de espécies vegetais. O Maranhão se destaca por ser um ponto de convergência entre distintas fisionomias dos biomas Amazônia, Cerrado e Caatinga, tornando-o uma região com alto valor biológico e biogeográfico. Considerando que ainda não existe uma lista abrangente e organizada das espécies de *Xylocopa* encontradas nessas áreas de transição, o objetivo central desta tese foi revisar e atualizar os registros de ocorrência de *Xylocopa*, investigar a diversidade e os padrões de distribuição, além de identificar os recursos florais utilizados por elas, com foco tanto em cenários climáticos atuais quanto em cenários futuros, levando em conta as projeções de mudanças climáticas. As informações foram compiladas através de inúmeros inventários realizados neste território, além da consulta direta em coleções científicas (CEDU, CZMA, LEACOL, LESPP e MPEG), os quais contam com muitos registros não publicados. Foram listadas 12 espécies pertencentes a três subgêneros: *Xylocopa* (*Neoxylocopa*) *amazonica* Enderlein, 1913, *X.* (*N.*) *aurulenta* (Fabricius, 1804), *X.* (*N.*) *cearensis* Ducke, 1910, *X.* (*N.*) *frontalis* (Olivier, 1789), *X.* (*N.*) *grisescens* Lepeletier, 1841, *X.* (*N.*) *hirsutissima* Maidl, 1912, *X.* (*N.*) *nigrocincta* Smith, 1854, *X.* (*N.*) *transitoria* Pérez, 1901, *X.* (*Schonnherria*) *macrops* Lepeletier, 1841, *X.* (*S.*) *muscaria* (Fabricius, 1775), *X.* (*S.*) *subcyanea* Pérez, 1901 e *X.* (*Stenoxylocopa*) sp. n. Destas, duas espécies são reportadas como primeiros registros para o Maranhão (*X. hirsutissima* e *X. subcyanea*), uma para o Brasil (*X. transitoria*) e uma para a ciência (*X.* (*Stenoxylocopa*) sp. n. – ainda não publicada). As abelhas foram coletadas em 109 espécies de plantas, pertencentes a 77 gêneros e 36 famílias. Uma rede ditrófica com 193 interações demonstrou uma correlação significativa entre a abundância de abelhas coletadas e a riqueza de plantas visitadas. As espécies de abelhas generalistas foram *X. cearensis* (61,5% de todas as plantas observadas), *X. frontalis* (37,6%) e *X. nigrocincta* (22%). Em contraste, *X. aurulenta* e *X. amazonica* visitaram apenas duas espécies de plantas cada. As plantas com mais registros de visitação foram *Chamaecrista hispidula* (9,9% dos indivíduos), *C. ramosa* (9,2%) (Fabaceae) e *Passiflora foetida* L. (7,8%) (Passifloraceae). Com a utilização de modelos de distribuição de espécies para prever possíveis impactos das mudanças do clima, descobriu-se que dez das doze espécies de *Xylocopa* que ocorrem na região, potencialmente, enfrentarão uma redução de adequabilidade climática no período de 2041 a 2060. As espécies que ocorrem apenas em florestas tropicais serão as mais afetadas, como a *X. aurulenta* que poderá perder toda a sua área de ocorrência no Maranhão, mesmo no cenário mais otimista. Por outro lado, duas espécies se beneficiarão no futuro, *X. hirsutissima* aumentará cerca de 23% de sua área total de ocorrência no estado, enquanto *X. grisescens* se expandirá por mais da metade de sua área, cobrindo mais de 80% do Estado do Maranhão, em todos os cenários. Apesar das mudanças previstas, a *X. frontalis,* provavelmente, continuará sendo a espécie com a maior distribuição na região. Observou-se ainda que, embora as espécies de *Xylocopa* tenham distribuições desiguais, a maioria delas está concentrada nas áreas do norte do estado, muitas das quais são legalmente protegidas. Por outro lado, as demais áreas de adequabilidade futura, sem proteção, que incluem o Cerrado na parte sul do estado e as áreas de transição intermediária na região central, serão fundamentais para o movimento das espécies e necessitam da implementação de planos de manejo e práticas agrícolas amigáveis para garantir a disponibilidade de recursos e, em última análise, a conservação desses polinizadores.

Palavras-chave: Mamangava; biogeografia; sistemática; polinização; conservação.

FERREIRA, Luciano André Chaves. **Distribution, Resources and Effects of Climate Change on carpenter bees (Apidae: Xylocopini) in transition areas, Maranhão, Brazil.** 2024. 210 f. Tese (PhD in Biodiversity and Biotechnology) – Federal University of Maranhão, São Luís – MA, Brazil, 2024.

ABSTRACT

Large carpenter bees are crucial in different types of ecosystems, acting as pollinators for a wide variety of plant species. Maranhão stands out as a point of convergence between different physiognomies of the Amazon, Cerrado and Caatinga biomes, making it a region of high biological and biogeographic value. Considering that there is still no comprehensive and organized list of *Xylocopa* species found in these transitional areas, the central objective of this thesis was to review and update the records of *Xylocopa* occurrence, study diversity and distribution patterns, and identify the floral resources used by them, with a focus on both current and future climate scenarios, taking into account climate change projections. The information was gathered through numerous inventories carried out in the area, in addition to direct consultation of scientific collections (CEDU, CZMA, LEACOL, LESPP and MPEG), which contain many unpublished records. Twelve species belonging to three subgenera have been listed: *Xylocopa* (*Neoxylocopa*) amazonica Enderlein, 1913, *X.* (*N.*) *aurulenta* (Fabricius, 1804), *X.* (*N.*) *cearensis* Ducke, 1910, *X.* (*N.*) *frontalis* (Olivier, 1789), *X.* (*N.*) *grisescens* Lepeletier, 1841, *X.* (*N.*) *hirsutissima* Maidl, 1912, *X.* (*N.*) *nigrocincta* Smith, 1854, *X.* (*N.*) *transitoria* Pérez, 1901, *X.* (*Schonnherria*) *macrops* Lepeletier, 1841, *X.* (*S.*) *muscaria* (Fabricius, 1775), *X.* (*S.*) *subcyanea* Pérez, 1901 and *X.* (*Stenoxylocopa*) sp. n. Of these, two species are reported as first records for Maranhão (*X. hirsutissima* and *X. subcyanea*), one for Brazil (*X. transitoria*) and one for science (*X.* (*Stenoxylocopa*) sp. n. - not yet published). Bees were collected on 109 plant species belonging to 77 genera and 36 families. A ditrophic network with 193 interactions showed a significant correlation between the abundance of collected bees and the richness of visited plants. Generalist bee species were *X. cearensis* (61.5% of all observed plants), *X. frontalis* (37.6%) and *X. nigrocincta* (22%). In contrast, *X. aurulenta* and *X. amazonica* visited only two plant species each. The plants with the most records were *Chamaecrista hispidula* (9.9% of individuals), *C. ramosa* (9.2%) (Fabaceae) and *Passiflora foetida* L. (7.8%) (Passifloraceae). Using species distribution models to predict the possible impacts of climate change, it was discovered that ten of the twelve *Xylocopa* species in the region will potentially face a reduction in climate suitability between 2041 and 2060. Species that only occur in tropical forests will be the most affected, such as *X. aurulenta*, which could lose its entire range in Maranhão, even in the most optimistic scenario. On the other hand, two species will benefit in the future: *X. hirsutissima* will increase by around 23% of its total area of occurrence in the state, while *X. grisescens* will expand by more than half of its area, covering more than 80% of Maranhão in all scenarios. Despite the predicted changes, *X. frontalis* will probably continue to be the most widely distributed species in the region. It was also observed that, although *Xylocopa* species have uneven distributions, most of them are concentrated in the northern areas of the state, many of which are legally protected. On the other hand, the remaining unprotected areas of future suitability, which include the Cerrado in the southern part of the state and the intermediate transition areas in the central region, will be fundamental for the movement of the species and require the implementation of management plans and friendly agricultural practices to guarantee the availability of resources and, ultimately, the conservation of these pollinators.

Keywords: Mamangava; biogeography; systematics; pollination; conservation.

LISTA DE FIGURAS

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Figura 1: Diversidade de coloração no gênero *Xylocopa.* Registros do iNaturalist: **(A)** *X.* (*Neoxylocopa*) *nigrocincta* ♀ Brasília – DF, Brasil, © Silvio Wolff; **(B)** *X.* (*Alloxylocopa*) *phalothorax* ♀ Aberdeen Reservoir, Hong Kong, © Keon Chiew; **(C)** *X.* (*Neoxylocopa*) *frontalis* ♀ Búzios – RJ, Brasil, © Jesús Macchi; **(D)** *X.* (*Koptortosoma*) *lateritia* ♀ Oichili, – KM, Comores, © Frank-Roland Fließ; **(E)** *X.* (*Koptortosoma*) *caffa* ♀ Ngquza – EC, África do Sul, © suncana; **(F)** *X.* (*Cyaneoderes*) *caerulea* ♀ Timur Laut – MY, Malásia, © CheongWeei Gan; **(G)** *X.* (*Schonnherria*) *splendidula* ♀ Cordillera – RM, Chile, © Peter Peterson; **(H)** *X.* (*Xylocopoides*) *cyanea* ♂ Zitácuaro – MC, México © Yizuz Arriaga; **(I)** *X.* (*Lestis*) *bombylans* ♀ Witta – QLD, Austrália, © Larney Grenfell; **(J)** *X.* (*Neoxylocopa*) *sonorina* ♂ Orange – CA, Estados Unidos, © Ramon(Ray) Evans; **(K)** *X.* (*Platynopoda*) *tenuiscapa* ♂ Pune – MH, Índia, © Vishal Jadhav; **(L)** *X.* (*Lestis*) *aerata* ♂ Blue Mountains – NS, Austrália, © Nature_Lover; **(M)** *X.* (*Neoxylocopa*) *augusti* ♂ Cordillera – RM, Chile, © Cristian Trejos Guerra; **(N)** *X.* (*Schonnherria*) micans ♂ Travis – TX, Estados Unidos, © Ken-ichi Ueda; **(O)** *X.* (*Schonnherria*) *viridigastra* ♂ Urubamba – CS, Peru, © Diego Balbuena **06**

Figura 2: Estudos sistematizados de abelhas realizados no Estado do Maranhão (MA) com registros de *Xylocopa* enumerados em ordem cronológica. **1** – GOTTSBERGER *et al.* (1988)**;** **2** – REBÊLO (1986); **3** – ARAÚJO (1994); **4** – BRITO (1994); **5** – FERREIRA (1994); **6** – MENDONÇA (1994); **7** – APOCALYPSE (1995); **8** – SANTOS (1996); **9** – ALBUQUERQUE (1998); **10** – PEREIRA (1998); **11** – BARBOSA (2003); **12** – MARTINS (2003); **13** – SERRA (2005); **14** – RÊGO *et al.* (2007); **15** – OLIVEIRA (2008); **16** – ARAÚJO (2010); **17** – OLIVEIRA (2010); **18** – SILVA (2010); **19** – GOSTINSKI (2011); **20** – ARAÚJO (2014); **21** – OLIVEIRA (2016); **22** – FERREIRA (2016); **23** – ANJOS (2018); **24** – SANTANA (2018); **25** – PINTO (2020); **26** – NEVES *et al.* (2021) **14**

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LISTA DE ABREVIATURAS E SIGLAS

Am	*Xylocopa* (*Neoxylocopa*) *amazonica*
AMNH	Museu Americano de História Natural
AMZ	Amazônia
APA	Área de Proteção Ambiental
AR6	Sexto Relatório de Avaliação
Au	*Xylocopa* (*Neoxylocopa*) *aurulenta*
Aw	Tipo climático tropical quente
BDiA	Banco de Informações Ambientais
BL	Comprimento do corpo
BVL	Marrom escuro/Violeta-azulado
C	Conectância
CA	Coeficiente de associação
CAA	Caatinga
Ce	*Xylocopa* (*Neoxylocopa*) *cearensis*
CEDU	Coleção Entomológica Danúncia Urban
CER	Cerrado
Chi	Quiropterofilia (polinização por morcegos)
CMIP6	Fase 6 do Projeto de Intercomparação de Modelos Acoplados
Cr	Liana
Ct	Cultivada
CZMA	Coleção Zoológica do Maranhão
D	Espécie dominante
DS	Floresta decidual estacional
FF	Campos alagados
Fr	*Xylocopa* (*Neoxylocopa*) *frontalis*
GBIF	Centro Global de Informações sobre Biodiversidade
GG	Marrom escuro/ Esverdeado-dourado
GLM	Modelo linear generalizado
Gr	*Xylocopa* (*Neoxylocopa*) *grisescens*
GVL	Marrom escuro/Violeta-esverdeado
Hb	Herbácea
HC	Hialino/Acobreado
Hi	*Xylocopa* (*Neoxylocopa*) *hirsutissima*
IO	Interações observadas
IP	Interações possíveis
IPCC	Painel Intergovernamental sobre Mudanças Climáticas
k	Grau médio
LEACOL	Coleção de Abelhas da Universidade Federal do Maranhão
LESPP	Laboratório de Ecologia e Sistemática de Insetos Polinizadores e Predadores
MA	Maranhão
Ma	*Xylocopa* (*Schonnherria*) *marops*
MAXENT	Máxima entropia

Mel	Melitofilia (polinização por abelhas)
MPEG	Museu Paraense Emílio Goeldi
Mu	*Xylocopa* (*Schonnherria*) *muscaria*
Myo	Miofilia (polinização por moscas)
n	Abundância
N	Aninhamento
N	Riqueza
Ne	Néctar
Ni	*Xylocopa* (*Neoxylocopa*) *nigrocincta*
NODF	Métrica de aninhamento de sobreposição e preenchimento decrescente
Nv	Nativa
Nz	Naturalizada
Ol	Óleo
Orn	Ornitofilia (polinização por aves)
P%	Frequência relativa de plantas visitadas
PH	Fisionomia
Po	Pólen
Psi	Psicofilia (polinização por borboletas)
R^2	Correlação de R-Quadrado
REBIO	Reserva Biológica do Gurupi
REF	Referências
S#	Esterno
SDM	Modelo de distribuição de espécies
SEMC	Museu Entomológico da Universidade de Kansas
Sh	Arbusto
SS	Savana estépica
SSP	Caminhos socioeconômicos compartilhados – projeções climáticas
St	*Xylocopa* (*Stenoxylocop*a) sp.
Su	*Xylocopa* (*Schonnherria*) *subcyanea*
T	Índice de temperatura
T#	Tergo
Tr	Árvore
Tr	*Xylocopa* (*Neoxylocopa*) *transitoria*
TSS	Estatística de habilidade verdadeira
UFBA	Universidade Federal da Bahia
UFC	Universidade Federal do Ceará
UFMA	Universidade Federal do Maranhão
UFPB	Universidade Federal da Paraíba
UFPR	Universidade Federal do Paraná
UNILA	Universidade Federal da Integração Latino-Americana
USP	Universidade de São Paulo
VL	Marrom escuro/Violeta
Z	Índice de uniformidade de Rayleigh

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1. INTRODUÇÃO

As abelhas da tribo Xylocopini compreendem cerca de 400 espécies reunidas em um único gênero, *Xylocopa* Latreille. Elas apresentam uma ampla distribuição geográfica, ocupando todos os continentes, mas são mais diversas nas regiões tropicais e subtropicais (HURD, 1978; MICHENER, 2007).

As espécies deste gênero são popularmente conhecidas como mamangavas de toco ou abelhas carpinteiras, pois, as fêmeas da maioria das espécies possuem o hábito de escavar seus ninhos em madeira viva ou morta, ramos ou em cavidades de bambu (HURD; MOURE, 1963). No geral, essas abelhas são consideradas solitárias, em que as fêmeas são autônomas em todas as etapas de construção e aprovisionamento de seus ninhos. No entanto, algumas espécies podem formar ninhos agregados, onde várias fêmeas compartilham o mesmo substrato, mas em fases reprodutivas diferentes (GERLING *et al.* 1989; HOGENDOORN e VELTHUIS, 1993).

As mamangavas também são conhecidas pelo seu porte corporal notavelmente robusto, tendo em média 20 a 30 mm de comprimento, o que lhes permite enfrentar ventos fortes e voar por distâncias mais longas em busca de alimento (GERLING *et al.* 1989). Uma das razões da qual são considerados organismos poliléticos é o hábito de visitarem diversas espécies botânicas durante a coleta de seus recursos florais, desempenhando assim um importante papel de polinizador em ambientes naturais e agrícolas (ROUBIK, 1995; NABHAN e BUCHMANN, 1997), podendo, inclusive, transportar o pólen por distâncias maiores do que aquelas alcançadas por outras abelhas de porte corpóreo menor.

Estes serviços ecossistêmicos, no entanto, estão enfrentando uma crescente vulnerabilidade devido às intervenções humanas aos seus habitats, além dos impactos causados pelas mudanças climáticas (GIANNINI *et al.* 2012, 2017). O declínio das populações destes polinizadores pode trazer sérias consequências na manutenção da diversidade genética de plantas (MEERBEEK *et al.* 2014), causar a redução da produção agrícola (GARIBALDI *et al.* 2011; GIANNINI *et al.* 2017), ameaçar o bem-estar e a saúde humana (NELSON *et al.* 2013), além de desestabilizar o ecossistema por conta da ruptura ou modificações das interações ecológicas (INNES *et al.* 2013; SCHENK *et al.* 2018). Assim, compreender os componentes (condições e recursos) necessários para permanência destas espécies nos ambientes naturais é fundamental.

Apesar de sua importância, o conhecimento sobre a ecologia da maioria das espécies desse grupo de abelhas é, entretanto, incipiente (BROWN e PAXTON, 2009; MURRAY *et al.* 2009). A falta de estudos de base em muitos táxons, ou a concentração de estudos realizados em locais de fácil acesso, seja por questões logísticas ou de conveniência, criam lacunas de conhecimento (Déficit Wallaceano) que dificultam, em última análise, as tomadas de decisões para a conservação e uso sustentado desses polinizadores (OLIVEIRA *et al.* 2016). Nesse contexto, tornou-se necessário a criação de novos métodos ou instrumentos que pudessem avaliar ou inferir a ocorrência das espécies em locais onde não houvesse registros prévios.

Os modelos computacionais que são baseados em testes estatísticos e probabilísticos tornaram-se uma ferramenta com grande potencial de preencher essas lacunas (ELITH *et al.* 2006; PHILLIPS e DUDÍK, 2008). Para informações sobre ocorrência de espécies, o mais adequado e usual são os modelos de distribuição de espécies (MDE) (ELITH *et al.* 2006).

Os MDE surgiram ao longo do avanço tecnológico da computação, com o intuito de auxiliar o entendimento dos padrões de adequabilidade ambiental dos organismos (GUISAN e THUILLER, 2005; ELITH e LEATHWICK, 2009). Essencialmente, os MDE consistem em associações entre variáveis ambientais de diferentes pontos de ocorrência de uma espécie-alvo, para definir os graus de tolerância, dentre os quais, as populações dessa dada espécie podem ser mantidas indefinidamente (GIANNINI *et al.* 2012a). Dessa forma, através de diferentes algoritmos e funções, podemos projetar em um mapa a probabilidade de presença ou ausência de determinada espécie em uma dada região geográfica (OLIVEIRA *et al.* 2019).

Através desse poder preditivo, os modelos nos permitem extrapolar ou interpolar informações para compreender a distribuição potencial das espécies-alvo, a fim de se localizar locais prioritários para sua conservação, ou mesmo a suscetibilidade de espécies bioinvasoras a determinados ambientes (WHITTAKER *et al.* 2005; SILVA *et al.* 2014; FERNÁNDEZ e HAMILTON, 2015; ACOSTA *et al.* 2016; OLIVEIRA *et al.* 2017; BELLARD *et al.* 2018).

Além do mapeamento das distribuições no cenário atual, podemos utilizar as variáveis ambientais como projeções de cenários futuros, demostrando tendências inerentes às dinâmicas populacionais das espécies, como aumento, diminuição ou deslocamento em função das alterações climáticas ou da paisagem (JIMÉNEZ-VALVERDE *et al.* 2011; PORFIRIO *et al.* 2014; MARTINS *et al.* 2015; SILVA *et al.* 2015).

As mudanças climáticas têm gerado preocupação crescente em escala global. Estações meteorológicas em todo o mundo apontam um aumento significativo da temperatura média do planeta a cada ano (WMO, 2022). No entanto, os efeitos reais dessas mudanças ainda não são compreendidos por completo para a maioria das espécies, especialmente nas regiões tropicais que abrigam uma grande diversidade de espécies e, consequentemente, teias ecológicas mais complexas (FEARNSIDE, 2008; ANTONELLI *et al.* 2018; PIRES *et al.* 2018).

Com intuito de suprir essas lacunas de conhecimento, este trabalho analisou os padrões de distribuição das espécies de *Xylocopa* e seus recursos florais no Estado do Maranhão (MA), região onde ocorre o encontro de três importantes biomas brasileiros (Amazônia, Cerrado e

Caatinga). Além disso, este trabalho contém informações sobre biogeografia, sistemática, redes de interação e sazonalidade das espécies.

Esta tese está organizada em três capítulos, no **Capítulo 1** foi feita a revisão e atualização dos registros de ocorrência de *Xylocopa* no Estado do Maranhão, a partir da análise taxonômica de material disponível em coleções biológicas. Além disso, investigou-se a diversidade e os padrões de distribuição por meio de mapas de ocorrência e foi oferecido subsídios taxonômicos, através da confecção de chaves de identificação para as espécies registradas.

No **Capítulo 2** foi feita a identificação dos recursos florais utilizados pelas espécies de *Xylocopa* nas fitofisionomias do Maranhão. Para isso analisou-se as métricas de interação ditrófica, como a conectância, grau médio e aninhamento e verificou-se informações gerais sobre os tipos de recursos, estratos verticais e padrões sazonais envolvidos nas interações.

No **Capítulo 3** foi feita uma modelagem de distribuição de espécies, com a utilização das informações constatadas nos capítulos anteriores. Com os modelos referentes ao cenário atual, foi avaliado o grau de adequabilidade climática das espécies em escala espacial e com os modelos referentes aos cenários futuros, foi possível analisar potenciais alterações na faixa de distribuição das espécies, como expansão, redução ou deslocamento.

1.1 OBJETIVO GERAL

Avaliar de forma abrangente a diversidade, distribuição geográfica e os recursos alimentares das abelhas pertencentes ao gênero *Xylocopa* Latreille, 1802, em áreas de transição no Estado do Maranhão. O foco foi examinar esses aspectos tanto em cenários climáticos atuais quanto em cenários futuros, levando em conta as projeções de mudanças climáticas.

1.2 OBJETIVOS ESPECÍFICOS

- Reunir informações sobre a diversidade das abelhas *Xylocopa* registradas no Maranhão;
- Identificar lacunas de amostragem e conduzir novas coletas nestas áreas;
- Revisar e atualizar as identificações das espécies encontradas no Maranhão;
- Confeccionar chaves de identificação dos subgêneros e espécies de *Xylocopa* da região;
- Indicar os recursos florais utilizados pelas espécies de *Xylocopa* do Maranhão;
- Analisar as interações exercidas entre as espécies de *Xylocopa* e suas plantas visitadas;
- Verificar o compartilhamento de nicho alimentar entre as espécies de *Xylocopa*;
- Construir modelos de adequabilidade climática para as espécies de *Xylocopa* em cenários atuais e futuros, de acordo com as projeções globais de mudanças do clima;
- Indicar as áreas prioritárias para a conservação das espécies de *Xylocopa* no Maranhão.

2. REVISÃO BIBLIOGRÁFICA

2.1 EMERGÊNCIA CLIMÁTICA E SUAS IMPLICAÇÕES

A interferência humana no meio ambiente, especialmente a partir da industrialização, vem alterando os padrões climáticos em larga escala. Desde o final do século XVIII, o aumento das emissões de gases de efeito estufa na atmosfera resultou em um incremento médio de 1,1ºC na temperatura global. Segundo o 6º Relatório (AR6) apresentado pelo IPCC (Painel Intergovernamental sobre Mudanças Climáticas – 2021), há ainda uma previsão de mais 2 a 5 ºC até 2100, caso as taxas de emissão não sejam controladas.

As alterações climáticas podem ocasionar diversos desarranjos nos ecossistemas, como mudanças nos padrões migratórios, e na composição e estrutura de comunidades (PECL *et al.* 2017). HARVEY *et al.* (2023) chamam atenção para os efeitos deletérios do aquecimento climático enfrentados pelos insetos, em termos de fisiologia, comportamento, fenologia, distribuição e interações. Os insetos são componentes fundamentais no ambiente, contribuindo de diversas maneiras para o funcionamento e fornecimento de serviços ecossistêmicos, como a reciclagem de nutrientes, controle de pragas e a polinização cruzada (DEVOTO *et al.* 2009; SCHOWALTER, 2013; SCHOWALTER *et al.* 2018; CONSTANTINO, 2024).

Estudos realizados ao longo dos últimos anos têm associado o aumento da temperatura média global a mudanças na fenologia de plantas (GILMAN *et al.* 2012; PIAO *et al.* 2019; KEHRBERGER 2021), o que, por sua vez, pode resultar na dessincronização de seus polinizadores (SCHENK *et al.* 2018; BEZERRA *et al.* 2019; FREIMUTH *et al.* 2022; HUANG *et al.* 2023). Estes impactos, juntamente com a degradação direta dos hábitats, são apontados como as principais ameaças às populações de abelhas (ZATTARA e AIZEN, 2021). Considerando que as abelhas constituem o grupo mais importante de insetos polinizadores, o declínio de suas populações representa um sério risco para a segurança alimentar humana a médio e longo prazo (POTTS *et al.* 2016; BROWN *et al.* 2016; SETTELE *et al.* 2016).

No Brasil, há pelo menos 10 anos, já se projetava perdas de adequabilidade para várias espécies de abelhas (GIANNINI *et al.* 2012). Mais tarde, um estudo concluiu que polinizadores de pelo menos 13 culturas agrícolas economicamente importantes sofrerão declínio em mais de 90% dos municípios produtores (GIANNINI *et al.* 2017) e, mais recentemente, uma avaliação das espécies de abelhas da Amazônia Oriental demostrou uma redução de suas áreas de ocorrência em até 95% (GIANNINI *et al.* 2020). Diante desse cenário, mesmo as espécies amplamente distribuídas e reconhecidamente generalistas, sofrerão algum impacto negativo. Este é o caso das abelhas carpinteiras, organismos pertencentes ao gênero *Xylocopa*, que constitui um dos principais grupos de polinizadores agrícolas (GIANNINI *et al.* 2013, 2015).

2.2 CARACTERÍSTICAS GERAIS DO GÊNERO *XYLOCOPA*

2.2.1 Aspectos morfológicos

As abelhas carpinteiras da tribo Xylocopini são geralmente reconhecidas pelo porte corporal grande, associado à coloração predominantemente preta do tegumento. Por conta disso, elas são frequentemente confundidas com besouros (Coleoptera), chamadas em muitas cidades do nordeste brasileiro de "besouro do maracujá" (SUSSI, 2017). Esta associação, apesar de discrepante, é compreensível, pois, embora haja espécies de *Xylocopa* relativamente pequenas (menores que 15 mm), a sua grande maioria mede em torno de 20 a 30 mm, e algumas espécies estão entre as maiores e mais robustas abelhas do mundo (MICHENER, 2007). No entanto, em termos de coloração, há muito mais variações do que apenas as formas totalmente melânicas (Fig. 1A) (HURD e MOURE, 1963). Em muitas espécies, há uma associação da pubescência preta com faixas brancas, amarelas, laranjas, vermelhas ou azuis, localizadas geralmente no tórax e tergos metassomais (Fig. 1B–F). Além disso, existem padrões de manchas no tegumento em várias espécies, e em alguns subgêneros os seus representantes possuem uma coloração metálica brilhante no corpo, variando entre os tons azulado e esverdeado (Fig. 1G–I) (HURD e MOURE, 1963).

As asas geralmente apresentam pigmentação marrom-escuro, acompanhada de uma iridescência violácea, mas exibem uma ampla variação com marcantes reflexos metálicos, que podem assumir tonalidades azuis, verdes ou violeta, (Fig. 1A–F) muitas vezes formando um gradiente da base ao ápice da asa (Fig. 1K). Por outro lado, também existem espécies sem nenhum desses padrões de cores e suas asas são totalmente acobreadas (Fig. 1G) ou mesmo hialinas (Fig. 1J).

Outra característica marcante do gênero *Xylocopa* é o dimorfismo sexual. Em alguns grupos, como os representantes do subgênero *Neoxylocopa,* as fêmeas são predominantemente pretas, enquanto os machos apresentam tegumento com coloração amarelada ou ferrugínea (Fig. 1J e 1M), além da pilosidade totalmente amarelada, e são extremamente semelhantes entre si, dificultando qualquer associação ou identificação específica (SILVEIRA *et al.* 2002; SCHLINDWEIN *et al.* 2003). Os machos dos demais subgêneros são dissociados das fêmeas, geralmente, pela presença de manchas amarelas ou brancas na face, geralmente em estruturas como clípeo, labro, mandíbulas e antenas (Fig. 1N–O). Em alguns casos, como os representantes do subgênero *Schonnherria* há também um forte processo de convergência na distância interorbital superior (Fig. 1N) (VILLAMIZAR *et al.* 2020).

Figura 1: Diversidade de coloração no gênero *Xylocopa*. Registros do iNaturalist: **(A)** *X.* (*Neoxylocopa*) *nigrocincta* ♀ Brasília – DF, Brasil, © Silvio Wolff; **(B)** *X.* (*Alloxylocopa*) *phalothorax* ♀ Aberdeen Reservoir, Hong Kong, © Keon Chiew; **(C)** *X.* (*Neoxylocopa*) *frontalis* ♀ Búzios – RJ, Brasil, © Jesús Macchi; **(D)** *X.* (*Koptortosoma*) *lateritia* ♀ Oichili, – KM, Comores, © Frank-Roland Fließ; **(E)** *X.* (*Koptortosoma*) *caffa* ♀ Ngquza – EC, África do Sul, © suncana; **(F)** *X.* (*Cyaneoderes*) *caerulea* ♀ Timur Laut – MY, Malásia, © CheongWeei Gan; **(G)** *X.* (*Schonnherria*) *splendidula* ♀ Cordillera – RM, Chile, © Peter Peterson; **(H)** *X.* (*Xylocopoides*) *cyanea* ♂ Zitácuaro – MC, México © Yizuz Arriaga; **(I)** *X.* (*Lestis*) *bombylans* ♀ Witta – QLD, Austrália, © Larney Grenfell; **(J)** *X.* (*Neoxylocopa*) *sonorina* ♂ Orange – CA, Estados Unidos, © Ramon(Ray) Evans; **(K)** *X.* (*Platynopoda*) *tenuiscapa* ♂ Pune – MH, Índia, © Vishal Jadhav; **(L)** *X.* (*Lestis*) *aerata* ♂ Blue Mountains – NS, Austrália, © Nature_Lover; **(M)** *X.* (*Neoxylocopa*) *augusti* ♂ Cordillera – RM, Chile, © Cristian Trejos Guerra; **(N)** *X.* (*Schonnherria*) micans ♂ Travis – TX, Estados Unidos, © Ken-ichi Ueda; **(O)** *X.* (*Schonnherria*) *viridigastra* ♂ Urubamba – CS, Peru, © Diego Balbuena.

No aspecto geral, as abelhas carpinteiras do gênero *Xylocopa* podem ser distinguidas dos demais gêneros através da seguinte diagnose (modificada de MICHENER 2007):

Abelhas robustas, comprimento médio de 13 a 30 mm, asas com célula marginal estreita e alongada, presença de três células submarginais, estigma ausente e terço apical da asa fortemente papilado. Cabeça geralmente arredondada lateralmente, com a face superior achatada; clípeo plano ou ligeiramente convexo; probóscide curta, antenas com o primeiro flagelômero mais comprido do que o segundo e o terceiro juntos; mandíbulas bi ou tridentadas. Fêmeas com escopa cerdosa, bem desenvolvida nas tíbias e nos basitarsos das pernas posteriores, arólios ausentes.

2.2.2 Distribuição geográfica

O gênero *Xylocopa* é um dos grupos de abelhas mais diversificados e amplamente distribuídos em todo o mundo. Essas abelhas são consideradas cosmopolitas, pois estão presentes em todos os continentes, embora sejam mais numerosas nas regiões tropicais e subtropicais (MICHENER, 2007). Com mais de 400 espécies válidas posicionadas em 31 subgêneros, estes organismos alcançam uma faixa geográfica aproximada de 50ºN – 40ºS, através de uma variedade de hábitats, desde áreas abaixo do nível do mar como no Vale da Morte, Califórnia (*X. californica arizonensis* Cresson), regiões montanhosas como Hindu Kush no Afeganistão à 5.000 metros de altitude (*X. valga* Gerstäcker) e vegetações isoladas na Cordilheira dos Andes (*X. viridigastra* Lepeletier) (HURD JR, 1978).

Algumas espécies possuem uma ampla distribuição ao longo de extensões continentais, como a *X. frontalis* Olivier, por exemplo, ocupando uma área enorme que abrange boa parte das Américas, estendendo-se do norte da Argentina até o México. Essa espécie é capaz de atravessar grandes distâncias ao longo de diferentes ecossistemas, incluindo regiões savânicas, costeiras e florestas úmidas, como a Floresta Atlântica e Amazônica (GONZALEZ *et al.* 2009). Outras espécies, no entanto, apresentam distribuições geográficas muito restritas como os casos de endemismo da *X. darwini* Cockerell nas Ilhas Galápagos, *X. clarionensis* Hurd nas Ilhas Revillagigedo e *X. bomboides* Smith nas montanhas de Taiwan (HURD, 1958, 1978).

De acordo com HURD e MOURE (1963), alguns subgêneros podem expandir suas áreas de ocupação em regiões de transições limítrofes. Aparentemente, as abelhas carpinteiras são potencialmente capazes de se estabelecerem com sucesso em novas áreas, se as barreiras físicas ou ecológicas intervenientes puderem ser ultrapassadas. A colonização das espécies do subgênero *Neoxylocopa* em diversos arquipélagos do continente americano fortalece a hipótese em questão. No entanto, a ausência dessas espécies no Pacífico Central pode ser atribuída às grandes distâncias de dispersão (HURD, 1958).

É muito provável que, além das condições climáticas favoráveis, outros componentes do nicho ecológico das espécies também exerçam limitações em relação às suas distribuições em uma região específica. Nesse contexto, a disponibilidade de locais adequados para nidificação, além dos recursos alimentares são fundamentais para a manutenção das populações (GERLING *et al.* 1989).

2.2.3 Utilização de recursos

A maioria das espécies de abelhas dependem essencialmente dos recursos florais oferecidos pelas plantas, os quais são fundamentais para sua sobrevivência (MICHENER, 1977; MINCKELY e ROULSTON, 2006). O pólen e o néctar são os principais alimentos explorados pelas abelhas (ROUBIK, 1989; MICHENER, 2007; VIT *et al.* 2018). Esses recursos são utilizados na alimentação dos indivíduos adultos e imaturos em fase de desenvolvimento (NEFF e SIMPSON, 1981; BUCHMANN, 1983; AUGUSTO e GARÓFALO, 2003; MINCLEY e ROULSTON, 2006; PEREIRA e GARÓFALO, 2010).

Devido ao tamanho corporal, as espécies do gênero *Xylocopa* tornaram-se os polinizadores ideais de plantas que produzem flores grandes, como a castanheira-do-Pará *Bertholletia* spp. (MAUÉS, 2002) e o maracujazeiro *Passiflora* spp. (CAMILLO 2003), os quais dependem deste processo para se reproduzir. Por outro lado, essas abelhas não dependem exclusivamente das plantas com essas características, pois, no geral, as espécies de *Xylocopa* são consideradas poliléticas, e visitam uma ampla variedade de plantas com antese diurna (HURD, 1978), as quais apresentam diferentes atributos, como tipos de recursos, cores, hábitos e padrões sazonais (ALBUQUERQUE *et al.* 2007; ALMEIDA *et al.* 2022).

Em algumas comunidades estudadas, estas abelhas estabeleceram redes de interações altamente entrelaçadas, sendo apontadas como organismos-chave destes ecossistemas (COSTA et al., 2002; PIGOZZO et al., 2007; NEVES et al., 2021). No entanto, algumas espécies são mais bem reconhecidas do que outras, e, apesar desta generalização, as relações das abelhas carpinteiras com a comunidade florística não são totalmente compreendidas (HURD, 1978; GERLING *et al.* 1989).

Alguns estudos envolvendo espécies de *Xylocopa* presentes na polinização agrícola demostraram os efeitos de sobreposição do nicho alimentar, em que os indivíduos particionam a preferência dos recursos florais de acordo com a sua disponibilidade no ambiente (PIGOZZO e VIANA, 2010; ARAÚJO et al., 2021).

O apontamento feito por HURD (1978), de que todas as espécies de *Xylocopa* do hemisfério ocidental são potencialmente poliléticas, continua relevante. No entanto, é fundamental realizar estudos mais detalhados para avaliar os efeitos da competição entre espécies, especialmente considerando a limitação de recursos ou restrições geográficas (a exemplo das espécies insulares) (HURD, 1958).

Embora os recursos florais sejam imprescindíveis para as abelhas, outro recurso igualmente fundamental para estas populações são os substratos adequados para nidificação (KROMBEIN, 1967; GERLING *et al.* 1989). Como o nome sugere, os sítios de nidificação das abelhas carpinteiras incluem madeira maciça, troncos de árvores vivas, ramificações ou troncos em decomposição (CAMILLO e GAROFALO, 1982; CAMILLO *et al.* 1986). Os representantes do subgênero *Stenoxylocopa,* por exemplo, são conhecidos pela utilização de colmos de bambu e plantas relacionadas em sua nidificação (SILVEIRA, 2002; SILVEIRA *et al.* 2002).

HURD e MOURE (1963) discutiram a relação entre a disponibilidade de locais de nidificação adequados com a limitação geográfica das espécies de *Xylocopa.* Segundo os autores, a destruição dos hábitats destes polinizadores pode extinguir as espécies localmente, até que os substratos voltem a estar disponíveis. A degradação ambiental, portanto, altera a dinâmica populacional destas espécies, frequentemente, isolando umas das outras e criando desarranjos ecológicos (LINSLEY, 1958).

Por outro lado, na mesma proporção em que os ambientes naturais são enfraquecidos pela ocupação humana, novos locais de nidificação têm sido oferecidos, através dos materiais utilizados na edificação de assentamentos, como madeiras estruturais e alvenaria. Alguns casos de dispersão geográfica por conta da maior disponibilidade de substratos foram registrados desde o século passado, como a disseminação de *X. violacea* (Linnaeus) em toda a Europa, *X. latipes* (Drury) em ilhas asiáticas (HURD, 1958; HURD JR, 1978) e mais recentemente o deslocamento de *X. pubescens* (Spinola) através do Mar Mediterrâneo (CATANIA, 2023).

Atualmente, há muito mais interferência humana na distribuição de certos grupos de abelhas, especialmente as espécies sociais como *Apis* spp. e *Bombus* spp. sendo utilizadas como subsídios incrementais na produção agrícola (WINTER *et al.* 2006; GARIBALDI *et al.* 2017). Para as espécies solitárias, a estratégia de manejo mais conhecida são os hotéis de abelhas, em que consistem em estruturas artificiais, geralmente de madeira, que simulam os substratos de nidificação de várias espécies, incluindo as abelhas carpinteiras (MACIVOR e PACKER, 2015). No entanto, em alguns casos, elas parecem ser pouco atraídas (GESLIN *et al.* 2020; GONZÁLEZ-ZAMORA *et al.* 2021) ou apenas poucas espécies acabam nidificando em armadilhas adaptadas (PEREIRA e GARÓFALO, 2010; JUNQUEIRA, 2012; RIBEIRO, 2022).

2.3 HISTÓRICO TAXONÔMICO DAS ESPÉCIES NEOTROPICAIS

Por se tratar de um grupo muito diversificado e com ampla distribuição geográfica, as espécies do gênero *Xylocopa* já passaram por inúmeras revisões taxonômicas e sistemáticas. Historicamente, os seus representantes são divididos em subgêneros do hemisfério oriental e ocidental, também designados como Velho e Novo Mundo, respectivamente (MICHENER, 2007). Dentro de cada continente há ainda a divisão por regiões zoogeográficas, que consistem em áreas delimitadas por condições físicas e composição faunística e florística similares (SCLATER, 1858; BAILEY, 1998). A Região Neotropical que abrange a América do Sul e Central (incluindo os arquipélagos) e parte Sul do México, é reconhecida como uma das áreas de maior diversidade biológica do mundo, apresentando ecossistemas complexos e muitos centros de endemismo (MORRONE, 2014). As espécies de *Xylocopa* presentes nesta região constituem um grupo distintamente isolado das espécies orientais, e por conta disso, nenhum subgênero ocorre naturalmente em ambos os hemisférios (MICHENER, 2007).

Até o início da década de 50, as espécies de *Xylocopa* do continente americano eram tratadas no sentido amplo, juntamente com outras espécies ao redor do mundo, sem uma sistemática fundamentada. MICHENER (1954), em seu estudo sobre as abelhas do Panamá, dividiu as espécies do Novo Mundo em três subgêneros (*Neoxylocopa, Schonnherria* e *Xylocopoides*). Posteriormente, os subgêneros *Notoxylocopa* e *Stenoxylocopa* foram propostos por HURD (1956) e HURD e MOURE (1960), respectivamente.

Uma revisão extensa e detalhada das abelhas carpinteiras de todo o mundo foi produzida por HURD e MOURE (1963). Na proposta geral de classificação das abelhas carpinteiras de grande porte, eles reconheceram três gêneros: *Lestis*, *Proxylocopa* e *Xylocopa*, reunidos em 51 subgêneros (17 no Novo Mundo e 34 no Velho Mundo). Essa foi a principal contribuição para o reconhecimento da maioria dos subgêneros presentes na Região Neotropical, e serve de base para estudos sistemáticos até os dias atuais.

De forma complementar, HURD (1978) publicou um catálogo com informações relevantes sobre a história natural das abelhas carpinteiras presentes no Hemisfério Ocidental. Por meio da consulta de espécimes em várias coleções renomadas, Hurd incluiu detalhes de suas anotações sobre os registros de ocorrência das espécies, os substratos de nidificação e as relações com parasitas e predadores. Além disso, neste mesmo trabalho, o subgênero *Stenoxylocopa* foi revisado e atualizado com novos registros.

Em 1998, MINCKLEY realizou um abrangente estudo filogenético utilizando caracteres morfológicos. Nesse estudo, ele tratou *Xylocopa* como um único gênero, enquanto *Lestis* e *Proxylocopa* foram considerados subgêneros. Além disso, Minckley propôs uma nova classificação, reduzindo para 11 subgêneros no Novo Mundo e 19 no Velho Mundo. Neste mesmo trabalho, o subgênero *Megaxylocopa* na qual inclui três das maiores abelhas da região, foi interpretado como sinônimo de *Neoxylocopa*. Posteriormente essas relações filogenéticas foram revisadas com análises moleculares feitas por LEYS *et al.* (2000, 2002).

OSPINA (2000) compilou um quadro sinóptico das abelhas carpinteiras da Região Neotropical e listou um total de 96 espécies válidas distribuídas em 12 subgêneros. Neste trabalho, foi apontado algumas lacunas de conhecimento, especialmente em relação aos machos e a distribuição de certas espécies.

Em 2002, SILVEIRA *et al.* publicaram o livro "Abelhas Brasileiras: sistemática e identificação", uma obra que incluiu vários aspectos do estudo das abelhas, desde a morfologia básica, história natural, procedimentos de coleta e montagem e classificação taxonômica. São apresentadas 5 famílias de abelhas para o Brasil, da qual o gênero *Xylocopa* se insere em Apidae – Xylocopinae – Xylocopini. Baseado na classificação de Minckley, neste livro foram listadas 50 espécies agrupadas em 10 subgêneros (*Cirroxylocopa, Dasyxylocopa, Diaxylocopa, Monoxylocopa, Nanoxylocopa, Neoxylocopa, Schonnherria, Stenoxylocopa, Xylocopoda* e *Xylocopsis*). Os autores ressaltaram a necessidade de uma revisão mais aprofundada dos grandes grupos *Neoxylocopa* e *Schonnherria*, devido à escassez de informações específicas que pudessem sustentar uma análise sistemática, bem como a produção de chaves de identificação para as espécies brasileiras.

Nos últimos 20 anos, diversos estudos na Região Neotropical têm enriquecido o nosso conhecimento sobre as abelhas carpinteiras, como: listas de espécies regionais (SCHLINDWEIN *et al.* 2003; SILVA *et al.* 2009; RAMIREZ-FREIRE *et al.* 2012; MARCHI e ALVES-DOS-SANTOS, 2013; LUCIA *et al.* 2015; MAWDSLEY, 2018; OLIVEIRA e ZANELLA, 2020), novas descrições (ZANELLA e SILVA, 2010; LUCIA *et al.* 2014; LUCIA *et al.* 2015; MELO, 2016, 2017; LUCIA e GONZALEZ, 2017; VILLAMIZAR *et al.* 2020; MÉRIDA-RIVAS *et al.* 2022; MELO, 2023), registros de ocorrência (MONTALVA *et al.* 2013; MAWDSLEY, 2018; VILLAMIZAR, 2020) e modelagem de distribuição (NASCIMENTO et al., 2022).

Existem outros subsídios importantes para o estudo das abelhas neotropicais, das quais incluem: a obra revisada de MICHENER (2007) "The Bees of the World", a qual representa um acervo de conhecimento a nível global, e o Catálogo de Abelhas Moure (MOURE *et al.* 2007) que reúne informações sobre classificação e registros de ocorrência, com foco na apifauna brasileira. É digno de nota que este Catálogo possui uma versão online (http://moure.cria.org.br/catalogue) (MOURE e MELO, 2023), tornando-se uma valiosa fonte de referência atualizada.

2.4 REGISTROS PRÉVIOS NO ESTADO DO MARANHÃO

O Maranhão (MA) é um estado brasileiro que se encontra em baixas latitudes da Região Neotropical (1º – 10º S), com área superior à maioria dos países europeus. O clima é predominantemente quente e úmido – Aw (KOEPPEN, 1948) e seu relevo é dividido em planícies e chapadas relativamente pequenas. Por outro lado, a cobertura vegetal é constituída pelo encontro de três grandes biomas (Amazônia, Cerrado e Caatinga) resultando em diferentes tipos de fitofisionomias de transição (ver sessão "Material and Methods – Sampling area" do capítulo 1), tornando o Maranhão uma região de grande interesse para estudos biológicos.

Os primeiros registros formais das abelhas do gênero *Xylocopa* no MA foram feitos por Adolpho Ducke no começo do século XX, por ocasião de suas explorações botânicas e entomológicas ao longo do norte e nordeste brasileiro (DUCKE, 1902, 1908, 1910). Durante esse intervalo, Ducke descreveu a espécie *X. cearensis* e fez os primeiros relatos de *X. frontalis* Olivier, na capital São Luís, além de *X grisescens* Lepeletier, *X. barbata* Fabricius (sinônimo de *X. muscaria*) e *X. viridis* Smith no interior do estado. É notável que, esta última espécie, apesar de possuir uma ampla distribuição na Região Neotropical, não foi mais registrada no Maranhão desde então.

Ao longo das décadas seguintes, observou-se apenas ocorrências ocasionais destas mesmas espécies amplamente distribuídas. Somente a partir do final dos anos 80, com o estabelecimento do curso de Ciências Biológicas na Universidade Federal do Maranhão, que levantamentos sistemáticos ganharam impulso (Fig. 2) (FERREIRA *et al.* 2020).

GOTTSBERGER *et al.* (1988) registraram pela primeira vez, nas dunas de São Luís, a *X. carbonaria* Smith (considerada nesta tese como *X. cearensis*) e *X. orthogonaspis* Moure, que assim como *X. viridis*, não foi mais observada posteriormente.

RÊGO *et al.* (2000) registraram pela primeira vez *X. aurulenta* Fabricius em uma área de floresta ombrófila aberta, localizada na Baixada Maranhense. Neste estudo, *X. aurulenta* foi consideravelmente menos abundante que as outras espécies do mesmo gênero, entretanto, ela foi mais expressiva em floresta ombrófila densa, em estudos posteriores (ANJOS, 2018; FERREIRA *et al.* 2019). Os registros de RÊGO *et al.* (2000) parecem ter sido o limite de ocorrência dessa espécie para leste do domínio amazônico.

Anos depois, RÊGO *et al.* (2007) conduziram um levantamento pioneiro na região mais ao sul do Maranhão, em uma área de Cerrado típico. Neste estudo, apenas espécies de grande porte foram observadas, dentre elas, uma forma indeterminada. Mais tarde foi esclarecido que se tratava da *X. amazonica* Enderlein, uma espécie que tem poucos registros ao longo das baixas latitudes da América do Sul, incluindo o nordeste brasileiro (HURD, 1978).

Xylocopa suspecta Moure & Camargo (considerada nesta tese como *X. nigrocincta* Smith) foi inicialmente identificada nos trabalhos de OLIVEIRA e SILVA (2010). No entanto, mesmo que seu primeiro registro para o MA só tenha sido formalmente publicado alguns anos depois (GOSTINSKI *et al.* 2016), essa espécie foi, por muito tempo, confundida com *X. carbonaria*, sendo observada desde os primeiros levantamentos (ALBUQUERQUE *et al.* 2001; APOCALYPSE, 1995; REBÊLO, 1995; SERRA, 2005).

Mais recentemente, FERREIRA *et al.* (2019) realizaram um inventário estruturado no extremo noroeste do MA, em uma área fragmentada de floresta ombrófila densa, característico do bioma Amazonia. Neste trabalho foi relatado a primeira ocorrência de *X. macrops* para o estado, que posteriormente foi ampliado por NEVES *et al.* (2021) em áreas de restinga do litoral.

Muitos destes estudos originaram-se de trabalhos de conclusão de curso, e por isso, nem todos foram publicados em periódicos científicos (REBÊLO *et al.* 2003; RÊGO e ALBUQUERQUE, 2012). Contudo, todos os registros resultantes desses esforços foram centralizados em uma única coleção (LEACOL – UFMA), simplificando a análise dos grupos e fornecendo um valioso material de referência de âmbito regional (FERREIRA *et al.* 2020).

Analisando o conjunto de dados depositados na LEACOL foi possível constatar que as abelhas carpinteiras do gênero *Xylocopa* têm tido uma presença constante em praticamente todos os levantamentos realizados no Maranhão. De modo geral, alguns padrões de distribuição puderam ser visualizados: *Xylocopa frontalis* foi registrada em todas as localidades estudadas, o que é esperado, considerando a sua ampla distribuição (MOURE e MELO, 2022); *Xylocopa cearensis* foi registrada massivamente em áreas litorâneas, dominando várias comunidades de restingas (ALBUQUERQUE *et al.* 2007; OLIVEIRA *et al.* 2010; GOSTINSKI *et al.* 2016; NEVES *et al.* 2021); *Xylocopa aurulenta* foi observada exclusivamente em áreas florestais, em contraste com *X. grisescens*, que esteve associada às áreas abertas; *X. nigrocincta* foi observada apenas nas regiões setentrionais, em contraste com os poucos indivíduos de *X. amazonica* na região meridional. Até então, havia apenas uma espécie do subgênero *Schonnherria*, *X. muscaria* sendo registrada predominantemente em áreas de florestais abertas.

Dessa forma, até o início desta tese, apenas sete espécies de *Xylocopa* haviam sido registradas no Maranhão. Apesar dos esforços recentes para digitalizar os dados da LEACOL (FERREIRA *et al.* 2020), nenhum desses registros estava disponível em plataformas online, como o *Specieslink* ou GBIF.

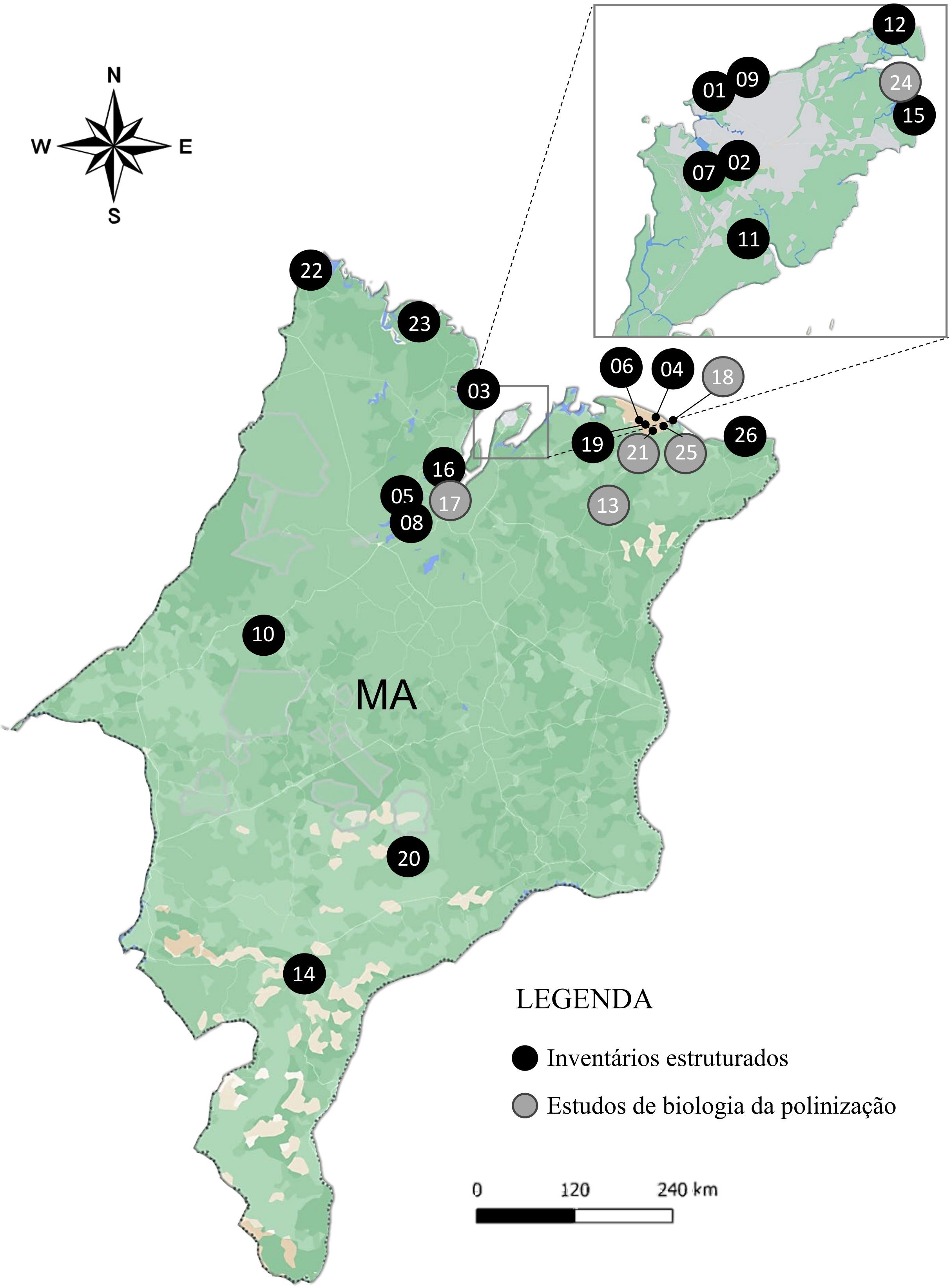

Figura 2: Estudos sistematizados de abelhas realizados no Estado do Maranhão (MA) com registros de *Xylocopa* enumerados em ordem cronológica. **1** – GOTTSBERGER *et al.* (1988)**;** **2** – REBÊLO (1986); **3** – ARAÚJO (1994); **4** – BRITO (1994); **5** – FERREIRA (1994); **6** – MENDONÇA (1994); **7** – APOCALYPSE (1995); **8** – SANTOS (1996); **9** – ALBUQUERQUE (1998); **10** – PEREIRA (1998); **11** – BARBOSA (2003); **12** – MARTINS (2003); **13** – SERRA (2005); **14** – RÊGO *et al.* (2007); **15** – OLIVEIRA (2008); **16** – ARAÚJO (2010); **17** – OLIVEIRA (2010); **18** – SILVA (2010); **19** – GOSTINSKI (2011); **20** – ARAÚJO (2014); **21** – OLIVEIRA (2016); **22** – FERREIRA (2016); **23** – ANJOS (2018); **24** – SANTANA (2018); **25** – PINTO (2020); **26** – NEVES *et al.* (2021)**.**

3. RESULTADOS

CAPÍTULO 1: CARPENTER BEES (APIDAE: XYLOCOPINI: *XYLOCOPA*) FROM MARANHÃO, NORTHEAST BRAZIL

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Carpenter bees (Apidae: Xylocopini: *Xylocopa*) from Maranhão, Northeast Brazil

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Abstract. We present a list of *Xylocopa* Latreille species that occur in Maranhão State, a region where several physiognomic formations characteristic of the Amazon, Cerrado, and Caatinga biomes overlap. The information was compiled through numerous surveys conducted in this territory, in addition to direct consultation in scientific collections, which have many unpublished records. Twelve species belonging to three subgenera were documented: *Xylocopa* (*Neoxylocopa*) *amazonica* Enderlein, 1913, *X.* (*N.*) *aurulenta* (Fabricius, 1804), *X.* (*N.*) *cearensis* Ducke, 1910, *X.* (*N.*) *frontalis* (Olivier, 1789), *X.* (*N.*) *grisescens* Lepeletier, 1841, *X.* (*N.*) *hirsutissima* Maidl, 1912, *X.* (*N.*) *nigrocincta* Smith, 1854, *X.* (*N.*) *transitoria* Pérez, 1901, *X.* (*Schonnherria*) *macrops* Lepeletier, 1841, *X.* (*S.*) *muscaria* (Fabricius, 1775), *X.* (*S.*) *subcyanea* Pérez, 1901 and *X.* (*Stenoxylocopa*) sp.. Of these, two species are reported as first records for Maranhão (*X. hirsutissima* and *X. subcyanea*), one for Brazil (*X. transitoria*), and one for science (*X.* (*Stenoxylocopa*) sp.– not yet published).

Key words: Anthophila, biogeography, conservation, diversity, systematics.

Introduction

The genus *Xylocopa* Latreille, 1802 consists of usually quite large bees widely distributed on all continents; however, they are more diverse in the old world and more abundant in tropical and subtropical regions where temperatures are higher (Hurd 1978; Michener 2007). *Xylocopa* comprises approximately 400 species, distributed in 31 subgenera, although there are estimates of up to 700 extant species (Silveira *et al.* 2002). Thus, this group is considered one of the largest evolutionary lineages of bees (Hurd & Moure 1963; Plant & Paulus 2016).

Xylocopa bees are popularly known as carpenter bees, as females make their nests in dead wood, twigs, or bamboo cavities, with the exception of the subgenus *Proxylocopa*, which nests in the soil (Hurd & Moure 1963). Some species are strictly solitary and may form aggregate nests (Sakagami & Laroca 1971; Pereira & Garófalo 2010), while others have facultatively social habits, in which females usually live together in the same nest but at different reproductive stages (Hogendoorn & Velthuis 1993; Richards 2011; Duff *et al.* 2023).

In general, carpenter bees are remarkably robust, reaching over 30 mm in length. For this reason, these bees can overcome the resistance of strong winds and can fly long distances, reaching radii of more than 10 km in search of food (Gerling *et al.* 1989). During this routed, flowers of various species can be visited, because these bees are polylectic and thus act as effective pollinators of many species of native and cultivated plants (Roubik 1995). Perhaps the best-known example is their role in passion fruit production, as, due to their morphometric adaptations, size, and abundant hairs, these bees act as a pollinator of *Passiflora* flowers, while smaller bees can only be robbers (Sazima & Sazima 1989; Camillo 2003). Other crops of commercial interest, such as tomato, pumpkin, and acerola are also pollinated by *Xylocopa*, making them an important agricultural pollinator (Giannini *et al.* 2020).

However, the ecosystem services provided by these bees are increasingly vulnerable due to human modifications to their habitats, making the need for baseline studies urgent (Schmeller & Bridgewater 2016). The lack of knowledge about taxonomic richness (Linnean Deficit) and geographic distribution (Wallacean Deficit) is an impediment to more in-depth studies, such as on ecological aspects, as well as an obstacle to decision-making aimed at environmental conservation (Neto & Loyola 2016).

Brazil holds an impressive diversity of *Xylocopa* and Silveira *et al.* (2002) called attention to the need for a broad taxonomic revision for the group. However, few papers have been published aiming to investigate the richness and distribution of Brazilian carpenter bees. Of these we highlight, the list of *Xylocopa* species from Rio Grande do Sul (Schlindwein *et al.* 2003), São Paulo (Marchi & Alves-dos-Santos 2013), the Northeast (Silva *et al.* 2009), and the Amazon Basin (Mawdsley 2018), the last two being poorly detailed, without distribution maps and with a large gap of records in the extreme eastern Amazon, where the State of Maranhão (MA) is located.

Rêgo & Albuquerque (2012) listed several species of bees that occur in the transition zones of MA, among them, seven species of *Xylocopa*, one without indication of specific identity. This information was provided from structured surveys conducted in the territory of Maranhão between 1994 and 2010, however, several unpublished data, such as graduation monographs and occasional studies, as well as historical information such as the first surveys in the region (Ducke 1910; Gottsberger *et al.* 1988), were disregarded. In addition, most surveys were conducted in the northern region of the state (Rebêlo *et al.* 2003), and although other works have been produced in the last 10 years (Gostinski *et al.* 2016; Ferreira *et al.* 2019; Neves *et al.* 2021), the bias of records concentrated to the north of MA remains.

This spatial under-sampling is particularly negative from a biogeographical point of view as it is an extremely heterogeneous region, which enables the overlapping of conditions and resources of the bordering biomes (Amazon, Cerrado, and Caatinga), thus supporting the occurrence of species with different niches (Rebêlo & Silva 1999).

Thus, the present study aims to review and update the records of the occurrence of *Xylocopa* in Maranhão State, based on the taxonomic analysis of a large amount of material available in the collections. Furthermore, we intend to investigate the diversity and distribution patterns by means of occurrence maps and to offer taxonomic subsidies by providing identification keys for the species, to facilitate future inventories in the region.

Material and Methods

Sampling area

Maranhão is the eighth largest Brazilian state, being 329.651 km^2, comparable to the size of Germany, and is situated in the Northeast Region of Brazil, between 01º01 ′ – 10º21 ′ S and 41º48 ′ – 48º50 ′ W (IBGE, 2021).

The state is divided into two very distinct topographical regions, the mid-north, characterized by coastal plains and lowlands and the mid-south, marked by the presence of plateaus, highlands, and tablelands. While the relief changes according to the latitude, the climate changes according to the longitude, that is, the predominant climate type is tropical hot, but it can be divided into three large regions: Humid Equatorial in the western portion, which corresponds to three dry months during the year, on average; Tropical Semi-humid Equatorial Zone, in the central portion, in which there are four dry months; and Tropical Semi-arid Equatorial Zone, in the eastern portion of the state, in which there can be up to six dry months throughout the year (NuGeo, 2021). The combination of these physical characteristics ends up promoting the establishment of distinct types of vegetation cover or phytophysiognomies in the different regions.

According to the Environmental Information Database (BDiA – IBGE, 2021), 32.41% of the territory of Maranhão is made up of contact areas or ecological tension, in the form of floristic interpenetration (ecotone or mixture) or interpenetration of physiognomies, without mixing (enclave). These contact areas permeate the following typologies: Ombrophylous Forest (30.41% of the territory), found especially in the west of the state, with an Amazonian vegetation characteristic, consisting of perennial macro and mesophanerophytes, the climate is hot and humid and under natural conditions suffers few changes throughout the year; Park/Wooded Savanna (43.25%), extending from the northeast to east and occupying almost the entire southern part of the state, characteristic of the Cerrado *stricto sensu*, where there is a predominance of grasses vegetation and shrubs with twisted trunks, that may occur in isolated form or grouped in small "islands", and, when associated with water bodies gallery forests or riparian forests with open-canopy are formed; Steppic Savanna (0.57%), in a small spot in the central-eastern portion of the state, that has typical elements of the Caatinga, with water scarcity resulting from the double climatic seasonality, presenting long dry periods during the year, followed by irregular rains, the vegetation, in turn, has xerophytic characteristics that are strategic to avoid water loss; Decidual Seasonal Forest (10.02%), is found in the eastern part of the state and is recognized for occupying restricted areas in climatic transition zones, defined by disjunctions or large discontinuous areas by the contact of ombrophilous forests and savannas; Pioneer Formations (4.09%), restricted to the extreme north of the state, where the coastline is located, with first occupation vegetation, which establishes itself on pedologically unstable soils and is in constant succession, in MA it occurs under the marine influence and dune formations (restingas), under the fluviomarine influence (mangrove and salt fields), and, under the fluvial or lacustrine influence, forming seasonally flooded fields, known as "Baixada maranhense" (Figure 1).

The percentage estimates of these areas are considered natural or predominant formations, this is because, according to the RADAM Project (Radar na Amazônia) from BDiA (2021), the regions of anthropic influences in Maranhão have a total of 48.54%, being composed of: Agricultural Sectors (30.28%), Secondary Vegetation (18.05%), and Urbanization (0.21%) (Figure 2). Deforestation and forest burning for pasture creation are the main sources of degradation of natural areas (Martins & Oliveira 2011). The most recent annual report on deforestation in Brazil shows an increasing rate of destruction of original formations, mainly in the forest (-24.5%) and savannah areas (-10%), placing Maranhão in 4th position in the national deforestation ranking (BDiA, 2021; MapBiomas 2022).

Occurrence records

The records were mostly obtained from the analysis of material deposited in the Coleção de Abelhas da Universidade Federal do Maranhão, São Luís, MA (LEACOL), as a result of significant field research in different localities, particularly involving many structured surveys, with systematic collections (biweekly or monthly) during at least twelve months, and carried out since 1994 (Rebêlo 1995; Gonçalves *et al.* 1996; Sodré *et al.* 2000; Albuquerque *et al.* 2001, 2007, 2010; Jesus *et al.* 2007; Rêgo *et al.* 2007; Oliveira 2008; Pinto *et al.* 2011; Araújo 2014; Gostinski *et al.* 2016; Ferreira *et al.* 2019; Neves *et al.* 2021). The collection also includes material from case studies, where collections were conducted according to the flowering period of a particular botanical species (Serra & Drummond 2006; Oliveira 2014; Oliveira *et al.* 2016; Santana 2018; Pinto *et al.* 2020), as well as sporadic collections (Ferreira *et al.* 2020). The *Xylocopa* specimens were selected and examined, and the provenience information, such as date and georeference, was extracted from individual labels, when possible, compared with the information contained in their respective papers.

Additional records were obtained from the following collections: Coleção Entomológica Danúncia Urban, Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, PR (CEDU); Coleção Zoológica do Maranhão, Universidade Estadual do Maranhão, Caxias, MA (CZMA); Coleção do Laboratório de Ecologia e Sistemática de Insetos Polinizadores e Predadores, Universidade Federal do Maranhão, São Luís, MA (LESPP), and Museu Paraense "Emílio Goeldi", Belém, PA (MPEG).

In a complementary approach, point collections were performed in areas with sampling gaps, aiming to achieve greater representativeness of the points in the state, as well as to reduce the effects generated by spatial concentration. For this, the bees were collected while visiting flowers, using an entomological net, at rest or in flight. They were then sacrificed and sent to the laboratory where they were subject to the identification process and incorporation into the collection (LEACOL).

Systematics

The individuals were examined based on the original descriptions of each species, with the support of the identification keys proposed by Schlindwein *et al.* (2003); Lucia & Abrahamovich (2010); Marchi & Alves-dos-Santos (2013); Mawdsley (2018); Villamizar & Vivallo (2020) and Mérida-Rivas *et al.* (2022) and through comparison with the material deposited at CEDU and LEACOL. Taxonomic classification and terminology were adopted according to revisions by Hurd & Moure, (1963) and Minckley (1998).

We considered previous identifications of *Xylocopa* (*Neoxylocopa*) *carbonaria* Smith, 1854 from northeastern Brazil as a melanistic variation of *X.* (*Neoxylocopa*) *cearensis* Ducke, 1910b (Zanella 2000; Silva *et al.* 2009) and *X.* (*Neoxylocopa*) *suspecta* Moure & Camargo, 1988 as a melanistic variation and junior synonym of *X.* (*Neoxylocopa*) *nigrocincta* Smith, 1854 (Agostini 2021).

The following terminology was used: N = number of species; n = number of individuals; BL = body length; T = terga, and S = sterna, enumerated for each segment in the anteroposterior direction (e.g. T1, T2, T3... S1, S2, S3). The punctation, when mentioned, was designated as: Dense = distance between punctures smaller than its diameter; Moderate = distance between punctures equivalent to its diameter; and Sparse = distance between punctures larger than its diameter.

The iridescence of the wings was analyzed under the same light conditions (fluorescent light-bulb, with direct and indirect light, under dorsal and lateral view) and the coloration patterns (VL = Dark brown/Violet; GVL = Dark brown/Violet-Greenish; BVL = Dark brown/Violet-Bluish; GG = Dark brown/Greenish-Golden; HC = Hyaline/Coppery) were established according to the predominance observed with or without the presence of associated metallic spots, in the base-apex direction (Figure 3).

Image capture and body length measurements of the bees deposited at LEACOL were performed using the software AxioVision (ver. SE64 Rel. 4.9.1), with the AxiCam ICc 1 coupled to the Zeiss Discovery V.8 stereoscopic microscope. The images obtained were enhanced with Adobe Photoshop® (ver. 23.4) and Adobe Lightroom® (ver. 11.4).

The maps were produced using QGIS Software (ver. 3.28) with layers of the phytoecological regions made available by the Environmental Information Database (BDiA – IBGE, 2021), with the symbology adapted, and the occurrence points of *Xylocopa* overlapping. To distinguish the density of the points, we used the heat map feature (kernel interpolation), with an estimator radius of 10 km and pixel size X of 400 as reference.

The labels were transcribed under the “Material examined” section in the following format: (n) **COUNTRY, STATE: Municipality**, (n) Specific locality, geographic coordinate, date, collector, COLLECTION, identification, responsible for identification (det.), year of identification.

Results

We analyzed 3515 individuals belonging to twelve species and three subgenera: *Xylocopa* (*Neoxylocopa*) *amazonica* Enderlein, 1913 (n = 12), *X.* (*Neoxylocopa*) *aurulenta* (Fabricius, 1804) (n = 11), *X.* (*Neoxylocopa*) *cearensis* Ducke, 1910 (n = 2053), *X.* (*Neoxylocopa*) *frontalis* (Olivier, 1789) (n = 924), *X.* (*Neoxylocopa*) *grisescens* Lepeletier, 1841 (n = 127), *X.* (*Neoxylocopa*) *hirsutissima* Maidl, 1912 (n = 27), *X.* (*Neoxylocopa*) *nigrocincta* Smith, 1854 (n = 197), *X.* (*Neoxylocopa*) *transitoria* Pérez, 1901 (n = 21), *X.* (*Schonnherria*) *macrops* Lepeletier, 1841 (n = 9), *X.* (*Schonnherria*) *muscaria* (Fabricius, 1775) (n = 117), *X.* (*Schonnherria*) *subcyanea* Pérez, 1901 (n = 5), and *X.* (*Stenoxylocopa*) sp. (n = 12).

Of these, two species are reported as first records for MA (*X. hirsutissima* and *X. subcyanea*), one for Brazil (*X. transitoria*) and one for science (*X.* (*Stenoxylocopa*) sp.) – not described, but being studied in a review of the subgenus).

In total, 180 occurrence points were recorded, distributed in 53 municipalities of MA. Of this set, only 49.3% of occurrences were in relatively preserved areas, 35.9% in areas with some urban influence, 12.9% in secondary vegetation, and 1.9% under direct influence of the agricultural sector. This results reflects the fact that the majority of the records were allocated in the northern portion of the state, in areas of urban influence, mainly in the region of the capital São Luís.

Despite this, it was possible to note the presence of *Xylocopa* in all sectors of Maranhão, including all areas with the main vegetation types (Figure 4). The physiognomy with the highest abundance was Pioneer Formation, characterized by dunes and restingas (n = 1871; 53.2% of the total) and the highest richness was Park/Wooded Savanna (N = 10; 83.3%).

Records had a time range of 117 years (1905–2022), although 67.7% of individuals were recorded between 2000 and 2022. This is reflected by the increase in baseline studies in the state since then, as 63.8% of all *Xylocopa* bees were collected in standardized surveys, 14.3% in pollination ecology studies, and another 21.8% in occasional collections. According to data obtained exclusively from the surveys, *Xylocopa* species were frequent in all months of the year, being slightly more abundant at the end of the rainy season and the beginning of the dry season (May, June, and August).

Systematics

Genus *Xylocopa* Latreille, 1802

Subgenus *Neoxylocopa* Michener, 1954

Apis (*Ancylosoma*) Dalla Torre, 1896: 206. Name not available, see: Michener (1997)
Xylocopa (*Neoxylocopa*) Michener, 1954: 157. Type species: *Apis brasilianorum* Linnaeus, 1767, by original designation.
Xylocopa (*Megaxylocopa*) Hurd & Moure, 1963: 151. Type species: *Apis frontalis* Olivier, 1789, by original designation. Minckley, 1998: 38, *Neoxylocopa* synonymy.

Diagnosis (Modified from Michener 2007). Its representatives are characterized by a strong sexual dimorphism in which the integument and pubescence are usually dark-colored in females and yellow or ferruginous in males. Including medium to large bees that have the following characters: apex of mandible bidentate, lower tooth equal to or larger than upper tooth; raised impunctate strip accompanies the whole epistomal suture; metasomal sterna with longitudinal carina; clypeus usually delimited by continuous smooth ridge. In males, posterior thoracic declivity begins on base of propodeum and mesosomal gland extremely large.

Distribution. It is the subgenus with the greatest diversity and geographic distribution in the Neotropical Region, with at least 50 described species, occurring from Argentina to the Southern United States and extending into more isolated island regions such as the Galápagos Islands and the West Indies (Vargas *et al.* 2015; Meurgey 2016). In Maranhão, it was the most diverse (N = 8) and most widely distributed subgenus, being found in basically all phytophysiognomies.

***Xylocopa* (*Neoxylocopa*) *amazonica* Enderlein, 1913**

(Figures 5, 17B, 17H)

Xylocopa amazonica Enderlein, 1913: 159-160. Holotype: Muzeum Instytut Zoologii, Warsaw, Poland (f#). Type locality: Brazil, Pará, Óbidos.

Diagnosis. Medium to large-sized bees, BL approximately 28.3 mm (25.2–29.5; n = 10); Females: integument and pubescence entirely black (Figure 5B-D); wings dark brown and iridescence predominantly GG; large inter-alveolar carina with "nose" shaped (Figure 5F), contrasting with small *X. nigrocincta* carina; dorsal surface of scutellum convex and smoothly rounded, transition with posterior surface forming a curved edge with an obtuse to right angle (Figure 5E), posterior surface with sparse punctation; T2 with moderate punctation on discal area. Males: medium-sized intra-alveolar carina; middle ocelli approximately the size of lateral ocelli (Figure 17B); metasomal terga with dense or moderately sparse punctation (Figure 17H).

Variation. Wings with iridescence GG in 72.7% of the individuals and GVL in 27.3%.

Distribution. Present along the Amazon Basin, in the states of Amapá, Amazonas, Pará, Mato Grosso, and Rondônia, however, it has been recorded outside this domain, in other areas of northeastern Brazil, such as Ceará and Paraíba states (Hurd 1978; Moure & Melo 2022; Oliveira & Zanella 2020). In Maranhão, 75% of the 12 individuals analyzed were recorded in regions where savanna predominates and 25% in areas of ombrophilous forest. Of the total, 83.3% of the bees were collected in areas without anthropic influence and 8.3% in secondary vegetation and urban areas (Figure 5A). As for seasonality, *X. amazonica* occurred in the months from June to December, a period characterized by the rainless period in the region.

Comments. In general, *X. amazonica* is very similar to *X. frontalis* (in body size) and *X. nigrocincta* (in the iridescent color of the wings), causing some erroneous identifications. It is probably for this reason that this species has not been reported in any of the surveys already conducted in MA (Rêgo & Albuquerque 2012). The presence of a prominent inter-alveolar carina in females also occurs in *X. nasica* Perez, 1901, according to the original description of this species, which has Chiriquí in Panama as its type locality. Thus, it is possible that they are closely related species or synonyms. But for caution, at this time, without analyzing material from Central America and intermediate regions, we chose to consider those from northern and northeastern Brazil as *X. amazonica*.

Material examined. (11f# 1m#) **BRAZIL, Maranhão: Balsas**, 3f# 1m# Povoado Santa Luzia, 15-VI, 17-VI and 15-IX-2001, Rêgo & Ramos, LEACOL, one female with label: *Xylocopa* (*Neoxylocopa*) *frontalis*. **Buriticupu**, 1f# Reserva Florestal da CVRD, 13-VIII-1996, Pereira & Pinto, LEACOL. **Carolina**, 1f# Riacho Estiva, 7°06'59.8"S 47°21'21.0"W, 15-VII-2013, Limeira-de-Oliveira, F., CZMA. **Chapadinha,** 2f# 15-X and 13-XI-1994, Brito & Rêgo, LEACOL. **Cururupu**, 2f# 21-VIII and 23-VIII-2015, Dos Anjos, J.V., LEACOL\CEDU, with label: *Xylocopa* (*Neoxylocopa*) *suspecta.* **Formosa da Serra Negra**, 1f# Parque Estadual do Mirador, 02-XII-2009, Maia, C.M., LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *nasica*, Silveira, F.A. det, 2015. **Mirador,** 1f# 11-X-2014, Costa, S.S., LEACOL.|

Xylocopa (*Neoxylocopa*) *aurulenta* (Fabricius, 1804)

(Figure 6)

Bombus aurulentus Fabricius, 1804: 351. Lectotype: University of Copenhagen Zoological Museum, Copenhagen, Denmark (f#). Subsequent designation: Moure, J. S. 1960: 143. Type locality: 'America meridionalis'.

Xylocopa medionitens Cockerell, 1916: 461. Holotype: American Museum of Natural History, New York, USA (f#). Type locality: Maroni, French Guiana.

Diagnosis. Medium to small-sized bees, BL approximately 20.5 mm (19–23.5; n = 10); Females: integument entirely black and mesosoma with strongly orange pubescence (Figure 6B-D); mesoscutum with smooth discal area; wings light-brown with distinctive HC pattern; pubescence of T1 entirely black; T2 with moderate punctation on discal area.

Distribution. Present along the Amazon Basin, there are records in Guyana, French Guiana, Peru, Suriname, and in Brazil, in the states of Acre, Amapá, Amazonas, Pará, Rio Branco, and Rondônia (Hurd 1978; Moure & Melo 2022). In Maranhão, the first records of *X. aurulenta* were reported by Ferreira *et al*. (2019), the distribution was recorded in the western portion, in ombrophilous forest (63.6%) and flooded fields (36.4%), areas which are currently under anthropic pressure converted into secondary vegetation and agricultural sectors, respectively (Figure 6A). The individuals of this species occurred from April to September, a period characterized by the transition between the rainy and dry seasons.

Comments. In general, *X. aurulenta* can be confused with *X. cearensis* - typical form, but it differs by the orange mesosomal pubescence and by the more translucent wing membrane, slightly brown, type HC. *Xylocopa aurulenta* has a distribution restricted to the Amazon biome, and the record in Maranhão possibly corresponds to the limit of occurrence to the east. Most records were collected in the 1990s, where, at the time, the collection sites were still preserved (Silva & Rebêlo 1999). Therefore, considering the annual degradation rates of this region, it is possible that the future occurrence of *X. aurulenta* in MA will be restricted to Protected Areas, such as the Gurupi Biological Reserve (REBIO) or Indigenous lands, such as Alto Turiaçu and Araribóia.

Material examined. (11f#) **BRAZIL, Maranhão: Buriticupu**, 6f# Reserva Florestal da CVRD, 20-IV, 18-V, 20-VI, 27-VII, 24-VIII and 07-IX-1996, Pereira & Pinto, LEACOL, all with label: *Xylocopa* (*Neoxylocopa*) *aurulenta*, Silveira, F.A. det, 2015. **Carutapera**, 1f# Sítio do Prata, 03-IX-2014, Ferreira, L.A.C., UFMG, with label: *Xylocopa* (*Neoxylocopa*) *aurulenta*, Silveira, F.A. det, 2015. **Vitória do Mearim**, 4f# Margem da ferrovia SLZ-Carajás, 24-IV and 15-VI-1992, Ferreira & Santos, LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *aurulenta*, Silveira, F.A. det, 2015.

Xylocopa (*Neoxylocopa*) *cearensis* Ducke, 1910

(Figures 7, 17F, 17I)

Xylocopa cearensis Ducke, 1910: 85. Lectotype: Museu Paraense 'Emílio Goeldi', Belém, Brazil (f#). Subsequent designation: Nascimento, P. T. R. 1979: 9. Type locality: Brazil, Ceará, Caridade.
Xylocopa branneri Cockerell, 1912: 42. Holotype: American Museum of Natural History, New York, USA (f#). Type locality: Brazil, Rio Grande do Norte, Natal.

Diagnosis. Medium to small-sized bees, BL approximately 18.9 mm (16–25.5; n = 2035); Females: integument entirely black, mesosoma with whitish-yellow pubescence - typical form (Figure 7B-D) or black to dark brown - melanic form (Figure 7E-F); wings dark brown and iridescence predominantly VL; dorsal surface of scutellum flattened, transition to posterior surface largely rounded (Figure 7E); posterior surface with dense punctation (Figure 7F); T2 with moderate to dense punctation on discal area. The typical form is similar to *X. grisescens* but is always smaller sized. Males: ventral surface of posterior tibia with a weak declivity and blackish pubescence (Figure 17F); metasomal terga with dense punctation (Figure 17I).

Variation. Wings with iridescence VL in 84.9% of the individuals, BVL in 11.6% and GVL in 3.4%. In females, 97.6% of the individuals had the melanic form and only 2.4% the typical form.

Distribution. Present across a wide geographic range, there are records in the Amazonian domain, as in the states of Amazonas, Rondônia, Mato Grosso, and Pará, however, the largest concentration is in the northeast of Brazil, in the states of Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Bahia, and extending to Minas Gerais (Hurd 1978; Moure & Melo 2022). In this region, bees were recorded predominantly in Caatinga areas, dunes, and restingas (Zanella 2000; Viana *et al.* 2002; Viana & Kleinert 2005). In Maranhão, this pattern was reinforced, as 79.7% of the individuals were collected on the coast, in dunes (47.7%) and restingas (32%). Another 12.6% were from ombrophilous forest, 5.1% from park savanna, 2.1% from flooded fields, and 0.6% from deciduous seasonal forest. Of the total, 55.1% of the bees were collected in areas without anthropic influence, 39.1% in urban areas, and 5.8% in secondary vegetation (Figure 7A). This was the species with the highest abundance observed in the state, accounting for 58.4% of all *Xylocopa* recorded, and even when we removed the information from specific surveys (which could bias this analysis), this species still represented 25% of the total abundance. Depending on the physiognomy, *X. cearensis* exhibited different seasonal patterns: in areas of ombrophilous and deciduous forests and savannas they were more frequent in the months of January to June, when there is more rainfall; in flooded fields it was the opposite, being more frequent in the second half of the year; and in areas of dunes and restingas they were abundant all year round (Gostinski *et al.* 2016). The melanic form of *X. cearensis* occupies a wide range of distribution in the mid-north sector of the state, concentrating mainly in areas of dunes and restingas, however, with no records in the flooded plains of the "Baixada maranhense". Otherwise, the typical form of the species has a more restricted distribution and is concentrated in flooded fields. Only two sites were common to both forms, the São Luís beaches and the extreme northeastern part of the state, and in these communities the melanic form was notably dominant.

Comments. In general, *X. cearensis* has numerous variations and therefore there are many incorrect identifications, in LEACOL this species was listed with at least five different names, and most (melanic) individuals were considered to be *Xylocopa* (*Neoxylocopa*) *carbonaria* Smith, 1854. Although the type locality of this species is from Pará (Rio Tapajós), this name was recognized by Moure (see Silva *et al.* 2009) and various authors (Rebêlo *et al.* 2003) for the melanic individuals from the northeast with dense T2 punctation. However, Zanella (2000) interpreted that entirely black specimens from the Caatinga and coast of the northeast correspond to the melanic form of *X. cearensis*, suggesting the need for revision with analysis of material covering the type locality area of the two nominal species, with two main possibilities, the occurrence of two valid species, with *X. carbonaria* restricted to or predominantly in the Amazon basin and *X. cearensis* predominantly in the Northeast, but with two forms (typical and melanic). Alternatively, they may be synonyms, in which case *X. carbonaria* will be the valid name. In MA, melanic individuals exhibited variation in T2 punctation from moderate to dense, the same pattern observed in individuals of the typical form of *X. cearensis*.

Material examined. (1945f# 108m#) **BRAZIL, Maranhão: Anajatuba**, 28f# Povoado São Benedito, 27-IX, 25-X, 22-XI, 21-XII, 26-VI and 25-VII-2009, Araújo & Carvalho, LEACOL, two females with label: *Xylocopa* (*Neoxylocopa*) *cearensis*, Silveira, F.A., 2015. 1m# *Ibidem*, 12-XII-2008, Oliveira & Vidigal, LEACOL. 12f# *Ibidem,* 14-IX, 19-IX, 01-X, 17-X, 13-VIII and 18-IX-2009, Oliveira, F.S., LEACOL, one female with label: *Xylocopa* (*Schonnherria*) *subcyanea*, Silveira, F.A., 2015. 2f# Centro, 13-VII and 11-VIII-2015, Oliveira, F.S., LEACOL. **Barreirinhas**, 6f# 20-IX, 29-II, 29-III, 27-VI and 22-VIII-1992, Brito & Mendonça, LEACOL, one female with label: *Xylocopa* (*Neoxylocopa*) *carbonaria*. 5f# Atins, 01-V, 30-IV, 17-VI and 18-VI-1989, Drummund, M.S., LEACOL. 4f# *Ibidem,* 16-VI, 17-VI and 18-

VI-1989, Glauco, LEACOL. 2f# *Ibidem,* 01-X-1987, Lacerda, L.M., LEACOL. 1f# *Ibidem*, 15-VI-1989, Sousa, D.C., LEACOL. 1f# 07-I-2015, Carvalho, G.C.A. LEACOL, with label: *Xylocopa* sp. 1f# 01-IX-1987, Maurício, LEACOL. 12f# Lençóis, 20-XI-2000, Rêgo, M.M.C., LEACOL, one female with label: *Xylocopa* sp. 11f# *Ibidem*, 07-VIII-2001, Cantanhede, LEACOL, four females with label: *Xylocopa* sp. 49f# 3m# Ponta do Mangue, 16-I, 17-I, 18-I, 19-I, 25-I, 13-II, 14-II, 17-II, 25-II, 26-II and 27-II-2015, Oliveira, F.S., LEACOL. 98f# 4m# *Ibidem*, 20-I, 18-II, 18-III, 25-IV, 19-V, 17-VI, 08-VII, 05-VIII, 05-IX, 09-X, 03-XI and 09-XII-2017, Pinto, R.S., LEACOL. 2f# *Ibidem*, 14-XI-2000, Rêgo, M.M.C., LEACOL. 1f# *Ibidem*, 04-I-2015, Silva, A.G., LEACOL, with label: *Xylocopa* sp. 67f# 7m# Povoado Cantinho, 30-VII, 21-VIII, 22-VIII, 25-IX, 29-X, 20-XI, 21-XI, 19-XII and 20-XII-2009, 13-I, 30-I, 04-II, 05-II, 04-III, 05-III, 05-IV, 06-IV, 01-V, 02-V, 06-V, 01-VI, 02-VI, 30-VI and 01-VII-2010, Gostinski & Carvalho, LEACOL\CEDU, four females with label: *Xylocopa* (*Neoxylocopa*) *cearensis,* four females with label: *Xylocopa* (*Neoxylocopa*) cfr. *carbonaria,* Silveira, F.A., 2015, two females with label: *Xylocopa* (*Neoxylocopa*) *aurulenta,* Silveira, F.A., 2015. 2f# *Ibidem*, 02-II-2008, Ribeiro, E., LEACOL, two females with label: *Xylocopa* (*Neoxylocopa*) cfr. *carbonaria,* Silveira, F.A., 2015. 1f# *Ibidem*, 16-V-2009, Silva, F.M.A., LEACOL. 2f# Povoado Queimado, 30-VIII-1989, Drummund, M.S., LEACOL. 4f# Povoado Rancharia, 28-VIII-1989, Drummund, M.S., LEACOL. **Buriticupu**, 20f# 22-I, 23-I and 24-I-1999, Pereira, C.Q.B., LEACOL\CEDU, three females with label: *Xylocopa* sp. **Cachoeira Grande**, 1f# 07-VII-2019, Ferreira, A.L., LEACOL. **Caxias**, 1f# Centro, 11-VI-2009, Moraes, P.A.M., CZMA. 1f# COHAB, 17-V-2009, Luz, L.A., CZMA. 1f# Morro do Alecrim, 26-VII-2011, Santos, A.A., CZMA. 1f# Seriema, 29-V-2009, Luz, L.A., CZMA. **Codó**, 8f# Centro, -4.457083 -43.879667, 21-III-2022, Ferreira, L.A.C., LEACOL. **Imperatriz**, 5f# Centro, -5.531528 -47.492250, 19-IV-2022, Ferreira, L.A.C., LEACOL. **Morros**, 1f# 20-XI-2010, Lima, J., LEACOL. **Paço do Lumiar**, 2f# 03-V-2010, Santos, D.F.P., LEACOL. **Peri Merim**, 1f#Parque AE. de Buritirana, -2.639500 -44.847600, 26-X-2013, Sardinha, T.L.M., LESPP. **Raposa**, 1m# Centro, 06-I-2006, Mendes & Santos, LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *carbonaria*. 3f# *Ibidem,* 06-I and 30-IX-2006, Santos, B.E., LEACOL, all with label: *Xylocopa* (*Neoxylocopa*) *cearensis*, Silveira, F.A., 2015. 60f# Ilha de Curupu, 04-VII, 15-VIII, 12-IX, 02-X, 03-X, 07-XI, 04-XII, 10-I, 09-II, 11-III, 12-III, 08-IV, 06-VI and 07-VIII-2000, Souza & Martins, LEACOL, one female with label: *Xylocopa* (*Neoxylocopa*) *carbonaria.* **Rosário**, 1f# 28-V-1991, Ferreira, K., LEACOL. **São Bento**, 1f# 08-IX-1982, Brenha, S., LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *cearensis*, Camargo, J.M.F. 1982. **São José de Ribamar**, 1f# Miritiua, 08-X-2009, Chaves, E.B., LEACOL. 2f# Praia de Panaquatira, Fabi & Carol, LEACOL. 2f# *Ibidem,* 22-XII-2016, Ferreira, L.A.C., LEACOL. 1f# *Ibidem,* 19-VII-2005, Mendonça & Rodrigues, LEACOL. 323f# 36m# *Ibidem,* 07-V, 08-V, 14-V, 22-V, 11-VI, 12-VI, 16-VI, 26-VI, 02-VII, 03-VII, 16-VII, 17-VII, 06-VIII, 07-VIII, 13-VIII, 14-VIII, 16-VIII, 27-VIII, 28-VIII, 18-IX, 24-IX, 25-IX, 06-X, 09-X, 22-X, 06-XI, 22-XI, 23-XI, 07-XII, 16-XII and 17-XII-2005, 08-I, 11-I, 14-I, 15-I, 28-I, 29-I, 12-II, 25-II, 12-III, 25-III, 26-III, 14-IV, 15-IV, 29-IV, 30-IV, 14-V, 27-V, 28-V, 25-VI, 25-VIII and 18-IX-2006, Oliveira & Mendonça, LEACOL\CEDU, six females with label: *Xylocopa* (*Neoxylocopa*) *cearensis.* 1f# *Ibidem,* 26-VI-2017, Santana, I.B.P.A., LEACOL, with label: *Xylocopa* sp. 9f# 1m# *Ibidem,* 09-V, 17-V, 08-VII, 04-VIII, 16-VIII and 14-IX-2014, Viana & Lacerda, LEACOL, four females with label: *Xylocopa* sp. **São Luís**, 1f# Bairro de Fatima, 30-IX-1991, Ribeiro, S., LEACOL. 1f# Centro, 26-VII-1985, Rêgo, F., LEACOL. 1f# *Ibidem*, 01-VIII-1987, Almeida, F, LEACOL. 1f# *Ibidem*, 11-IX-1991, Ribeiro, S., LEACOL. 1f# *Ibidem*, 18-X-1992, Gama, LEACOL. 1f# *Ibidem*, 21-XI-1992, Muniz, Z.M., LEACOL. 1f# Cidade Operária, 25-VI-1995, Isabel, LEACOL. 1f# UEMA, 01-VIII-1987, Eugênio, W., LEACOL. 7f# *Ibidem*, -2.574909 -44.206159, 28-IV-2022, Ferreira, L.A.C., LEACOL. 1f# 04-IV-1984, Silma, LEACOL. 1f# 28-VII-1984, Muniz, LEACOL. 1f# 28-VII-1985, Rodrigues, J.O., LEACOL. 1f# 23-I-1987, Lopes, A., LEACOL. 1f# 24-I-1987, Lopes, A., LEACOL. 1f# 01-VIII-1987, Ribeiro, V., LEACOL. 1f# 01-VIII-1987, LEACOL. 1f# 23-XI-1987, Willian, LEACOL. 1f# 10-VIII-1988, Matos, R., LEACOL. 1f# 12-V-1991, Fecury, LEACOL. 1f# 29-VII-1991, Brito, C., LEACOL. 1f# 17-VIII-1991, Trindade. G, LEACOL. 1f# 21-X-1991, Carvalho, G, LEACOL. 1f# 14-XII-1992, Sousa, LEACOL. 1f# 18-XII-1992, Sousa, LEACOL. 1f# 14-VII-1995, Mourão, LEACOL. 1f# 31-VII-1999, Gomes, LEACOL. 1f# 04-IV-2001, Cutrim, F, LEACOL. 1f# 04-IV-2001, Mendes, F., LEACOL. 1m# 26-IV-2001, Santos, R., LEACOL. 1m# 30-X-2001, Mendes, LEACOL. 1f# 23-V-2002, Morais, L., LEACOL. 1f# 20-XII-2002, Santos, LEACOL. 1f# 16-II-2003, Fonseca, LEACOL. 1f# 17-VII-2003, Campos, LEACOL. 1f# 15-VIII-2003, Sousa, LEACOL. 1f# 15-X-2003, Campos, LEACOL. 1f# 15-XII-2003, Luso, A.G.P, LEACOL. 1f# 15-XII-2003, Mascarenhas, L, LEACOL. 1m# 15-XII-2003, Sousa, LEACOL. 1f# 23-VI-2004, Ramos, LEACOL. 1f# 08-I-2007, Azevedo, LEACOL. 2f# 08-I-2007, Soares, E.A.S., LEACOL. 2f# 25-V-2007, Muniz, D.B., LEACOL. 1f# 15-XI-2007, Araújo & Carvalho, LEACOL. 1f# 22-II-2008, Medeiros, R.P., LEACOL. 1f# 19-IV-2008, Bezerra, A.C., LEACOL. 1f# 05-V-2008, Miranda, A.P.R., LEACOL. 1f# 06-V-2008, França, C., LEACOL. 1f# 15-V-2008, Sousa, A.C., LEACOL. 1f# 27-V-2008, Moreira, A.F.S., LEACOL. 1f# 05-VI-2008, Martins, A.P.B., LEACOL. 1f# 08-VI-2008, Sousa, F.M., LEACOL. 2f# 25-X-2008, Dutra, LEACOL. 1f# 03-XI-2008, Santos, J., LEACOL. 1m# 10-XI-2008, Santana, LEACOL. 1m# 11-XI-2008, Dutra, LEACOL. 2f# 14-XI-2008, Martins, LEACOL. 1f# 15-XI-2008, Tayllon, R, LEACOL. 1f# 28-XI-2008, Santos, J., LEACOL. 3f# 05-XII-2008, Pacheco, LEACOL. 1f# 10-XII-2008, Santana, LEACOL. 2m# 11-XII-2008, Martins, LEACOL. 1f# 22-IV-2009, Soares, M.D.S., LEACOL. 1f# 25-IV-2009, Lima, N.F.M., LEACOL. 1f# 03-V-2009, Castro, M.C., LEACOL. 1f# 17-V-2009, Amorim, I.F., LEACOL. 1f# 20-V-2009, Mendes, R.J.A., LEACOL. 1f# 27-V-2009, Araújo, W.A., LEACOL. 1f# 29-V-2009, Miranda, R.B., LEACOL. 1f# 10-VI-2009, Saraiva, C.C.F., LEACOL. 1f# 14-VI-2009, Serra & Sousa, LEACOL. 1f# 23-VIII-2009, Serra, B.V.C., LEACOL. 1f# 26-IX-2009, Araújo, A.C.M., LEACOL. 1f# 15-X-2009, Amorim, I.F., LEACOL. 1f# 17-X-2009, Firmino, A.G.L., LEACOL. 1f# 24-X-2009, Araújo, A.C.M., LEACOL. 1f# 05-XI-2009, Lindoso, N., LEACOL. 1f# 15-XII-2009, Serra, B.V.C., LEACOL. 1f# 10-IV-2010, Oliveira, C.C., LEACOL. 1f# 10-IV-2010, Silva, J.A., LEACOL. 1f# 20-V-2010, Sousa, E., LEACOL. 1f# 02-VI-2010, Calvet, LEACOL. 1f# 06-VI-2010, Sousa, E., LEACOL. 1f# 19-VI-2010, Silva, LEACOL. 1f# 27-IV-2011, Martins, K., LEACOL. 1f# 27-IV-2011, Serra, S., LEACOL. 1f# 15-VI-2011, Silva & Liborió, LEACOL. 1f# 16-VI-2011, Silva & Liborió, LEACOL. 1f# 16-VI-2011, Silva & Mendonça, LEACOL. 1f# 22-VI-2011, Silva & Mendonça, LEACOL. 1f# 24-VI-2011, Serra, S., LEACOL. 1f# 01-V-2015, Francileide, LEACOL. 1f# 20-VI-2016, LEACOL. 1f# 29-VI-2016, LEACOL. 1f# 08-I-2017, Veloso, S.R., LEACOL. 1f# 25-V-2017, Camargo, S.P., LEACOL. 1f# 08-VI-2017, Júnior, W.R.D.S., LEACOL. 5f# 09-VI-2017, Ferreira, L.A.C., LEACOL. 1f# 15-XI-2018, Noleto, LEACOL. 1f# 29-VI-2019, Mendes, M.R., LEACOL. 5f# Trindade, E., LEACOL. 1f# COHAB, 28-IX-1991, Gonçalves, LEACOL. 1f# COHAJAP, 14-VII-1985, Ramos, M., LEACOL. 20f# 1m# Estação Ecológica do Rangedor, 29-V, 12-VI, 30-VII, 25-VIII, 27-VIII, 10-IX, 11-IX, 29-IX, 11-XII and 12-XII-2010, 16-I, 29-I, 13-III, 18-III, 31-III and 16-IV-2011, Silva & Conceição, LEACOL, six females with label: *Xylocopa* sp. 1f# Olho d'água, 01-XII-1992, LEACOL. 1f# Praça Gonçalves Dias, 29-V-1991, Gonçalves, LEACOL. 576f# 13m# Praia de São Marcos, 23-XI, 24-XI, 25-XI and 23-XII-1993, 21-I, 19-II, 20-II, 14-III, 20-III, 18-IV, 18-V, 15-VI, 14-VII, 12-VIII, 09-IX, 10-IX, 08-X, 09-X, 18-X, 20-XI and 12-XII-1994, Albuquerque & Ferreira, LEACOL, eleven females with label: *Xylocopa* (*Neoxylocopa*) *cearensis*, Silveira, F.A., 2015, three females with label: *Xylocopa* (*Neoxylocopa*) *carbonaria*. 1f# Recanto Vinhais, 17-VIII-1992, Félix, W., LEACOL. 4f# Reserva Florestal da CVRD, 05-VI, 12-VI and 20-VI-1991, Rodrigues, J.O., LEACOL. 2f# Mata da CAEMA, Azevedo, A, LEACOL. 1f# Reserva Florestal do Sacavém, 13-I-1986, Brenha & Rebêlo, LEACOL, with label: *Xylocopa* (*Schonnherria*) *subcyanea*, Silveira, F.A. det., 2015. 3f#1m# *Ibidem*, 18-VIII and 27-XII-1982, 17-VII and 01-VIII-1983, Brenha, S., LEACOL, one female with label: *Xylocopa* (*Neoxylocopa*) *carbonaria*, Camargo, J.M.F.

det.,1982. 3f# *Ibidem*, 27-XI-1990 and 04-XII-1992, Lobato, A., LEACOL. 2f# *Ibidem*, 29-III-1984, Rêgo, M.M.C., LEACOL. 11f# Santa Bárbara, 24-III, 30-III, 09-IV, 16-IV, 07-V, 07-V and 28-V-2005, Machado & Botão, LEACOL. 1f# São Francisco, 01-VIII-1987, Moreira, H, LEACOL. 40f# 23-I and 24-I-1999, Brenha & Rebêlo, LEACOL. 3f# Tirirical, 08-X, 14-X and 16-X-1992, Oliveira, LEACOL.1f# Turú, 26-II-1983, Albuquerque, P.M.C., LEACOL. 1f# *Ibidem*, 20-VI-1985, Monteiro, S., LEACOL. 1f# Vinhais, 13-XII-1992, Lobato, A., LEACOL. **Tutóia**, 395f# 33m# Ilha Grande do Paulino, 11-VII, 12-VII, 23-VIII, 23-IX, 30-X, 31-X, 27-XI, 28-XI, 27-XII, 28-XII, 19-I, 23-II, 24-II, 17-III, 18-III, 17-IV, 18-IV, 22-V, 23-V, 10-VI, 24-VI, 25-VI, 15-VII, 16-IX, 14-X, 18-XI and 09-XII-2018, Neves JR & Barros, LEACOL, all with label: *Xylocopa* (*Neoxylocopa*) *cearensis*, Santos-Júnior, J.E. det., 2018. **Urbano Santos**, Margem da MA-224, -3.243100 -43.424500, 10-XI-2005, Maia, C.M., LESPP.

***Xylocopa* (*Neoxylocopa*) *frontalis* (Olivier, 1789)**

(Figures 8, 17A, 17D, 17G)

Apis frontalis Olivier, 1789: 64. Holotype: locality unknown (f#). Type locality: French Guiana, Cayenne.

Xylocopa fasciata Lepeletier, 1841: 202. Holotype: Museum Natural d'Histoire Naturelle Paris, France (m#). Type locality: Brazil.

Xylocopa nitens. Lepeletier, 1841: 176. Holotype: locality unknown (f#). Type locality: French Guiana, Cayenne.

Xylocopa frontalis quadrimaculata Meunier, 1890: 64. Holotype: locality unknown (m#). Type locality: Ecuador, Pichincha, Quito.

Xylocopa morio callichlora Cockerell, 1911: 287. Holotype: American Museum of Natural History, New York, USA (f#). Locality: Peru, Piura.

Xylocopa frontalis var. coeruleomicans Enderlein, 1913: 158. Holotype: Academie Polonaise des Sciences, Warsaw, Poland (f#). Type locality: Brazil, Espírito Santo.

Xylocopa frontalis var. viridimicans Enderlein, 1913: 158. Holotype: Academie Polonaise des Sciences, Warsaw, Poland (f#). Type locality: Panama, Chiriquí.

Xylocopa frontalis fabricii Cockerell, 1926: 658. Holotype: American Museum of Natural History, New York, USA (f#). Locality: French Guiana, Maroni.

Xylocopa frontalis roseata Cockerell, 1926: 658. Syntypes: National Museum of Natural History, Washington, D.C., USA (f#). Type locality: Ecuador.

Xylocopa frontalis trinitatis Cockerell, 1926: 658. Syntype: American Museum of Natural History, New York, USA (m#). Type locality: Trinidad and Tobago.

Xylocopa frontalis var. obscuripennis Cockerell, 1949: 484. Holotype: National Museum of Natural History, Washington, D.C., USA (m#). Type locality: Honduras, Zamorano.

Xylocopa frontalis var. purpureipennis Cockerell, 1949: 484. Holotype: National Museum of Natural History, Washington D.C., USA (m#). Type locality: Honduras, Zamorano.

Xylocopa americana Prance 1976: 238. (*nomen nudum*).

Xylocopa (*Megaxylocopa*) *frontalis*, Hurd & Moure, 1963: 151; Minckley 1998: 151.

Diagnosis. Large bees, BL approximately 31.2 mm (19.8–36; n = 902); Females: integument black with reddish bands on metasoma - typical form or entirely black - melanic form, and black pubescence (Figure 8B–D); wings dark brown and varied iridescence; presence of subocellar carina forming two arc-shaped elevations on frons (Figure 8F); inter-alveolar carina absent, in contrast to *X. amazonica* carina; lateral margins of clypeus elevated; upper line of mesosoma, in lateral view, strongly rounded (Figure 8E); posterior surface with dense punctation; T1 glabrous and T2 with sparse punctation on discal area. Males: middle ocellus smaller than the inter-lateral ocelli distance (Figure 17A); ventral surface of posterior tibia with a strong declivity (Figure 17D); metasomal terga with finer and sparser punctation (Figure 17G).

Variation. Wings with iridescence GVL in 37.5% of the individuals, GG in 20.6%, VL in 20.4%, and BVL in 4.4%. In females, 96.3% of the individuals had the melanic form and only 3.7% the typical form.

Distribution. This is the species with the greatest geographic range and occurs in most of the continental neotropical region. It is distributed from Buenos Aires, Argentina to southern Mexico (Mérida-Rivas *et al.* 2022). In Maranhão, *X. frontalis* was recorded in all systematic surveys, covering 102 of the 180 sampled points, along all physiognomies, except the steppic savanna. Of the total, 36.4% of the bees were recorded in ombrophilous forest, 32.3% in savannas, 21.2% in dunes and restingas, and 8% in flooded fields, in addition to occasional records in other ecosystems. Of this contingent, 45.9% of the bees were collected in areas without anthropic influence, 30.5% in urban areas, and 21.8% in secondary vegetation (Figure 8A). As for seasonality, *X. frontalis* was frequent in all months of the year, regardless of physiognomy.

Comments. Variations in the iridescence of the wings of *X. frontalis* have caused many invalid descriptions (Hurd 1978), therefore, the use of this character is not recommended for identification. However, *X. frontalis* is easily recognized by the presence of the subocellar carina on frons, there are two other species with similar characteristics, *X.* (*Neoxylocopa*) *fimbriata* Fabricius, 1804, with elevated prominences adjacent to ocelli with appearance of "horns" and *X.* (*Neoxylocopa*) *nautlana* Cockerell, 1904, in which the carina is narrower, and the median ocelli is above the upper margin of the eyes. *Xylocopa fimbriata* occurs in Brazil, in areas north of the Amazon and extends through Central America, while *X. nautlana* is restricted to Central America and Mexico (Mérida-Rivas *et al.* 2022). These three species form the subgenus *Megaxylocopa* Hurd & Moure (1963) which was included in *Neoxylocopa* by Minckley (1998).

Material examined. (887f# 37m#) **BRAZIL, Maranhão: Açailândia**, 1f# Margem da BR-222, -4.798861 -47.227528, 26-II-2022, Ferreira, A.W.C., LEACOL. **Alcântara**, 1f# Centro, 29-XII-1984, Brenha, S., LEACOL. 2f# Pepital, 21-VI and 20-VIII-1992, Araújo & Gonçalves, LEACOL. **Anajatuba**, 7f# Centro, 09-X-2005, 15-I-2011, 12-VII and 11-VIII-2015, Oliveira, F.S., LEACOL. 22f# 2m# Povoado São Benedito, 29-VII, 27-IX, 25-X, 20-XII and 21-XII-2008, 23-I, 24-I, 25-IV, 26-IV, 26-VI and 23-X-2009, Araújo & Carvalho, LEACOL. 26f# 6m# *Ibidem*, 09-X-2005, 11-VIII, 14-VIII, 17-VIII, 12-X, 17-X and 05-XI-2008, 27-VIII, 18-IX, 07-X and 09-X-2009, 15-I, 12-VII, 11-VIII and 15-VIII-2015, Oliveira, F.S., LEACOL. **Arari**, 1f# 23-II-2019, LEACOL. **Axixá**, 2f# 11-V-2014, Moura, LEACOL. **Bacabal**, 1f#

Fazenda Estiva, 05-I-1989, Cazuza, MPEG. **Bacabeira**, 1f# Estreito dos mosquitos, 10-VI-2016, Fontes, E., LEACOL. **Balsas**, 1f# Centro, 01-II-2011, LEACOL. 4f# Povoado Santa Luzia, 12-VI, 14-VI and 15-VI-2001, Rêgo & Ramos, LEACOL. 7f# Serra do Gado Bravo, 09-VI, 22-VII, 22-VIII and 24-IX-2006, 23-I, 27-II and 25-III-2007, Jesus & Silva, LEACOL. **Barra do Corda**, 1f# 12-VI-1978, França, W., MPEG. 2f# 20-IV-1986, Kerr, W.E., LEACOL. **Barreirinhas**, 18f# 20-IX-1991, 18-X, 18-XI, 19-XI, 20-XI-1991 and 30-IV-1992, Brito & Mendonça, LEACOL. 1m# Ponta do Mangue, 18-II-2017, Pinto, R.S., LEACOL. 3f# *Ibidem*, 14-XI-2000, Rêgo, M.M.C., LEACOL. 1m# Povoado Cantinho, 31-VII-2009, Gostinski & Carvalho, LEACOL. 49f# 2m# *Ibidem,* 16-V and 18-VII-2008, 16-V, 21-V, 12-VI, 18-VII and 19-VII-2009, 22-IV, 23-IV, 22-V, 25-V, 29-VI, 30-VI and 22-IX-2010, Silva, F.M.A., LEACOL. 4f# *Ibidem,* 01-VI-2003, 29-II and 23-IV-2004, Silva, O., LEACOL. 50f# Povoado Tabocas, 31-I, 03-III, 04-III, 08-III, 15-III, 25-III, 14-IV, 16-IV, 22-VI, 04-VIII, 22-XI and 07-XII-2005, 12-II, 26-III, 30-IV and 28-V-2006, Serra, B.D.V., LEACOL. **Buriticupu**, 1f# Centro, 02-X-1978, França, W., MPEG. 1f# *Ibidem,* 16-VIII-1984, Melo, A., LEACOL. 47f# Reserva Florestal da CVRD, 27-II, 14-III, 23-III, 06-IV, 15-IV, 15-VI, 07-VII, 10-VII, 13-VII, 27-VII, 29-VII, 10-VIII, 13-VIII, 14-VIII, 27-VIII and 02-XII-1996, Pereira & Pinto, LEACOL. **Cachoeira Grande**, 1f# 07-VII-2019, Costa, T.E.B., LEACOL. **Cajari**, 1f# 10-IV-2009, Serra & Sousa, LEACOL. **Carolina**, 1f# 01-VIII-2013, Limeira-de-Oliveira, F, CZMA. **Carutapera**, 8f# Sítio do Prata, 03-IX, 23-X, 24-X, 29-XI-2014 and 08-XII-2018, Ferreira, L.A.C., LEACOL. **Caxias**, 1f# Trezidela, 31-V-2009, Silva, M.M.L., CZMA. **Chapadinha**, 3f# 25-XI-2011, Barbosa & Pinto, LEACOL. **Colinas**, Centro, -6.029053 -44.239475, 24-III-2022, Ferreira, L.A.C., LEACOL. **Cururupu**, 44f# 21-VIII, 22-VIII, 23-VIII and 29-IX-2015, 09-IV, 07-V, 23-VII, 24-VII, 27-VIII and 28-VIII-2016, Dos Anjos, J.V., LEACOL. 1f# 19-VIII-2014, Azevedo, G.G., LESPP. 3f# 19-VIII and 22-VIII-2014, Marinho, D.P, LESPP. **Formosa da Serra Negra**, 1f# 25-IX-2009, Muniz, D.B., LESPP. 1f# Parque Estadual do Mirador, 29-XI-2009, Maia, C.M., LEACOL. 1f# *Ibidem*, 03-XII-2009, Mendonça, M.W.A., LEACOL. 1f# *Ibidem*, 10-XII-2012, Araújo & Brito, LEACOL. **Fortaleza dos Nogueiras**, 1f# Fazenda Santa Maria, 07-V-2010, Ferreira, A.C.S., CZMA. 1f# Margem da MA-006, -7.226917 -45.892472, 23-II-2022, Ferreira, A.W.C., LEACOL. **Grajaú**, 1f# Centro, -5.817687 -46.138721, 20-IV-2022, Ferreira, L.A.C., LEACOL. **Icatu**, 1f# -2.792224 -43.853261, 21-III-2022, Ferreira, A.W.C., LEACOL. **Lago da Pedra**, 1m# Fazenda Gloriosa, 17-II-2022, Jonna, LEACOL. **Lima Campos**, 1f# 19-II-2021, Ribeiro, R., LEACOL. **Maranhãozinho**, 1f# Ximborendá, 08-XII-2000, Rêgo, M.M.C., LEACOL. **Matinha**, 2f# 15-X-2007, Farias & Pinto, LEACOL. **Paço do Lumiar**, 1f# 03-V-2010, Santos, D.F.P., LEACOL. **Peri Mirim**, 1m# Parque AE. de Buritirana, -2.639500 -44.847600, 20-V-2013, Azevedo, G.G., LESPP. 2f# 1m# *Ibidem*, -2.639500 -44.847600, 26-V-2013 and 08-IV-2014, Sardinha, T.L.M., LESPP. **Raposa**, 2f# Ilha de Curupu, 07-XI-1999 and 07-VII-2000, Souza & Martins, LEACOL. 1f# 29-VI-2018, Borges, P.D., LEACOL. **Riachão**, Margem da BR-230, -7.410556 -46.376111, 23-II-2022, Ferreira, A.W.C., LEACOL. **Rosário**, 1f# 03-II-1995, Silva, A., LEACOL. **Santa Inês**, 2f# 26-X-2000, Carvalho & Luz, LEACOL. **Santo Amaro do Maranhão**, 1f# 10-IV-2009, Oliveira, K.K.C., LEACOL. 1f# 07-XII-2009, Costa, D.S.F., LEACOL. **São João dos Patos**, 2f# Centro, -6.487472 -43.694750, 24-III-2022, Ferreira, L.A.C., LEACOL. **São José de Ribamar**, 1m# Miritiua, 07-XI-2009, Chaves, E.B., LEACOL. 1f# Parque Vitória, 05-V-1998, Coelho, LEACOL. 2f# Praia de Panaquatira, 22-XII-2016, Ferreira, L.A.C., LEACOL. 114f# 1m# *Ibidem,* 07-V, 08-V, 22-V, 12-VI, 17-VI, 26-VI, 03-VII, 07-VIII, 13-VIII, 14-VIII, 28-VIII, 06-IX, 24-IX, 25-IX, 09-X, 21-X, 06-XI, 23-XI, 06-XII and 07-XII-2005, 07-I, 08-I, 11-I, 14-I, 15-I, 28-I, 29-I, 02-II, 11-II, 12-II, 24-II, 25-II, 12-III, 26-III, 14-IV, 15-IV, 30-IV, 14-V, 22-V, 28-V, 28-VI and 23-XI-2006, Oliveira &

Mendonça, LEACOL. 21f# *Ibidem,* 22-I, 28-V, 25-VI, 30-VII, 27-VIII, 27-IX and 30-XII-2017, Santana, I.B.P.A., LEACOL. 1f# *Ibidem,* 28-V-2006, Silva & Conceição, LEACOL. 1f# *Ibidem,* 30-VIII-2014, Viana & Lacerda, LEACOL. 1f# Sítio Aguahy, 22-X-2007, Azevedo, G.G., LESPP. 2f# *Ibidem,* 13-XI-2010, Castro, M.C., LEACOL. 1f# *Ibidem,* 19-X-2007, Lacerda, L.M., LESPP. 1f# *Ibidem,* 20-X-2006, Soares, E.A.T., LEACOL. 1f# 06-III-1983, Brenha, S., LEACOL. 1f# 16-V-2010, Silva, A.P.S., LEACOL. 1f# 24-VI-2017, Gabriella, R., LEACOL. 1f# 16-II-2019, LEACOL. **São Luís**, 1f# Bacanga, 18-XI-1992, Gama, LEACOL. 1f# 1m# Bairro de Fátima, 09-IV-1991, Ribeiro, S., LEACOL. 1f# Centro, 12-V-1991, Ferreira, K., LEACOL. 1f# *Ibidem*, 12-X-1992, Gama, LEACOL. 1f# *Ibidem*, 17-X-1989, Glauco, LEACOL. 3f# *Ibidem*, 27-X-1989, Glauco, LEACOL. 10f# UEMA, 28-IV-2022, Ferreira, L.A.C., LEACOL. 31f# Estação Ecológica do Rangedor, 25-III-2006, 29-I-2009, 29-V, 29-X, 10-XII, 11-XII, 12-XII and 28-XII-2010, 03-I, 15-I, 16-I, 28-I, 29-I, 09-VI and 03-I-2012, Silva & Conceição, LEACOL. 33f# Alumar, 22-VIII, 27-XI, 28-XI, 29-XI, 05-XII, 06-XII, 12-XII, 19-XII, 26-XII and 28-XII-2002, 03-I and 09-I-2003, Carvalho, C.C., LEACOL. 3f# *Ibidem,* 30-X and 12-XI-1999, Cruz & Sodré, LEACOL. 1f# Itapiracó, 14-IX-1992, Oliveira, LEACOL. 1f# Maracanã, 20-VII-2013, Ferreira, L.A.C., LEACOL. 1f# Maracanã, 08-VI-2019, Lima, L.S., LEACOL. 1f# Praça Gonçalves Dias, 17-II-1991, Apocalipse, M.S., LEACOL. 1f# *Ibidem*, 02-V-1991, Araújo, A., LEACOL. 46f# Praia de São Marcos, 24-XI-1993, Albuquerque & Ferreira, LEACOL. 24-XI-1993, 21-I, 10-II, 19-II, 20-II, 18-IV, 18-V, 15-VI, 14-VII, 12-VIII, 10-IX and 09-X-1994, Albuquerque & Ferreira, LEACOL. 5f# 1m# Reserva Florestal da CVRD, 27-II, 23-VII, 05-VIII, 23-VIII, 18-IX and 21-XII-1991, Apocalipse & Rodrigues, LEACOL. 31f# 1m# Reserva Florestal do Sacavém, 17-VII, 01-VIII, 12-X, 23-X, 06-XI, 21-XI and 18-XII-1983, 04-II, 21-II, 11-III, 28-IV, 21-VI, 21-VII, 16-IX and 23-VII-1985, Brenha & Rebêlo, LEACOL. 1f# Turú, 03-VIII-2002, Aragão-Filho, W.C., LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *grisescens.* 3f# UFMA, 17-XI-2003, Souza, LEACOL. 1f# *Ibidem*, 12-VIII-2016, Barros, H.C., LEACOL. 1f# *Ibidem*, 09-VI-2017, Ferreira, L.A.C., LEACOL. 1f# *Ibidem*, 08-II-2018, Pereira, G.C.S., LEACOL. 2f# *Ibidem*, 03-IV-2019, Ferreira, A.W.C., LEACOL. 1f# 12-I-1980, Lima, LEACOL. 1f# 01-VIII-1987, Pacheco, R., LEACOL. 1f# 10-VII-1988, Garcia, LEACOL. 1f# 27-X-1989, Glauco, LEACOL. 1f# 20-X-1990, Nogueira, LEACOL. 1f# 11-XI-1990, Macedo, R., LEACOL. 1f# 15-XI-1990, Ferreira, LEACOL. 1f# 15-XI-1990, Silva, S., LEACOL. 1f# 20-XI-1990, Garcia, R.S., LEACOL. 1f# 28-XI-1990, Lobato, A., LEACOL. 1f# 05-XII-1990, Sousa, S., LEACOL. 1f# 23-VII-1991, Rodrigues, J.O., LEACOL. 1f# 05-VIII-1991, Rodrigues, J.O., LEACOL. 1f# 29-VIII-1991, Brito, C., LEACOL. 1f# 17-XI-1992, Boas, V., LEACOL. 1f# 18-VIII-1994, Bessa, C.N., LEACOL. 1f# 26-VI-1995, Francinaldo, LEACOL. 1f# 16-VI-1996, Lira, M.C., LEACOL. 1f# 17-VI-1996, Araújo, J.C., LEACOL. 1f# 26-VII-1999, Gomes, LEACOL. 1f# 20-IV-2001, Maia, C., LEACOL. 1f# 26-V-2001, Viana, LEACOL. 1f# 25-IV-2002, Patrício, LEACOL. 7f# 15-XII-2003, Vasconcelos, G, LEACOL. 1f# 04-IV-2005, Miranda, W.S., LEACOL. 1f# 29-VI-2005, Carneiro, E., LEACOL. 1f# 28-I-2007, Mendes, LEACOL. 1f# 25-V-2007, Costa, B.R.R., LEACOL. 1f# 14-VI-2007, Souza, A.B., LEACOL. 1f# 17-VII-2007, Muniz, D.B., LEACOL. 1f# 27-X-2007, Ribeiro & Silva, LEACOL. 1f# 02-XI-2007, Ferreira, D.I.S., LEACOL. 1f# 04-XI-2007, Ferreira, D.I.S., LEACOL. 1f# 05-V-2008, Medeiros, R.P., LEACOL. 1f# 20-X-2008, Oliveira, D., LEACOL. 1f# 05-XI-2008, Costa, C., LEACOL. 1f# 28-XI-2008, Lopes, L., LEACOL. 1f# 03-XII-2008, Oliveira, D., LEACOL. 1f# 12-XII-2008, Cardoso, LEACOL. 1f# 12-XII-2008, Santos, J., LEACOL. 1f# 18-IV-2009, Sena, J.J.B., LEACOL. 1f# 08-V-2009, Lemos, A.W.S., LEACOL. 1f# 10-V-2009, Ferreira, B.R.A., LEACOL. 1f# 16-V-2009, Ferro, J.C.B., LEACOL. 1f# 19-V-2009, FIgueiredo, C.E.C., LEACOL. 1f# 27-V-2009, Silva, W.F., LEACOL. 1f# 27-V-2009, Silva, W.S., LEACOL. 1f# 29-V-2009, Serra & Sousa, LEACOL. 1f# 06-VI-2009, Carlos, LEACOL. 1f# 14-VI-2009, Coelho, P.L., LEACOL. 1f# 15-VI-2009, Ferro, J.C.B., LEACOL. 1f# 17-IX-2009, Aguiar, I.R.G., LEACOL. 1f# 12-X-2009, Santos, W.C., LEACOL. 1f# 17-X-2009, Amorim, I.F., LEACOL. 1f# 18-X-2009, Coelho, R.C., LEACOL. 1f# 28-X-2009, Serra, F.C.V., LEACOL. 1f# 10-XI-2009, Carvalho, L.M., LEACOL. 1f# 21-XI-2009, Firmino, A.G.L., LEACOL. 1f# 22-XI-2009, Santos, W.C., LEACOL. 1f# 05-XII-2009, Santos, W.C., LEACOL. 1f# 29-III-2010, Bandeira, M, LEACOL. 1f# 31-III-2010, Silva, R.S., LEACOL. 1f# 16-IV-2010, Silva, R.S., LEACOL. 1f# 24-IV-2010, Araújo, B.O., LEACOL. 1f# 24-IV-2010, Tavares, D.B., LEACOL. 1f# 30-IV-2010, Oliveira, L.K., LEACOL. 1f# 04-V-2010, Silva, R.S., LEACOL. 1f# 17-V-2010, Bandeira, M, LEACOL. 1f# 31-V-2010, Martins, S.S., LEACOL. 1f# 04-VI-2010, Bras, X.L., LEACOL. 2f# 04-VI-2010, Cerqueira, A.S., LEACOL. 1f# 04-VI-2010, Rodrigues, R.C., LEACOL. 1f# 06-VI-2010, Calvet, LEACOL. 1f# 06-VI-2010, Seixas & Silva, LEACOL. 2f# 06-VI-2010, Sousa, E., LEACOL. 1f# 09-VI-2010, Almeida, C., LEACOL. 1f# 11-VI-2010, Rodrigues, R.C., LEACOL. 1f# 11-VI-2010, Santos, R.M., LEACOL. 1f# 16-VI-2010, Oliveira, F.F., LEACOL. 1f# 17-VI-2010, Almeida, C., LEACOL. 1f# 18-VI-2010, Sousa, E., LEACOL. 2f# 20-VI-2010, Sousa, E., LEACOL. 1f# 15-IX-2010, Pereira, D.M., LEACOL. 1f# 17-X-2010, Rocha, T.K.M., LEACOL. 1f# 06-IV-2011, Ferreira, LEACOL. 1f# 27-IV-2011, Martins, K., LEACOL. 1f# 05-V-2011, Oliveira, C.B.C., LEACOL. 1f# 15-V-2011, Silva & Libório, LEACOL. 1f# 06-VI-2011, Silva, W.C., LEACOL. 1f# 18-VI-2011, Silva & Mendonça, LEACOL. 1f# 09-I-2012, Carvalho, G.C.A., LEACOL. 14f# 14-III-2014, Silva, W & Carvalho, J, LEACOL. 1f# 08-VI-2014, Silva, A., LEACOL. 1f# 22-VI-2014, Oliveira, F., LEACOL. 1f# 07-VII-2016, LEACOL. 1f# 15-VIII-2016, LEACOL. 1f# 04-VII-2017, Araújo, T.C., LEACOL. 1f# 26-VII-2017, Veloso, R.S., LEACOL. 1f# 24-V-2018, Araújo, A.C.C., LEACOL. 1f# 24-V-2018, Souza, E.R., LEACOL. 1f# 15-VI-2019, Silva, S.P., LEACOL. 1f# 29-VI-2019, Ferreira, G.F., LEACOL. **Timon**, 1f# Centro, -5.108167 -42.833889, 22-III-2022, Ferreira, L.A.C., LEACOL. **Tutóia**, 2f# Ilha Grande do Paulino, 19-I-2018 and 24-II-2018, Neves JR & Barros, LEACOL. **Urbano Santos**, 8f# 1m# Fazenda Paineiras, 18-V, 26-IX and 13-XII-2003, Mendes & Ramos, LEACOL, one female with label: *Xylocopa* (*Neoxylocopa*) *grisescens*. 90f# Povoado Cajueiro, 27-XI-2004, 31-I, 03-III, 04-III, 08-III, 09-III, 15-III, 21-III, 24-III, 25-III, 14-IV and 16-IV-2005, Serra, B.D.V., LEACOL. **Vitória do Mearim**, 7f# Margem da ferrovia SLZ-Carajás, 20-II, 04-VI, 24-VI, 25-VI, 28-VIII, and 24-X-1992, Ferreira & Santos, LEACOL\CEDU, one female with label: *Xylocopa* (*Neoxylocopa*) *frontalis.* 1f# 04-VI-1991, Rêgo, M.M.C., LEACOL. 1f# 04-VI-1991, Santos, C.S., LEACOL.

***Xylocopa* (*Neoxylocopa*) *grisescens* Lepeletier, 1841**

(Figures 9, 17C, 17E)

Xylocopa lanigera Illiger, K. 1806: 151 (*nomen nudum*).

Xylocopa grisescens Lepeletier, A. L. M. 1841: 178. Holotype: Museo Regionale di Scienze Naturale, Torino, Italy (f#). Type locality: 'Patrie inconnue'.

Diagnosis. Large bees, BL approximately 30 mm (26–32.5; n = 84); Females: integument entirely black, mesosoma with whitish-yellow pubescence (Figure 9B–D); wings dark brown and iridescence predominantly GVL; central axis of the vertex with a distinct elevation (Figure 9F) and posterior margin with whitish-yellow pubescence; T2 with dense punctation on discal area (Figure 9E). Males: middle ocelli larger than the lateral ocelli (Figure 17C); vertex with sparse and short pubescence; metasomal terga with dense punctation.

Distribution. Present in Paraguay and Brazil, in the states of Alagoas, Amapá, Bahia, Ceará, Goiás, Maranhão, Mato Grosso, Minas Gerais, Paraíba, Pará, Pernambuco, Piauí, Rio Grande do Norte, Sergipe, São Paulo, and Tocantins (Hurd 1978; Moure & Melo 2022). In Maranhão, *X. grisescens* had a wide distribution with a predominance of records in open areas, 71% of the individuals were recorded in park savanna, 12.1% in restingas, 4% in flooded fields, and 2.4% in deciduous seasonal forest. There were no records in the northwest, where there is influence of the Amazon Rainforest, but the number of records of any species in this sector is limited. Of the total, 49.2% of the bees were collected in areas without anthropic influence, 39.5% in urban areas, and 8.9% in secondary vegetation (Figure 9A). *Xylocopa grisescens* was frequent in all months of the year, regardless of physiognomy.

Comments. In a general aspect, *X. grisescens* is very similar to *X. cearensis* - typical form, with a clear difference in size between them, however, although *X. grisescens* has few morphological variations, some individuals exhibited sizes smaller than 28 mm, which may generate uncertainty in the identification. This species is common in open areas, and is predominant in northeastern Brazil, in areas of Cerrado and Caatinga (Zanella 2000; Silva *et al.* 2009).

Material examined. (124f# 3m#) **BRASIL, Maranhão: Arari**, 1f# Lago da Morte, 25-XII-2021, Ferreira, L.A.C., LEACOL. **Bacabal**, 2f# Fazenda Estiva, 03-I-1989, Cazuza, MPEG. **Balsas**, 5f# Povoado Santa Luzia, 12-VI and 14-VI-2001, 16-IX, 17-IX and 18-IX-2002, Rêgo & Ramos, LEACOL. 5f#Serra do Gado Bravo, 23-I-2006 and 27-II-2007, Carvalho & Jesus, LEACOL. 8f# *Ibidem*, 23-I-2006 and 27-II-2007, Jesus & Silva, LEACOL. **Barreirinhas**, 11f# 19-II, 09-VIII, 28-IX and 28-XII-1991, 29-III, 30-IV, 20-V, 26-VI and 22-XII-1992, Brito & Mendonça, LEACOL. 3f# 04-I-2015, Carvalho, G.C.A., LEACOL. 1f# Lençóis, 05-VIII-2001, Cantanhede, LEACOL. 6f# Ponta do Mangue, 17-I, 18-I and 19-I-2015, Oliveira, F.S., LEACOL. 8f# *Ibidem,* 20-I, 18-III, 25-IV, 19-V, 08-VII, 05-VIII and 09-XII-2017, Pinto, R.S., LEACOL. 1f# Povoado Cantinho, 30-VI-2010, Silva, F.M.A., LEACOL. 4f# *Ibidem,* 01-VI-2003, 24-IV and 13-VII-2004, Silva, O., LEACOL. 1m# Povoado Tabocas, 22-VI-2005, LEACOL. **Carolina**, 1f# 28-XII-2020, Isabela, LEACOL. **Caxias**, 1f# Centro, 21-IV-2011, Ferreira, A.C.S., CZMA. 35f# Centro, CZMA. **Codó**, 2f# 21-V-1907 and 18-VI-1907, Ducke, A., MPEG. **Formosa da Serra Negra**, 8f# Parque Estadual do Mirador, 09-XII-2011, 03-III, 04-V, 09-VI, 09-VII and 11-VII-2012, Araújo & Brito, LEACOL. 1f# *Ibidem,* 03-XII-2009, Mendonça, M.W.A., LEACOL. **Imperatriz**, 1f# 13-VI-1978, França, W., MPEG. **Riachão**, 1f# Centro, 24-II-2022, Ferreira, A.W.C., LEACOL. **São Bento**, 2m# 08-IX-1982, Brenha, S., LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *grisescens*, Camargo, J.M.F. det, 1982. **São Luís**, 4f# Estação Ecológica do Rangedor, 23-IV, 29-VI and 30-VI-2010, Silva & Conceição, LEACOL. 9f# Reserva Florestal do Sacavém, 04-IX, 06-IX and 08-IX-1982, 21-XI-1983 and 19-IV-1984, Brenha & Rebêlo, LEACOL. **Sítio Novo**, 1f# 26-IX-2009, Muniz, D.B., LESPP. **Tutóia**, 1f# Ilha Grande do Paulino, 08-XII-2019, Barros, H.C., LEACOL. **Urbano Santos**, 1f# 18-V-2003, LEACOL. 1f# 26-IX-2003, LEACOL. 1f# 27-II-2004, LEACOL. **Vitória do Mearim**, 1f# Margem da ferrovia SLZ-Carajás, 12-VIII-1991, Ferreira & Santos, LEACOL.

***Xylocopa* (*Neoxylocopa*) *hirsutissima* Maidl, 1912**

(Figure 10)

Xylocopa hirsutissima Maidl, 1912: 315. Syntype: Naturhistorisches Museum in Wien, Wien, Austria (f#). Type locality: Paraguay, 'San Luis'.

Diagnosis. Medium-sized bees, BL approximately 23.2 mm (21.1–24.9; n = 10); Females: integument entirely black, mesosoma with black and plumose pubescence (Figure 10B–D); wings dark brown and iridescence predominantly BVL; metasoma with long dense pubescence, with a velvety appearance (Figure 10E–F).

Distribution. Present in Bolivia, Paraguay, and Brazil, in the states of Bahia, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Pará, Piauí, Rio de Janeiro, Rondônia, and São Paulo (Hurd 1978; Moure & Melo 2022). For Maranhão we present the first records, distributed in park savanna (81.5%), deciduous seasonal forest (11.1%), and steppic savanna (7.4%). Of this total, 59.3% of the bees were collected in urban areas, 33.3% in preserved areas, and 3.7% in secondary vegetation (Figure 10A). As for seasonality, *X. hirsutissima* was recorded in all months of the year, but more frequently during the months of March to June, a period characterized by the rainy season in the region.

Comments. In general, *X. hirsutissima* can be confused with *X. cearensis* - melanic form but can be easily recognized by the long and dense pubescence on the metasoma. The occurrence of *X. hirsutissima* is more extensive and occupies other transition areas (Marchi & Alves-dos-Santos 2013), frequently associated with open areas. In Maranhão, *X. hirsutissima* was the only species recorded in steppic savanna and in contact areas with Caatinga, and a notable concentration of records was observed in the southern Cerrado of the state.

Material examined. (27f#) **BRAZIL, Maranhão: Balsas**, 4f# Serra do Gado Bravo, 24-IX-2006, 27-II and 25-III-2007, Jesus & Silva, LEACOL\CEDU, one female with label: *Xylocopa* (*Neoxylocopa*) *frontalis,* three females with label: *Xylocopa* (*Neoxylocopa*) *cearensis.* 2f# *Ibidem,* 25-X and 26-XI-2006, Silva, F.M.A., LEACOL. **Barão de Grajaú**, 2f# Centro, -6.754583 43.023750, 23-III-2022, Ferreira, L.A.C., LEACOL. **Caxias**, 1f# Cangalheiro, 17-IV-2009, Costa, A.L., CZMA. 1f# Centro, 14-V-2004, Silva, V.M., CZMA. 2f# *Ibidem*, 13-IV-2009, Moraes, P.A.M., CZMA. 1f# *Ibidem*, 01-V-2009, Bezerra, F. A., CZMA. 1f# *Ibidem*, 01-VI-2009, Santos, F.J.L., CZMA. 1f# *Ibidem*, 05-VI-2009, Pinho, A.N., CZMA. 1f# Centro, 13-VI-2009, Moraes, P.A.M., CZMA. 1f# Fazenda Bode, 18-I-1997, Oliveira, F.L., CZMA. 1f# Morro do Alecrim, 10-VI-2009, Barbosa, E.A.S., CZMA. 1f# *Ibidem*, 30-VI-2011, Barbosa, E.A.S., CZMA. 1f# Multirão, 24-V-2011, Lima, E.S., CZMA. 1f# Povoado Coités, 31-VII-2015, Limeira-de-Oliveira, F., CZMA. 1f# Povoado Poço Dantas, 29-V-2010, Reis, L.L., CZMA. 1f# Volta Redonda, 04-VII-2011, Nascimento, D.C., CZMA. **Formosa da Serra Negra**, 2f# Parque Estadual do Mirador, 03-XII-2009, Rêgo, M.M.C., LEACOL. **Parnarama**, 1f# Povoado Brejo de São Félix, 5°29'44.6"S 43°29'30.9"W, 03-VI-2010, Sousa, S.S.S., CZMA. **Timon**, 1f# Centro, -5.108167 -42.833889, 22-III-2022, Ferreira, L.A.C., LEACOL.

***Xylocopa* (*Neoxylocopa*) *nigrocincta* Smith, 1854**

(Figure 11)

Xylocopa nigro-cincta Smith, 1854: 354. Holotype: locality unknown (f#). Type locality: 'South America'.

Xylocopa nigrocinta jujuyensis Brèthes, 1916: 410. Lectotype: Museo Argentino de Ciencias Naturales (f#). Subsequent designation: Hurd & Moure 1961: 183. Type locality: Argentina, Jujuy.

Xylocopa schulthesii Dusmet & Alonso, 1924: 52. Holotype: Museo Nacional de Ciencias Naturales, Madrid, Spain (f#). Type locality: Brazil, Rio Grande do Sul.

Xylocopa (*Neoxylocopa*) *suspecta* Moure & Camargo, 1988: 209. Holotype: Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (f#). Type locality: Brazil, Ribeirão Preto. synonymy by Agostini, 2021: 52.

Diagnosis. Medium-sized bees, BL approximately 22.7 mm (20–25.2; n = 159); Females: integument black with reddish bands on metasoma – typical form or entirely black – melanic form, and black pubescence (Figure 11B–D); wings dark brown and strong metallic iridescence, predominantly GG and GVL; small inter-alveolar carina and absence of subocellar carina; dorsal surface of scutellum convex and smoothly rounded, transition with posterior surface forming a curved edge with obtuse angle (Figure 11E); posterior surface with sparse punctation; T2 with moderate punctation on discal area. Males: ventral surface of posterior tibia with entirely yellowish pubescence; metasomal terga with moderately sparse punctation.

Variation. Wings with iridescence GG in 41.7% of the individuals, GVL in 40.2%, BVL in 10.6%, and VL in 7.6%. All individuals listed had only the melanic form.

Distribution. Present in Argentina, Bolivia, Uruguay, Paraguay, and Brazil, in the states of Acre, Amapá, Amazonas, Bahia, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Roraima, Santa Catarina, São Paulo, and Tocantins (Hurd 1978; Moure & Melo 2022). In Maranhão, *X. nigrocincta* was first reported by Gostinski *et al.* (2016) (identified as *X. suspecta*). The listed records are mostly distributed in the northern region of the state and are in the following physiognomies: ombrophilous forest (50.5%), park savanna (24.7%), flooded fields (18.6%), and dunes/restingas (5.1%). Most records were in areas with anthropic influence: 42.3% in urban areas, 26.8% in secondary vegetation, and 4.6% in agricultural sectors (Figure 11A). In MA, *X. nigrocincta* exhibited different seasonal patterns depending on the physiognomy: in forested areas, they were more frequent in the months of June to September, an interval characterized by the end of the rainy season and the beginning of the dry season; in savanna areas, the opposite pattern was observed, that is, the highest frequency was in the first semester, especially in March and April, when there is the highest rainfall in the state.

Comments. In general, *X. nigrocincta* has distinct variations, the iridescence of the wings, for example, can be presented in almost all the patterns listed here. It is likely that due to this, many individuals have been incorrectly identified, such as *X. cearensis* associated with pattern VL and *X. frontalis* with pattern GVL or BVL. For these cases, the dissociation is due to the scutellum form and punctation of its posterior surface and the absence of the subocellar carina, respectively. In Maranhão, *X. nigrocincta* had only the melanic form, previously designated as *X. suspecta*, where it was recently synonymized by Agostini (2021), based on morphological and molecular data. The typical form, therefore, presents the same pattern of reddish bands on metasoma of *X. frontalis* - typical form and its distribution is concentrated in southern Brazil and northern Argentina (Lucia *et al.* 2014).

Material examined. (194f# 3m#) **BRAZIL, Maranhão: Anajatuba**, 2f# 11-VIII and 12-VIII-2015, Oliveira, F.S., LEACOL. 7f# Povoado São Benedito, 27-VIII, 27-IX, 25-X and 21-XII-2008, 25-IV, 26-IV and 25-VI-2009, Araújo & Carvalho, LEACOL, all with label: *Xylocopa* (*Neoxylocopa*) *frontalis.* 7f# *Ibidem,* 14-IX, 01-X and 05-XI-2008, 20-III, 18-IX and 07-X-2009, Oliveira & Vidigal, LEACOL\CEDU, four females with label: *Xylocopa* sp. 11f# *Ibidem,* 01-II, 14-VIII, 17-X and 05-XI-2008, 14-VIII, 27-VIII, 28-VIII, 18-IX, 17-X, 11-VIII and 12-VIII-2015, Oliveira, F.S., LEACOL, three females with label: *Xylocopa* sp. **Bacabal:** 1f# Fazenda Estiva, 04-I-1989, Cazuza, MPEG. 1f# *Ibidem*, 05-I-1989, Torres, M.F., MPEG. **Balsas:** 1f# 22-VIII-2006, Jesus & Silva, CEDU, with label: *Xylocopa* (*Neoxylocopa*) *frontalis.* **Barra do Corda:** 2f# 12-VI-1978, Torres, M.F., MPEG. **Barreirinhas:** 1f# Atins, 19-VI-1989, Cordeiro, J., LEACOL. 1f# *Ibidem*, 19-VI-1989, Drummond, M.S., LEACOL. 2f# *Ibidem,* 16-VI and 17-VI-1989, Glauco, LEACOL. 4f# Lençóis, 14-XI and 20-XI-2000, Rêgo, M.M.C., LEACOL, all with label: *Xylocopa* sp. 1f# 31-VII-2010, Silva & Conceição, LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *suspecta*. 1f# Rêgo, M.M.C., CEDU, with label: *Xylocopa* sp. 2f# Ponta do Mangue, 18-III and 09-X-2017, Pinto, R.S., LEACOL. 4f# Povoado Cantinho, 20-XII-2009, 13-I and 05-II-2010, Gostinski & Carvalho, LEACOL. 1f# *Ibidem*, 11-IX-2010, Ribeiro, E., CEDU, with label: *Xylocopa* (*Neoxylocopa*) *cfr. carbonaria*, Silveira, F.A. det., 2015. 15f# *Ibidem*, 12-VI-2009, 22-IV, 23-IV, 21-V and 30-VI-2010, Silva, F.M.A., LEACOL\CEDU, six females with label: *Xylocopa* sp. 1f# *Ibidem*, 01-VI-2003, Silva, O., LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *frontalis*. 17f# Povoado Tabocas, 11-II, 04-III, 25-III, 16-IV and 31-V-2005, Serra, B.D.V., CEDU, three females with label: *Xylocopa* (*Neoxylocopa*) *suspecta,* Zanella, F.C.V. det., 2009, seven females with label: *Xylocopa* (*Neoxylocopa*) *carbonaria* and seven females with label: *Xylocopa* sp. **Carutapera:** 1f# Sítio do Prata, 12-VIII-2013, Ferreira, L.A.C., LEACOL, with label: *Xylocopa* (*Neoxylocopa*) *suspecta*. **Caxias:** 1f# Reserva Ecológica Ilhamum, 17-IV-2009, Santos, S.M., CZMA. **Chapadinha:** 1f# Centro, 25-VI-2011, Barbosa & Pinto, LEACOL, with label: *Xylocopa* sp. **Morros:** 1f# 22-III-2022, Ferreira, A.W.C., LEACOL. **Peri Mirim:** 1f# 1m# Parque AE. de

Buritirana, -2.639500, -44.847600, 08-III and 02-IV-2014, Sardinha, T.L.M., LESPP. **Santa Inês:** 1f# 05-X-1978, Neto, R.B., MPEG. **São José de Ribamar:** 1f# 30-VI-2017, Santos, A.L.G., LEACOL. 1f# Sítio Aguahy, 13-X-2007, Lacerda, L.M., LESPP. 1m# *Ibidem*, 23-I-2011, Trindade, O., LESPP. **São Luís:** 1f# Bacanga, 20-IV-1998, Pinheiro, LEACOL. 1f# 01-XI-1992, Melo, R., LEACOL. 1f# 12-VIII-1999, França, LEACOL. 3f# UEMA, -2.574909 -44.206159, 28-IV-2022, Ferreira, L.A.C., LEACOL. 1f# 17-IV-2005, Sousa, R.M.S., LEACOL. 1f# 10-IX-2007, Abreu, J., LEACOL. 1f# 01-V-2008, Medeiros, R.P., LEACOL. 1f# 01-V-2008, Oliveira, L.P., LEACOL. 1f# 03-V-2008, Medeiros, R.P., LEACOL. 1f# 05-V-2008, Moraes, L.S., LEACOL. 1f# 08-V-2008, Freitas, M., LEACOL. 1f# 24-V-2008, Pinheiro, L, LEACOL. 1f# 14-VI-2009, França, H.S., LEACOL. 1f# 21-IX-2009, Silva, T.H.D., LEACOL. 1f# 29-III-2010, Siqueira, A.I.N., LEACOL. 1f# 03-VI-2010, Santana, I.B.P.A., LEACOL. 1f# 21-X-2010, Gomes, L., LEACOL. 1f# 03-XII-2010, Carvalho, L.M., LEACOL. 1f# 06-IV-2011, Fonseca, LEACOL. 1f# 08-V-2017, Silva, L.A.S., LEACOL. 1f# 01-VII-2017, Marques, L.L., LEACOL. 1f# 05-VI-2018, Silva-Filho, A.F.A., LEACOL. 1f# Ferreira, R.G., LEACOL. 45f# Estação Ecológica do Rangedor, 15-IV-2006, 30-VII, 31-VII, 27-VIII, 28-VIII, 10-IX, 11-IX, 24-IX, 29-X, 30-XII-2010 and 16-I-2011, Silva & Conceição, LEACOL, eight females with label: *Xylocopa* sp., Silveira, F.A. det., 2015, one female with label: *Xylocopa* (*Neoxylocopa*) *suspecta.* 15f# Alumar, 21-VIII, 04-IX, 18-IX and 16-XII-1999, 11-III, 27-V, 09-VI, 24-VI, 10-VII, 09-X and 30-X-2000, Cruz & Sodré, LEACOL, two females with label: *Xylocopa* sp. 1f# Praia de São Marcos, 18-V-1994, Albuquerque & Ferreira, LEACOL. 1f# Reserva Florestal da CVRD, 26-VI-1991, Apocalipse & Rodrigues, CEDU, with label: *Xylocopa* (*Neoxylocopa*) *suspecta*, Zanella, F.C.V. det., 2009. 6f# Reserva Florestal do Sacavém, 14-XI-1982, 02-I, 30-VIII 16-IX-1984, Brenha & Rebêlo, LEACOL. **Urbano Santos:** 1f# 08-I-2000, LEACOL. 1f# Povoado Cajueiro, 03-III-2005, Serra, B.D.V., CEDU, with label: *Xylocopa* (*Neoxylocopa*) *carbonaria*. 1f# *Ibidem*, 24-III-2005, Serra, B.D.V., CEDU, *Xylocopa* sp. **Viana:** 1f# 31-X-2009, Carvalho, L.G., LEACOL. **Vitória do Mearim:** 7f# Margem da ferrovia SLZ-Carajás, 30-III-1992 and 24-IV-1992, Ferreira & Santos, LEACOL, all with label: *Xylocopa* sp. 1f# *Ibidem*, 04-VI-1991, Rêgo, M.M.C., LEACOL.

***Xylocopa* (*Neoxylocopa*) *transitoria* Pérez, 1901**

(Figure 12)

Xylocopa transitoria Pérez, 1901: 95. Holotype: Muséum National d'Histoire Naturelle, Paris, France (f#). Type locality: 'Argentine, Mérida (Vénézuele)'.

Xylocopa submordax Cockerell, 1935. Holotype: Natural History Museum, London, England (f#). Type locality: Trinidad & Tobago, 'Patos Island'.

Diagnosis. Medium-sized bees, BL approximately 22.4 mm (21.2–25; n = 16); Females: integument and pubescence entirely black (Figure 12B–D); wings dark brown and iridescence predominantly GVL; dorsal surface of scutellum concave, transition with posterior surface forming a carinate edge with an acute angle (Figure 12E–F); T2 with moderate punctation on discal area.

Distribution. Present in northern South America, it is present in Colombia, Dominica, French Guiana, Guyana, Trinidad and Tobago, and Venezuela (Moure & Melo 2022). We present the first records for Brazil, in Maranhão occurrence was mainly in areas of ombrophilous forest (71.4%), dunes (14.3%), flooded fields (9.5%), and wooded savanna (4.8%). Of the total, 81%

of the bees were collected in areas with anthropic influence: 47.6% in secondary vegetation, 28.6% in urban areas, and 4.8% in agricultural sectors (Figure 12A). In MA, *X. transitoria* did not show a clear seasonal pattern, although it was more frequent in the months of June to August.

Comments. In general, *X. transitoria* resembles the other entirely melanic species listed here, but it is easily recognized by the scutellum form, which has a concavity that extends to the margin, forming an acute angle between the dorsal and posterior surfaces. This character is found in *Xylocopa* (*Neoxylocopa*) *orthogonaspis* Moure, 2003, a species that occurs in the Amazon basin, however, this species presents light brown wings, following the HC pattern, in contrast to the dark brown with GVL iridescence of *X. transitoria* (Moure 2003; Mawdsley 2018). In one of the first inventories conducted in MA, Gottsberger *et al.* (1988) recorded the supposed occurrence of *X. orthogonaspis* on the coast of São Luís, but the species had not yet been formally described, and, although we did not have access to the specimens of this work, we know from the publication of Moure (2003), that there was no individual from the type series from Maranhão. Our data suggest a probable sympatry in the Amazon basin between these species, a fact that should be investigated with new surveys in the region, as well as a nominal revision between them.

Material examined. (21f#) **BRAZIL, Maranhão: Alcântara**, 1f# 05-V-1990, Bezerra & Fernandes, LEACOL. **Anajatuba**, 1f# Povoado São Benedito, 29-VIII-2009, Araújo & Carvalho, CEDU, *Xylocopa* (*Neoxylocopa*) *frontalis*. **Carutapera**, 2f# Sítio do Prata, 13-VIII-2013 and 03-IX-2014, Ferreira, L.A.C., LEACOL\CEDU, all with label: *Xylocopa* (*Neoxylocopa*) *suspecta*. **Godofredo Viana**, 1f# 06-XII-2019, Rodrigo, LEACOL. **São Domingos do Azeitão**, 1f# -6.783333 -44.483333, 01-IV-2015, Pereira, J.R.M.S., LESPP. **São José de Ribamar**, 3f# Praia de Panaquatira, 08-V-2005, 26-III and 14-V-2006, Oliveira & Mendonça, LEACOL\CEDU, two females with label: *Xylocopa* (*Neoxylocopa*) cf. *transitoria*, Silveira, F.A. det., 2015 and one female with label: *Xylocopa* (*Neoxylocopa*) *cearensis*. **São Luís**, 1f# UEMA, -2.574909 -44.206159, 28-IV-2022, Ferreira, L.A.C., LEACOL. 1f# UFMA, 15-VI-2007, Costa, B.R.R., LEACOL. 1f# *Ibidem*, 07-VI-2009, Saraiva, C.C.F., LEACOL. 1f# *Ibidem*, 23-X-2009, Amaral, L.P.R., LEACOL. 5f# Alumar, 21-VIII and 18-IX-1999, 11-III, 09-VI and 10-VII-2000, Cruz & Sodré, LEACOL, all with label: *Xylocopa* (*Neoxylocopa*) *cf. transitoria*, Silveira, F.A. det., 2015. 2f# Reserva Florestal da CVRD, 23-VII and 21-VIII-1991, Apocalipse & Rodrigues, LEACOL, one female with label: *Xylocopa* (*Neoxylocopa*) *carbonaria.* **Vitória do Mearim**, 1f# Margem da ferrovia SLZ-Carajás, 04-VI-1991, Rêgo, M.M.C., LEACOL.

Subgenus *Schonnherria* Lepeletier, 1841

Schonnherria Lepeletier, 1841: 207. Subsequent designation: Sandhouse, 1943: 598. Type species: *Xylocopa micans* Lepeletier, 1841, by subsequent designation.

Schonherria Dalla Torre, 1896: 202. (unjustified emendation of *Schonnherria* Lepeletier, 1841).

Schoenherria Hurd, & Moure, 1963: 118. (unjustified emendation of *Schonnherria* Lepeletier, 1841).

Diagnosis (Modified from Michener 2007). Including small to medium bees that have the following characters: tegument usually metallic; gradulus only present on T1; metasomal sterna without longitudinal carina; clypeus without a continuous smooth ridge; In males, eyes converge upwards.

Distribution. It is the second most diverse subgenus of the Neotropical Region, with at least 30 recognized species, and is widely distributed in the Americas, especially in the tropical regions (Hurd 1978; Silveira *et al.* 2002; Villamizar *et al.* 2020). In Maranhão, according to Moure & Melo (2022), four species of this subgenus are listed, however, the species *Xylocopa* (*Schonnherria*) *viridis* Smith, 1854 was observed by Ducke (1910a) and has not been recorded since, even with the numerous surveys already mentioned. In addition, no specimens of *X. viridis* were found in our examined material, justifying its exclusion from the listing. Thus, we report three species of *X.* (*Schonnherria*) in MA, distributed predominantly in the north in forested areas and flooded fields.

***Xylocopa* (*Schonnherria*) *macrops* Lepeletier, 1841**

(Figures 13, 18B, 18D)

Xylocopa macrops Lepeletier, 1841: 209. Holotype: locality unknown (m#). Type locality: Brazil.
Xylocopa crotalariae Schrottky, 1901: 212-214. (*nomen nudum*).
Xylocopa crotalariae Schrottky, 1902: 472. Holotype: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (f#). Type locality: Brazil, São Paulo, Campinas.

Diagnosis. Medium to small-sized bees, BL approximately 19.7 mm (18.4–21.1; n = 9); Females: integument black with barely perceptible bluish sheen and black pubescence (Figure 13B–D), except for white hairs on S3–5; wings dark brown and iridescence predominantly VL; genal area and T1–2 with very sparse punctation (Figure 13E–F). Males: superior interocular distance small, similar to the middle ocellus diameter; scape with yellowish patch (Figure 18B); whitish or yellowish pubescence on T1 (Figure 18D).

Distribution. Present in Argentina, Bolivia, Colombia, Paraguay, Peru, and Brazil in the states of Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Maranhão, Mato Grosso, Minas Gerais, Paraná, Pará, Pernambuco, Rio Grande do Sul, Rio de Janeiro, Rondônia, Santa Catarina, and São Paulo (Hurd 1978; Moure & Melo 2022). In Maranhão, *X. macrops* was first reported by Ferreira *et al.* (2019), in an area of ombrophilous forest, however, most records are from dunes and restingas (77,8%). Of this total, only 22% of the bees were collected in areas with anthropic influence (Figure 13A). *Xylocopa macrops* was collected in January, February, June, July, September, and December and did not show a clear seasonal pattern, since it was considered an occasional species in the respective surveys, Ferreira *et al.* (2019) and Neves *et al.* (2021).

Comments. The barely perceptible bluish sheen of *X. macrops* viewed superficially, may be confused with other entirely melanic bees, e.g., *X. cearensis* by the body size (this is the largest species of *Schonnherria* listed here). However, they are easily separated by considering the whole distinct set of characters between the subgenera. This is a species that did not show relevant variations, however, it is necessary to consider the limited number of records. Only one individual was collected occasionally, thus, we highlight the importance of conducting structured surveys, especially in still preserved areas, to increase the contingent of *X. macrops* and better understand the ecological patterns of this species in transition areas.

Material examined. (9f#) **BRAZIL, Maranhão: Carutapera**, 1f# Sítio do Prata, 14-VII-2013, Ferreira, L.A.C., LEACOL. **São Bento**, 1f# 08-IX-1982, Brenha, S., LEACOL, with label: *Xylocopa* (*Schonnherria*) *macrops*, Camargo, J.M.F. det., 1982. **Tutóia**, 7f# Ilha Grande do Paulino, 19-I, 24-II and 25-VI-2018, 08-XII-2019, Neves JR & Barros, LEACOL.

Xylocopa (*Schonnherria*) *muscaria* (Fabricius, 1775)

(Figures 14, 18A, 18E)

Apis muscaria Fabricius, 1775: 386. Holotype: Natural History Museum, London, England (m#). Type locality: 'Nova Hollandia'.

Xylocopa barbata Fabricius, 1804: 341. Lectotype: University of Copenhagen Zoological Museum, Copenhagen, Denmark (f#). Subsequent designation: Moure, 1960: 140. Type locality: 'America meridionalis'.

Xylocopa affinis Lepeletier, 1841: 210. Holotype: Museo Regionale di Scienze Naturale, Torino, Italy (m#). Type locality: French Guyana, Cayenne.

Diagnosis. Small bees, BL approximately 14.2 mm (12–16.5; n = 108); Females: integument black with barely perceptible bluish sheen and black pubescence (Figure 14B-D), except for plumose white hairs on paraocular and genal area, S4–5 and T4–5, (Figure 14E–F); dark brown wings and iridescence predominantly VL. Males: superior interocular distance small, less than the middle ocellus diameter; scape entirely black (Figure 18A); blackish pubescence on T1 (Figure 18E).

Distribution. Present in Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, Guyana, French Guiana, Guatemala, Honduras, Mexico, Panama, Paraguay, Peru, Trinidad and Tobago, Venezuela, and Brazil in the states of Alagoas, Amapá, Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Paraná, Paraíba, Pará, Pernambuco, Rio Grande do Norte, Rio de Janeiro, Rondônia, São Paulo, and Tocantins (Hurd 1978; Moure & Melo 2022). In Maranhão, *X. muscaria* was the species with the highest abundance and distribution among the bees of the subgenus *Schonnherria*. Its records were distributed in most physiognomic forms but were more frequent in ombrophilous forest (57.2%) and flooded fields (35.9%), the coastal areas (dunes and restingas) had only 3.7% of occurrences. The wide distribution of *X. muscaria* is reflected in 83.8% of the records in areas with anthropic influence, of which 59% is secondary vegetation, 14.5% urban areas, and 10.3% agricultural sectors (Figure 14A). As for seasonality, *X. muscaria* was most frequent in the months from June to December, characterized by the rainless period in the region.

Comments. In general, *X. muscaria* has no relevant variations, it is a small species and can be easily identified by the dense white pubescence on the genal area, because of this, most individuals were correctly identified. According to Rebêlo *et al.* (2003), *X. muscaria* is one of the most frequent species in MA, and can move between different physiognomies in the northern part of the state.

Material examined. (109f# 8m#) **BRAZIL, Maranhão: Alcântara**, 2f# Pepital, 21-VI-1992 and 28-II-1993, Araújo & Gonçalves, LEACOL. **Anajatuba**, 4f# 19-IX-2000, 11-VIII and 12-VIII-2015, Oliveira, F.S., LEACOL, one female with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. 5f# Povoado São Benedito, Araújo & Carvalho, LEACOL, all with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. 21f# *Ibidem,* 12-VIII, 13-VIII, 14-VIII, 01-X, 07-X, 17-X, 05-XI, 26-VIII and 18-IX-2009, Oliveira, F.S., LEACOL, all with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. **Barreirinhas**, 1f# Povoado Cantinho, 20-XII-2009, Gostinski & Carvalho, LEACOL, with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. 2f# 1m# 28-XII-1991 and 29-IV, 26-VI-1992, Brito & Mendonça, LEACOL. **Carutapera**, 4f#Sítio do Prata, 13-VIII, 14-VIII and 23-XII-2013, Ferreira, L.A.C., LEACOL. **Cururupu**, 11f# 19-VI and 28-IX-2015, 18-VI and 27-VIII-2016, Dos Anjos, J.V., LEACOL\CEDU, three females with label: *Xylocopa* (*Schonnherria*) *muscaria*. **Peri Mirim**, 2f# Parque AE. de Buritirana, -2.639500 -44.847600, 28-VI and 30-VII-2013, Sardinha, T.L.M., LESPP. 1m# *Ibidem*, 26-X-2013, Muniz, D.B., LESPP. 1f# *Ibidem*, 28-IX-2014, Azevedo, G.G., LESPP. **Santa Inês**, 3m# 26-X-2000, Carvalho & Luz, LEACOL. 1f# *Ibidem*, Maurício, P., MPEG.**São Domingos do Azeitão**, 1f# -6.783333 -44.483333, 01-IV-2015, Pereira, D.M., LESPP. **São José de Ribamar**, 1f# Sítio Aguahy, -2.645700 -44.141300, 2010, Ferreira, B.R.A., LESPP. **São Luís**, 27f# 2m# Alumar, 21-VIII, 13-X, 30-X and 01-XII-1999, 04-VI, 09-VI, 24-VI, 10-VII and 25-VII-2000, Cruz & Sodré, LEACOL, all with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. 1f# *Ibidem*, 03-I-2003, Carvalho, C.C., LEACOL, with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. 1f# Praia de São Marcos, 12-VIII-1994, Albuquerque & Ferreira, LEACOL. 2f# Estação Ecológica do Rangedor, 12-VI-2010, Silva & Conceição, LEACOL, one female with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. 2f# Reserva Florestal da CVRD, 21-X and 21-XI-1991, Apocalipse & Rodrigues, LEACOL. 1f# 25-VIII-1991, Santos, LEACOL. 1f# 03-XI-2007, Farias & Pinto, LEACOL. 1f# 06-VI-2010, Silva, LEACOL. 1f# 11-VI-2010, Tavares, D.B., LEACOL. **Tutóia**, 2f# 1m# Ilha Grande do Paulino, 31-X-2017 and 08-XII-2019, Neves JR & Barros, LEACOL. **Urbano Santos**, 1f# 25-IX-2003, Mendes & Ramos, LEACOL, with label: *Xylocopa* (*Schonnherria*) *muscaria*, Silveira, F.A. det., 2015. **Vitória do Mearim**, 12f# Margem da ferrovia SLZ-Carajás, 13-VIII and 09-XI-1991, 31-III, 24-IV, 25-IV, 21-V, 25-VI and 29-VIII-1992, Ferreira & Santos, LEACOL. **Zé Doca**, 1f# 06-X-1978, Torres, M.F., MPEG.

***Xylocopa* (*Schonnherria*) *subcyanea* Pérez, 1901**

(Figures 15, 18C)

Xylocopa caerulea Illiger, 1806:150. (*nomen nudum*).
Xylocopa subcyanea Pérez, 1901:74. Holotype: Muséum National d'Histoire Naturelle, Paris, France (f#). Type locality: Brazil, Mato Grosso.
Xylocopa burmeisteri Friese, 1903: 203. Syntype: Museum für Naturkunde, Humboldt-Universität zu Berlin, Berlin, Germany (f#). Type locality: Argentina, 'Banda Oriental'. Brazil, São Paulo.
Xylocopa melanopogon Moure, 1949: 452. Holotype: Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (f#). Type locality: Brazil, São Paulo, Rio Claro.

Diagnosis. Small bees, BL approximately 14.2 mm (13–16; n = 4); Females: tegument black except for barely perceptible bluish sheen on metasoma; pubescence black (Figure 15B–D), except for white hairs on S3–4; wings light brown and iridescence predominantly VL; genal area with very dense punctation (Figure 15F), contrasting with sparse punctation genal area of *X. macrops*; T2 with moderate to dense punctation on discal area (Figure 15E). Males: superior interocular distance large, more than 5x the middle ocellus diameter; yellowish paraocular area extending beyond the lateral ocelli (Figure 18C); genal area with moderate black pubescence.

Distribution. Present in Argentina, Bolivia, Paraguay, Uruguay, and Brazil in the states of Alagoas, Bahia, Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Paraná, Pará, and São Paulo (Hurd 1978; Moure & Melo 2022). For Maranhão we present the first records, distributed exclusively in open areas: wooded savanna (80%), without anthropic influence, and park savanna (20%), with urbanization influence (Figure 15A). *X. subcyanea* was collected in April, May, June, and December, and did not have a clear seasonal pattern due to the limited number of records.

Comments. For patterns of the genus *Xylocopa*, *X. subcyanea* is a considerably small species, some individuals exhibited below-average sizes observed by Mawdsley (2018) and Villamizar *et al.* (2020). In addition to the very small body size, this species can be separated from the other *X. Schonnherria* by the presence of very dense punctation on the genal area. *Xylocopa subcyanea* has a very dispersed distribution, in Brazil it occurs in the South American dry diagonal from northwestern Argentina to northeastern Brazil. Silva *et al.* (2009) recorded its presence in areas of dunes and restinga and called attention to its absence in areas of the northeastern Cerrado. In MA, the records demonstrated the opposite pattern, since no individual, until then, was observed in the coastal regions. Despite this sample increment for the northeast, we reinforce the need to expand studies on bees in Cerrado areas.

Material examined. (4f# 1m#) **BRAZIL, Maranhão: Balsas**, 1f# 09-VI-2006, Jesus & Silva, LEACOL. **Barreirinhas**, 1f# Povoado Cantinho, 15-XII-2003, Silva, O., LEACOL, with label: *Xylocopa* (*Schonnherria*) *subcyanea*, Silveira, F.A., 2015. **Formosa da Serra Negra**, 1f# Parque Estadual do Mirador, 03-XII-2009, Maia, C.M., LEACOL, with label: *Xylocopa* (*Schonnherria*) *subcyanea*, Melo, G.A.R., 2009. **São Domingos do Azeitão**, 1f# 01-IV-2015, Sardinha, T.L.M., LESPP. **Urbano Santos**, 1m# 17-V-2003, LEACOL.

Subgenus *Stenoxylocopa* Hurd & Moure, 1960

Stenoxylocopa Hurd, & Moure, 1960: 809. Type species: *Xylocopa artifex* Smith, 1874 by original designation.

Diagnosis (Modified from Michener 2007). Including small to medium-sized bees which have similar characteristics to *Neoxylocopa* such as: metasomal sterna with longitudinal carina; clypeus usually delimited by a continuous smooth ridge; the apex of the mandible is bidentate, however, differing in the size of the upper tooth, which is larger than the lower tooth. (Figure 16E-F).

Comments. Three species are present in Brazil, *Xylocopa* (*Stenoxylocopa*) *artifex* Smith, 1874 and *X.* (*S.*) *nogueirai* Hurd & Moure, 1960 are distributed in the south-central part of the country, while *X.* (*S.*) *ruficollis* Hurd & Moure, 1963 is restricted to the Amazon basin. In Maranhão, Zama & Silveira (2015) were responsible for the first record of this subgenus, discovering a new species (not yet published) (Figure 16B–D). In this paper, we expand the distribution records of *Xylocopa* (*Stenoxylocopa*) sp. n (Figure 16A).

Material examined. (10f# 2m#) **BRAZIL, Maranhão: Balsas**, 1f# 24-IX-2006, Jesus & Silva, LEACOL. 1f# Povoado Santa Luzia, 26-XI-2006, Silva, F.M.A., UFMG. **Barreirinhas**, 7f# 2m# Povoado Cantinho, 05-II, 04-III and 07-VIII-2010, Gostinski & Carvalho, LEACOL\UFMG. **Tutóia**, 1f# 05-I-1986, Brenha, S., UFMG.

Discussion

We recognized 12 species in Maranhão, of which one species is reported as a first record for Brazil (*X. transitoria*) and one for science (*X.* (*Stenoxylocopa*) sp.). Two species (*X. viridis* and *X. orthogonaspis*) have been recorded previously (Ducke 1908; Gottsberger *et al.* 1988), but were not found in the material examined, so their presence must still be confirmed.

The distribution of phytophysiognomies is complex in Maranhão, since in this state there is the contact of three major biomes from Brazil, and extensive transition areas (Figure 1). This scenario was more complex due to anthropization of many areas (Figure 2), wich can be assumed to favor the expansion of open vegetation species. Additionally, the mapping of Cerrado and Caatinga, do not indicate the presence of evergreen forests, in the form of enclaves or riparian forest. Most of bee surveys, especially those most structured (monthly collections for 24 consecutive months conducted in the last two decades (Rêgo & Albuquerque 2012) were undertaken in transition areas, mainly in the northeastern and in the region near the capital São Luís.

Although the sampling effort is very uneven across the sectors of the state, it was able to detect evidence for different patterns of distribution between species. *Xylocopa aurulenta* was recorded almost exclusively in areas of ombrophilous forest and represent a sample from the Amazonian fauna. It is possible that *X. transitoria* is another representant of this fauna, but the records in Maranhão includes transition areas in the region of São Luís, and one isolated point in the south of the state, in an area that includes Cerrado vegetation and transition areas. We suggest that it is occurrence in this area must be verified, in order to confer it is in an enclave of ombrophilous forest.

In contrast, *X. grisescens*, *X. hirsutissima*, *X. subcyanea* and *X.* sp. were only found in open vegetation areas. *Xylocopa grisescens* was intensively collected in the northeastern region and near São Luis, in dunes and restinga and also transition areas. For this species the absence of records in the extensive areas of savanna in the southern region is interpreted as the result of limitation of surveys since it is broadly distributed in Cerrado and Caatinga vegetations (Zanella 2000; Silva *et al.* 2009). *X. hirsutissima* was apparently more associated to savanna vegetation, since it was the only species recorded in the southern Cerrado of the state. It was also recorded in some transition areas in central eastern area, but it is also notable its absence in other areas of open vegetation, in the north, where most of collection effort was done.

Xylocopa cearensis can be included in this group, since most of the records were near the coast in dunes and restinga vegetation and in transition areas near São Luís. Its southern records were in transition area and one in ombrophilous forest was in an anthropized area (Figure 1 and 7A). The same for *X. nigrocincta*, also with a high number of records in open vegetation areas in the northeastern region and near São Luís, but with a record in the extreme northwestern region and in southern region, in transition zones (Figure 1 and 11A). The clearest case of a broad distribution in the state is *X. frontalis*, what is expected since the extensive records of this species in Brazilian biomes (Moure & Melo 2022).

In this study we expanded the knowledge about the distribution and systematics of bees of the genus *Xylocopa* in Maranhão, a strategic region for the study of biological diversity and conservation plans, due to its complex transition zones between three major biomes from Brazil. The taxonomic resources provided will be valuable support for future research involving the precise recognition of species of the genus *Xylocopa* in this region.

Key to subgenus of the *Xylocopa* present in Maranhão State

Females:

(Modified from Silveira *et al.* 2002)

1. Metasomal sterna with distinct longitudinal carina; clypeus delimited by a continuous smooth ridge along the epistomal suture; integument without bluish sheen **2**
– Metasomal sterna with indistinct or without longitudinal carina; clypeus without a continuous smooth ridge along the epistomal suture; integument with barely perceptible bluish sheen . . . . ***Schonnherria***

2. Mandible with the lower tooth equal to or larger than the upper tooth . . . . . ***Neoxylocopa***
– Mandible with the lower tooth smaller than the upper tooth (Fig. 16E–F) . ***Stenoxylocopa***

Males:

(Modified from Minckley 1998)

1. Integument and pubescence predominantly yellowish-orange . . . . ***Neoxylocopa***
– Integument predominantly black; pubescence predominantly blackish, sometimes partly whitish, or yellowish **2**

2. Integument usually metallic sheen; clypeus entirely yellowish . . . . ***Schonnherria***
3. Integument without metallic sheen; clypeus yellowish only on the sides . . ***Stenoxylocopa***

Key to species of the *Xylocopa* (*Neoxylocopa*) present in Maranhão State

Females:

1. Subocellular carina present (Fig. 8F); inter-alveolar carina absent; lateral margins of clypeus elevated and with broad smooth glossy band above in paraocular; upper line of mesosoma, in lateral view, strongly rounded (Fig. 8E) . . . . ***X. frontalis***
– Subocellular carina absent; inter-alveolar carina present (Fig. 5F); lateral margins of clypeus flat; upper line of mesosoma, in lateral view, smoothly rounded (Fig. 7E) **2**

2. Dorsal surface of scutellum flattened, transition to posterior surface largely rounded; posterior surface with dense punctation (Fig. 7F) **3**
– Dorsal surface of scutellum smoothly rounded, transition to posterior surface forming a curved edge with obtuse to a right angle (Fig. 5E) or acute angle (Fig. 12E); posterior surface with sparse punctation, with smooth areas between points larger than its diameter (Fig. 11F) **6**

3. Punctation of genal area and vertex, sparse and moderate, respectively **4**
– Punctation of genal area and vertex, moderate and dense, respectively. **5**

4. Mesosoma with orange pubescence (Fig. 6B–D); wings light brown with a coppery pattern. . . . . ***X. aurulenta***
– Mesosoma with whitish-yellow pubescence (Fig. 7B–D) or dark brown (Fig. 7E–F); wings dark brown with a violaceous pattern . . . . ***X. cearensis***

5. Central axis of the vertex without elevation; mesosoma with black and plumose pubescence (Fig. 10B–D); metasoma with dense and long pubescence (Fig. 10E–F) . . . . ***X. hirsutissima***

– Central axis of the vertex with a distinct elevation (Fig. 9F); mesosoma with whitish-yellow pubescence (Fig. 9B–D); metasoma with dense and short pubescence . . . . ***X. grisescens***

6. Dorsal surface of scutellum concave, transition with posterior surface forming a carinate edge with an acute angle (Fig. 12E–F) . . . . ***X. transitoria***

– Dorsal surface of scutellum convex, transition with posterior surface forming a curved edge with obtuse to a right angle (Fig. 5E) **7**

7. Large inter-alveolar carina, with "nose" shaped (Fig. 5F); metasoma always entirely black . . . . ***X. amazonica***

– Small inter-alveolar carina; metasoma entirely black (Fig. 11C–D) or with reddish bands (Fig. 8C–D) . . . . ***X. nigrocincta***

Males:

Note: Because of the absence of keys that include several species of *Neoxylocopa*, the key presented is based on a few characters that are easier to visualize, based on the analysis of specimens from Maranhão, combined with some data from other papers: Lucia *et al.* (2014) and Merida-Rivas *et al.* (2022). *Xylocopa aurulenta, X. hirsutissima* and *X. transitoria* are not known from material studied.

1. Large-sized bees, length approximately 30 mm **2**

– Small to medium bees, length less than 25 mm **4**

2. Middle ocellus smaller than the inter-lateral ocelli distance (Fig. 17A); ventral surface of posterior tibia with a strong declivity (Fig. 17D); metasomal terga with finer and sparser punctation (Fig. 17G) . . . . ***X. frontalis***

– Middle ocellus size similar to the inter-lateral lateral ocelli distance; ventral surface of posterior tibia with a moderate (Fig. 17E) to weak declivity (Fig. 17F); metasomal terga with dense or moderately sparse punctation **3**

3. Medium-sized intra-alveolar carina; middle ocellus approximately the size of lateral ocelli (Fig. 17B); vertex with long and dense pubescence; metasomal terga with moderately sparse punctation (Fig. 17H) . . . . ***X. amazonica***

– Small-sized intra-alveolar carina; middle ocelli larger than the lateral ocelli (Fig. 17C); vertex with short and sparse pubescence; metasomal terga with dense punctation . . . . ***X. grisescens***

4. Medium overall body size, length approximately 23 mm; ventral surface of posterior tibia with entirely yellowish pubescence; metasomal terga with moderately sparse punctation . . . . ***X. nigrocincta***

– Smaller overall body size, length approximately 20 mm; ventral surface of posterior tibia with blackish pubescence (Fig. 17F); metasomal terga with dense punctation (Fig. 17I) . . . . ***X. cearensis***

Key to species of the *Xylocopa* (*Schonnherria*) present in Maranhão State

Females:

1. Medium-sized bees, length approximately 20 mm, genal area with sparse punctation and hairs (Fig. 13F) . . . . ***X. macrops***

– Small bees, length less than 15 mm, genal area with dense punctation and hairs (Fig. 15F) **2**

2. Genal area with dense white pubescence (Fig. 14F); vertex and metasoma with moderate and sparse punctation, respectively; white hairs on S-T4-5 (Fig. 14E) . . . . . ***X. muscaria***

– Genal area without white pubescence but with dense punctation (Fig. 15F); vertex and metasoma with dense punctation (Fig. 15E); white hairs on S3–4 . . . . ***X. subcyanea***

Males:

(Modified from Villamizar *et al.* 2020)

1. Superior interocular distance large, more than 5x the middle ocellus diameter; yellowish paraocular area extending beyond the lateral ocelli (Fig. 18C); genal area with moderate black pubescence . . . . ***X. subcyanea***

– **S**uperior interocular distance small, similar or less than the middle ocellus diameter; yellowish paraocular area extending only to the antennal sockets (Fig. 18A–B); genal area with dense white pubescence **2**

2. Overall body size length approximately 20 mm; scape with yellowish patch (Fig. 18B); whitish or yellowish pubescence on T1 (Fig. 18D) . . . . ***X. macrops***

– Overall body size length less than 15 mm; scape entirely black (Fig. 18A); blackish pubescence on T1 (Fig. 18E) . . . . ***X. muscaria***

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Legends of illustrations

Figure 1. State of Maranhão highlighting the main original vegetation typologies. The Amazon (AMZ), Cerrado (CER) and Caatinga (CAA) biomes are represented by color gradients: green, orange and yellow, respectively. Source: BDiAWeb – Vegetação (1º nível).

Figure 2. State of Maranhão highlighting the main original vegetation typologies, and areas of anthropic influence. The Amazon (AMZ), Cerrado (CER) and Caatinga (CAA) biomes are represented by color gradients: green, orange and yellow, respectively. Source: BDiAWeb – Vegetação (2º nível).

Figure 3. Coloration patterns (Color/Iridescence) of the wings of *Xylocopa* individuals recorded in Maranhão State. A = Dark brown/Violet (VL); B = Dark brown/Violet-Greenish (GVL); C = Dark brown/Violet-Bluish (BVL); D = Dark brown/Greenish-Golden (GG); E = Hyaline/Coppery (HC).

Figure 4. Distribution records of *Xylocopa* in Maranhão State; Kernel density: red points = 100 individuals; Estimator radius: 10 km. Source: BDiAWeb – Vegetação.

Figure 5: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *amazonica* in Maranhão, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Scutellum in lateral view; (F) Inter-alveolar carina in profile. Scale bar: 2 mm.

Figure 6: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *aurulenta* in Maranhão, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus. Scale bar: 2 mm.

Figure 7: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *cearensis* in Maranhão, kernel index: red dots = highest density; (B) Frontal view – typical form; (C) Dorsal habitus – typical form; (D) Lateral habitus – typical form; (E) Scutellum in lateral view – melanic form; (F) Scutellum in frontal view – melanic form. Scale bar: 2 mm.

Figure 8: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *frontalis*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Scutellum in lateral view; (F) Subocellar carina in frontal view. Scale bar: 2 mm.

Figure 9: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *grisescens*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Vertex in frontal view. Scale bar: 2 mm.

Figure 10: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *hirsutissima*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasomal pubescence in dorsal view; (F) Metasomal pubescence in lateral view. Scale bar: 2 mm.

Figure 11: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *nigrocincta*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Scutellum in lateral view; (F) Scutellum in frontal view. Scale bar: 2 mm.

Figure 12: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *transitoria*, kernel index: red dots = highest density; (B) frontal view; (C) dorsal habitus; (D) lateral habitus; (E) Scutellum in lateral view; (F) Scutellum in frontal view. Scale bar: 2 mm.

Figure 13: (A) Occurrence records of *Xylocopa* (*Schonnherria*) *macrops*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Genal area in lateral view. Scale bar: 2 mm.

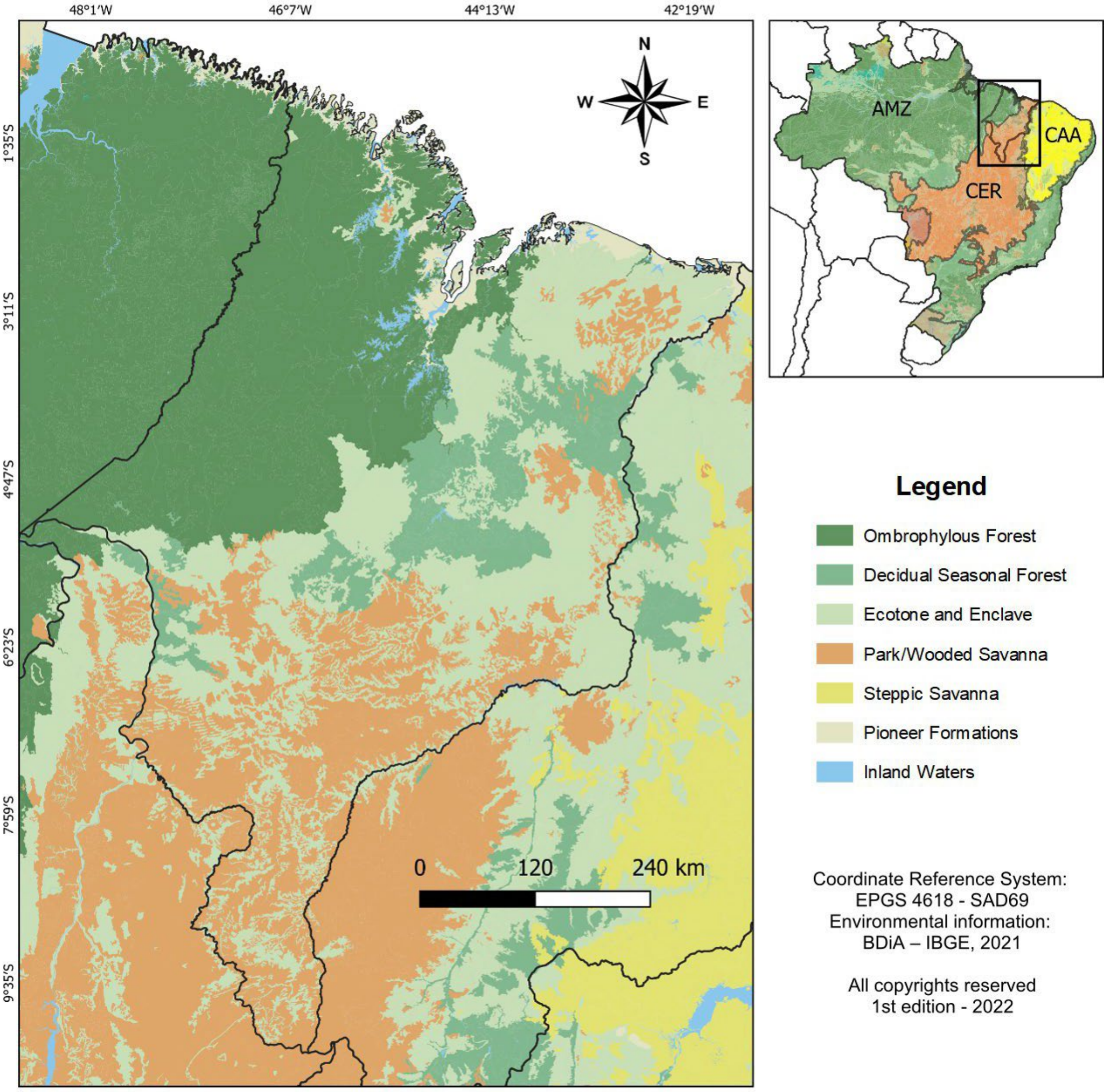
Figure 14: (A) Occurrence records of *Xylocopa* (*Schonnherria*) *muscaria*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Genal area in lateral view. Scale bar: 2 mm.

Figure 15: (A) Occurrence records of *Xylocopa* (*Schonnherria*) *subcyanea*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Genal area in lateral view. Scale bar: 2 mm.

Figure 16: (A) Occurrence records of *Xylocopa* (*Stenoxylocopa*) sp. n., kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Mandible teeth in frontal view; (F) Mandible teeth in profile. Scale bar: 2 mm.

Figure 17: Middle ocellus size of (A) *X. frontalis*, (B) *X. amazonica* and (C) *X. grisescens*; lateral view of posterior tibia of (D) *X. frontalis,* (E) *X. grisescens* and (F) *X. cearensis*; metasoma punctation of (G) *X. frontalis*, (H) *X. amazonica* and (I) *X. cearensis*. Scale bar: 2 mm.

Figure 18: Head details of (A) *X. muscaria*, (B) *X. macrops* and (C) *X. subcyanea*; T1 pubescence of (D) *X. macrops* and (E) *X. muscaria.* Scale bar: 2 mm.



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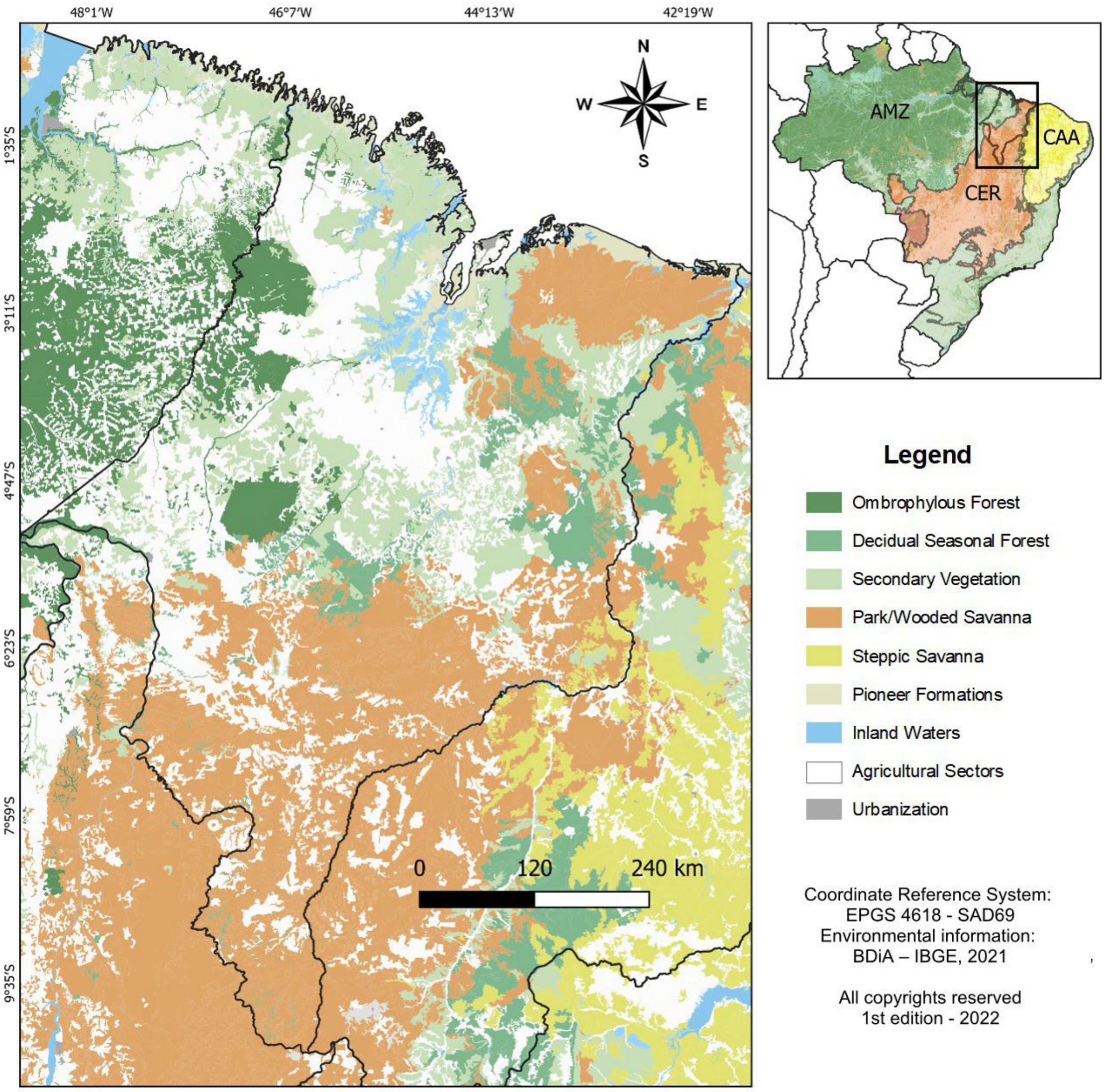

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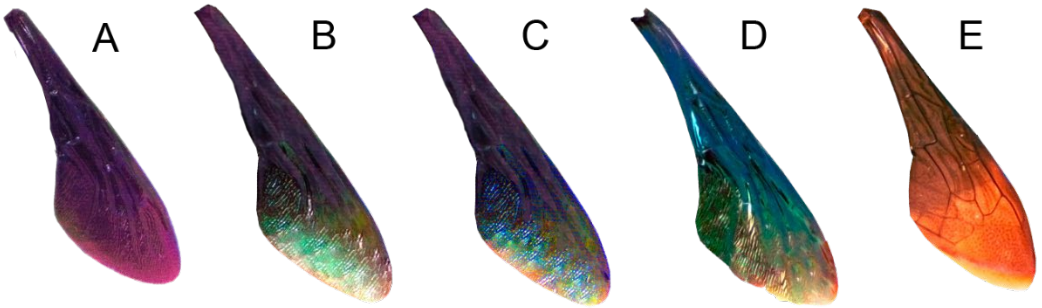

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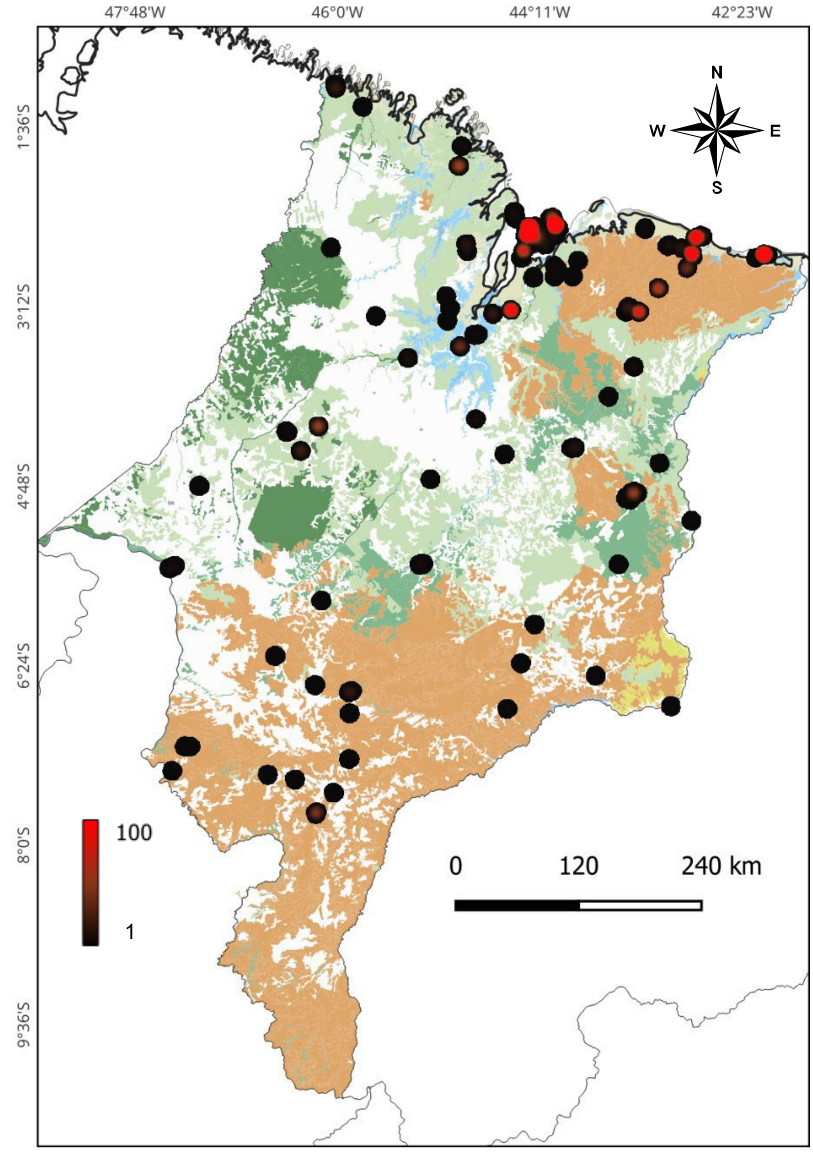

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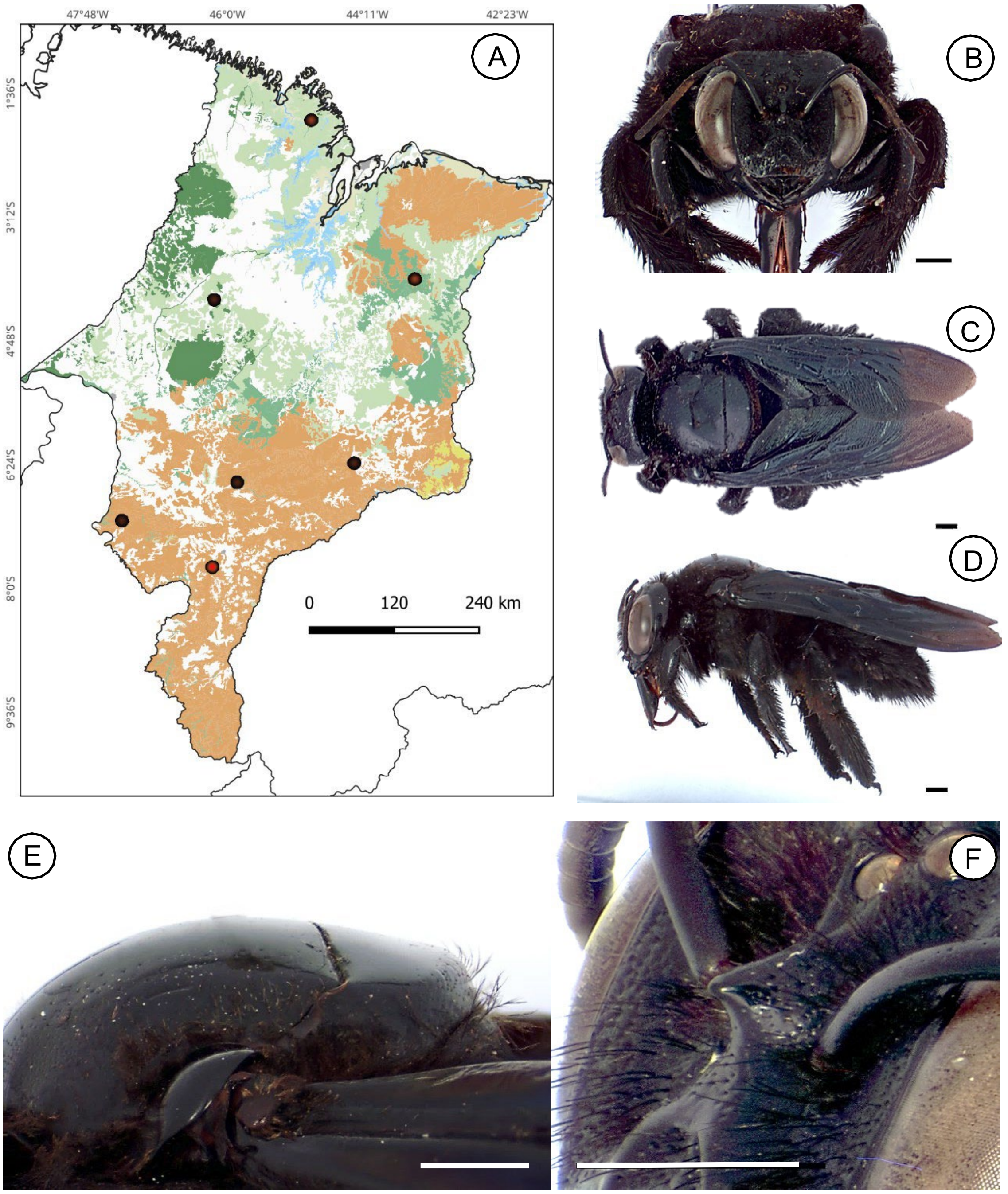

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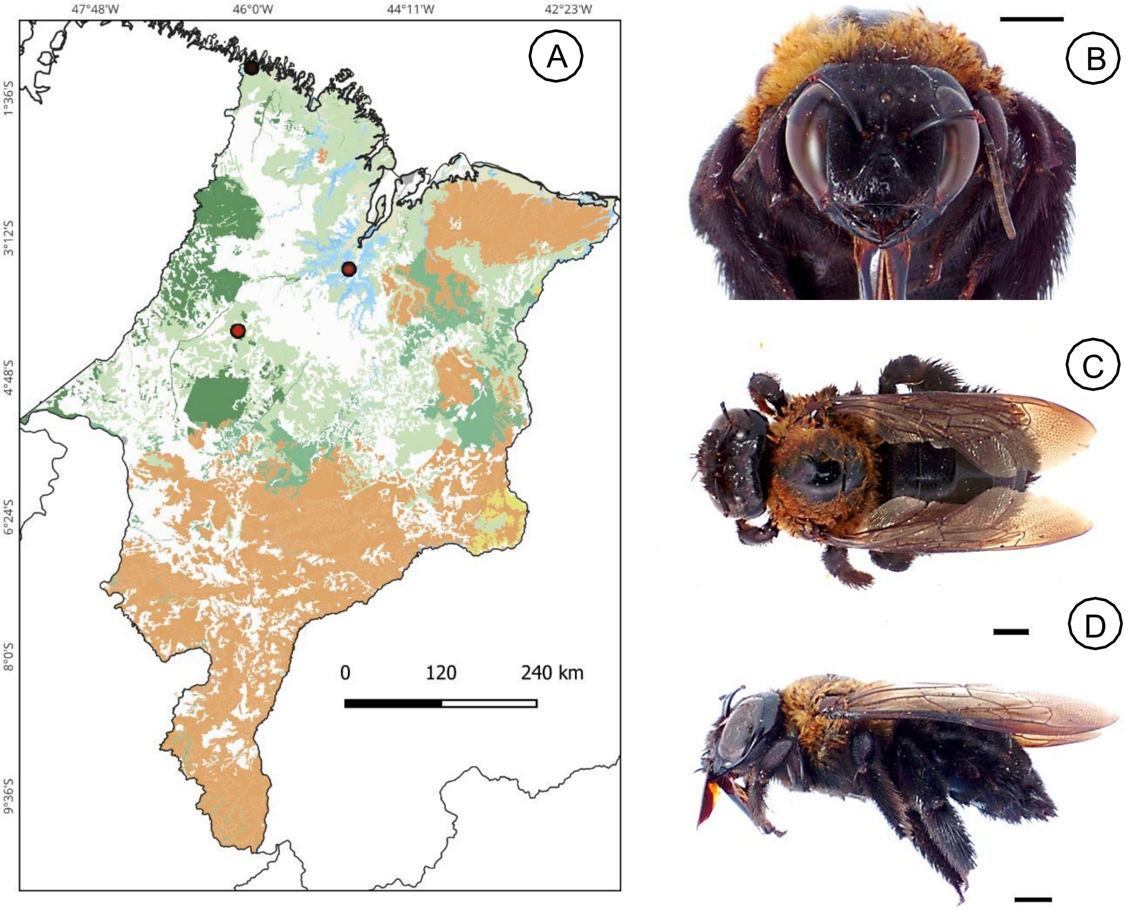

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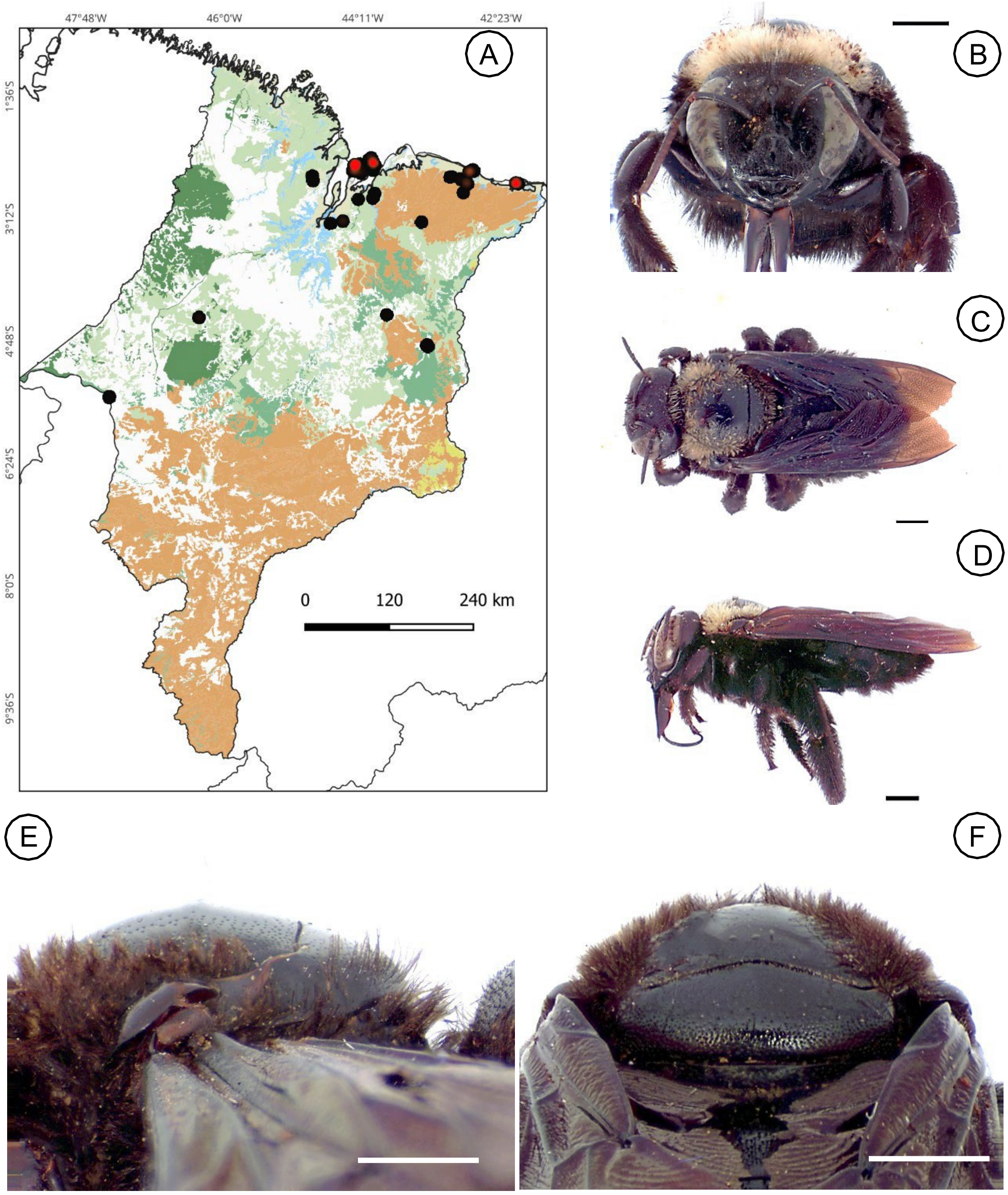

Figure 7: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *cearensis* in Maranhão, kernel index: red dots = highest density; (B) Frontal view – typical form; (C) Dorsal habitus – typical form; (D) Lateral habitus – typical form; (E) Scutellum in lateral view – melanic form; (F) Scutellum in frontal view – melanic form. Scale bar: 2 mm.

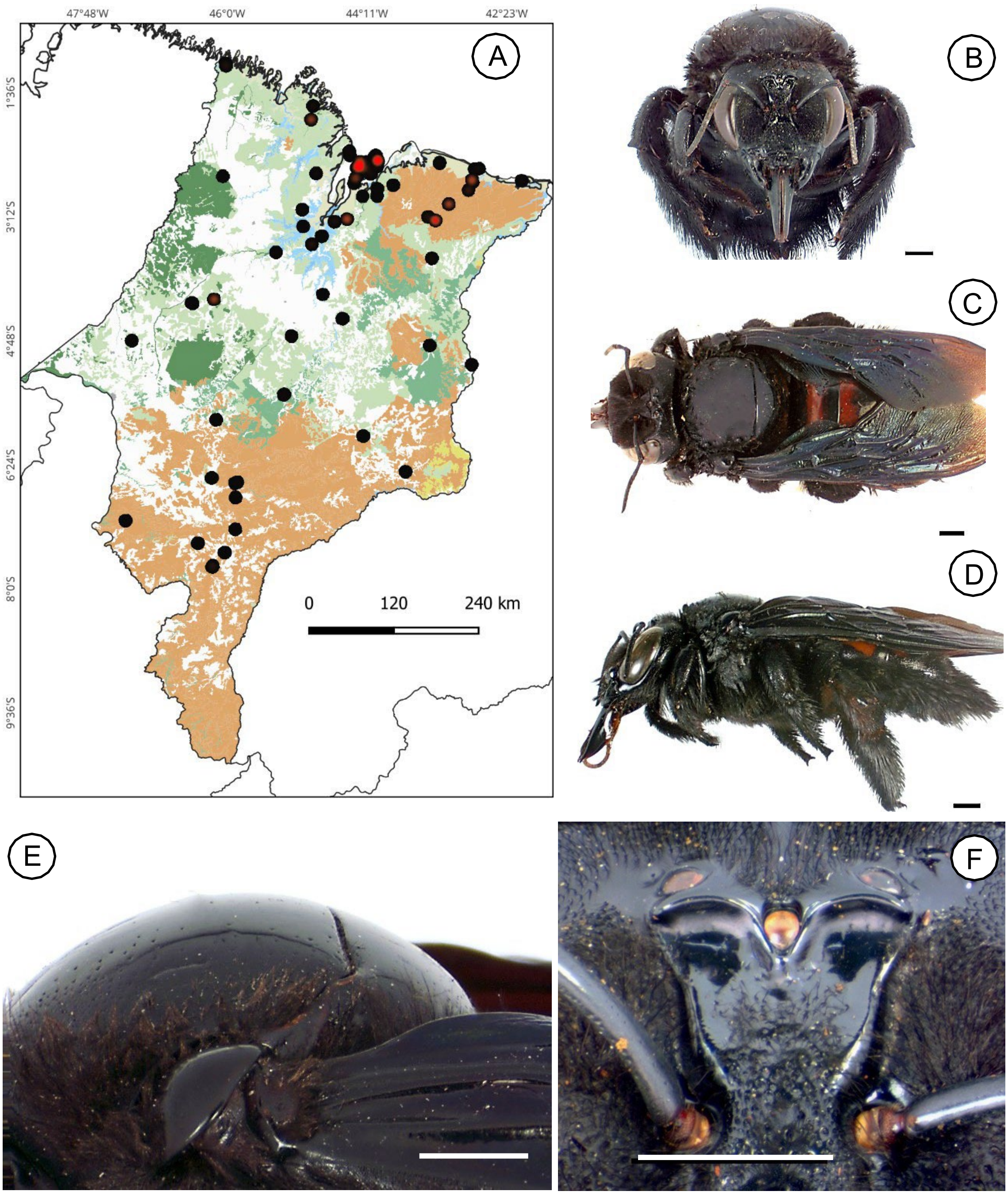

Figure 8: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *frontalis*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Scutellum in lateral view; (F) Subocellar carina in frontal view. Scale bar: 2 mm.

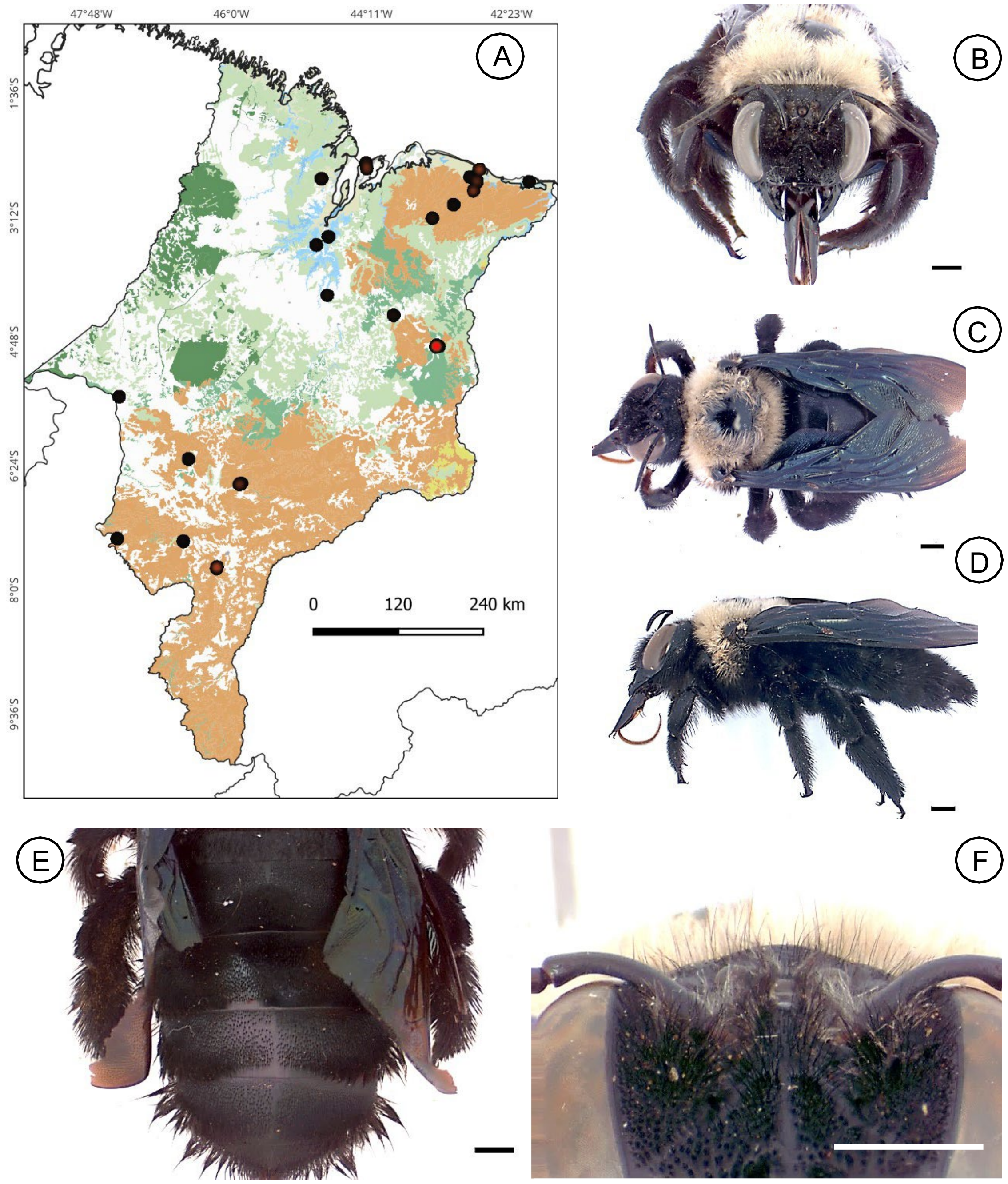

Figure 9: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *grisescens*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Vertex in frontal view. Scale bar: 2 mm.

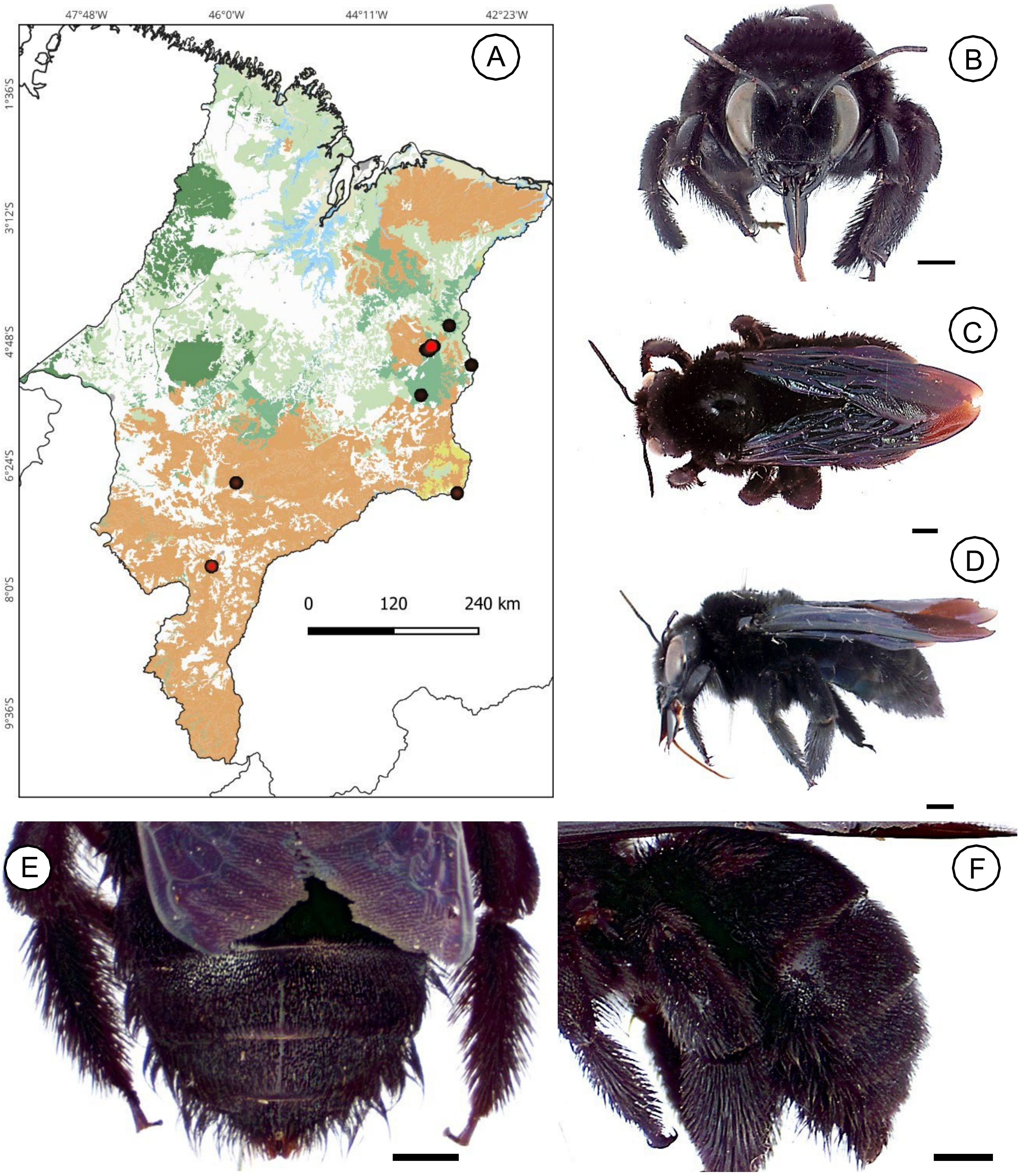

Figure 10: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *hirsutissima*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasomal pubescence in dorsal view; (F) Metasomal pubescence in lateral view. Scale bar: 2 mm.

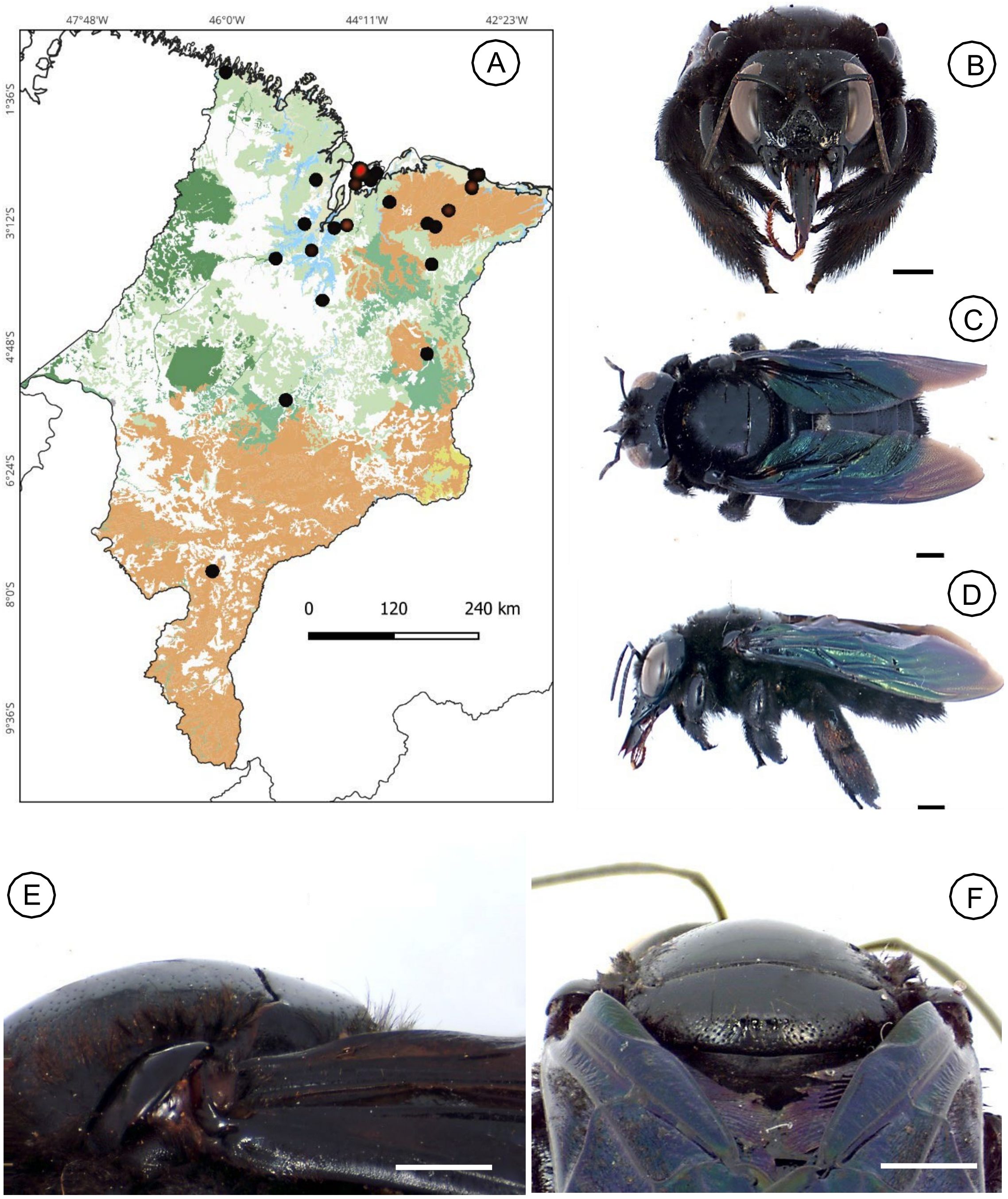

Figure 11: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *nigrocincta*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Scutellum in lateral view; (F) Scutellum in frontal view. Scale bar: 2 mm.

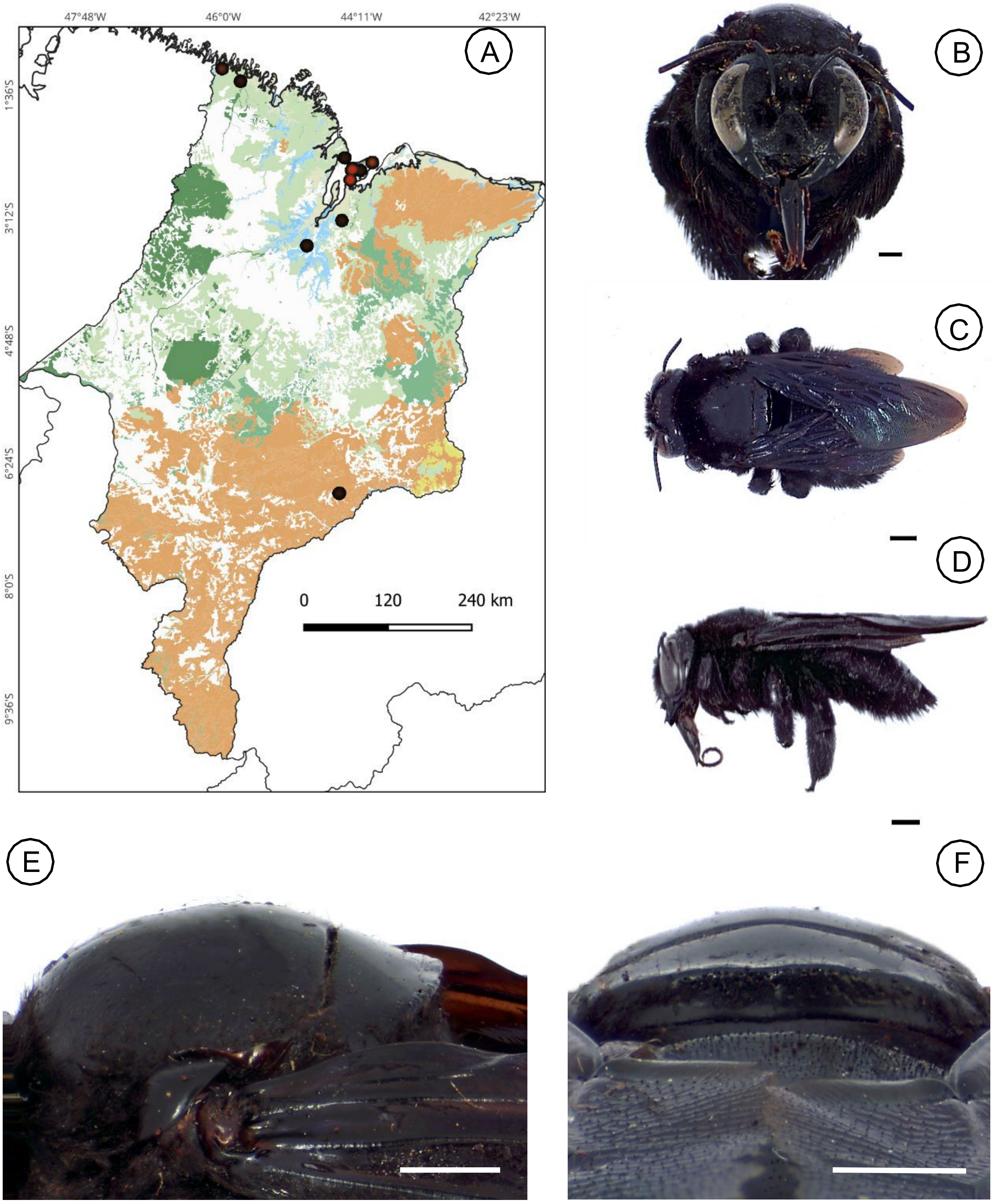

Figure 12: (A) Occurrence records of *Xylocopa* (*Neoxylocopa*) *transitoria*, kernel index: red dots = highest density; (B) frontal view; (C) dorsal habitus; (D) lateral habitus; (E) Scutellum in lateral view; (F) Scutellum in frontal view. Scale bar: 2 mm.

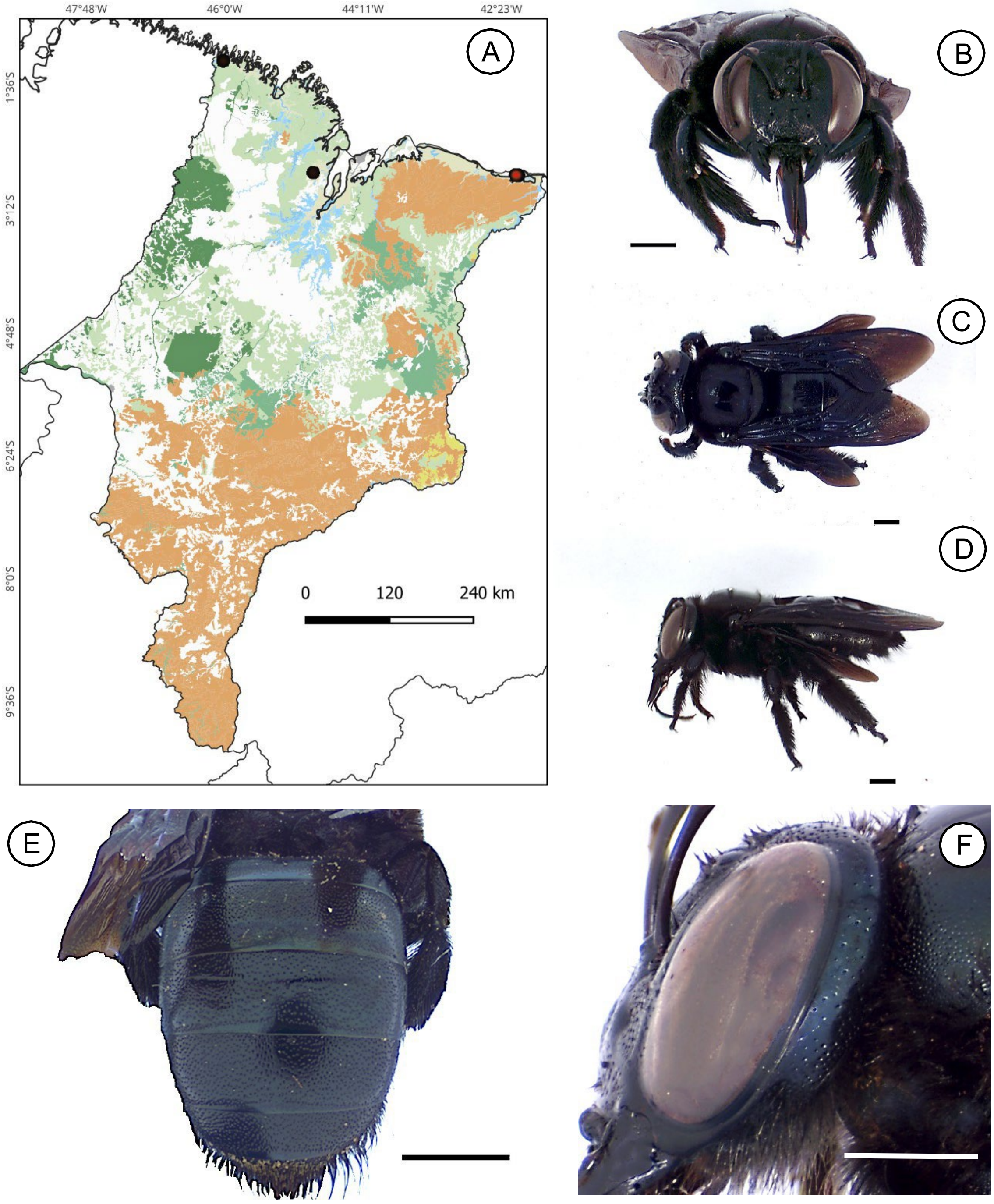

Figure 13: (A) Occurrence records of *Xylocopa* (*Schonnherria*) *macrops*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Genal area in lateral view. Scale bar: 2 mm.

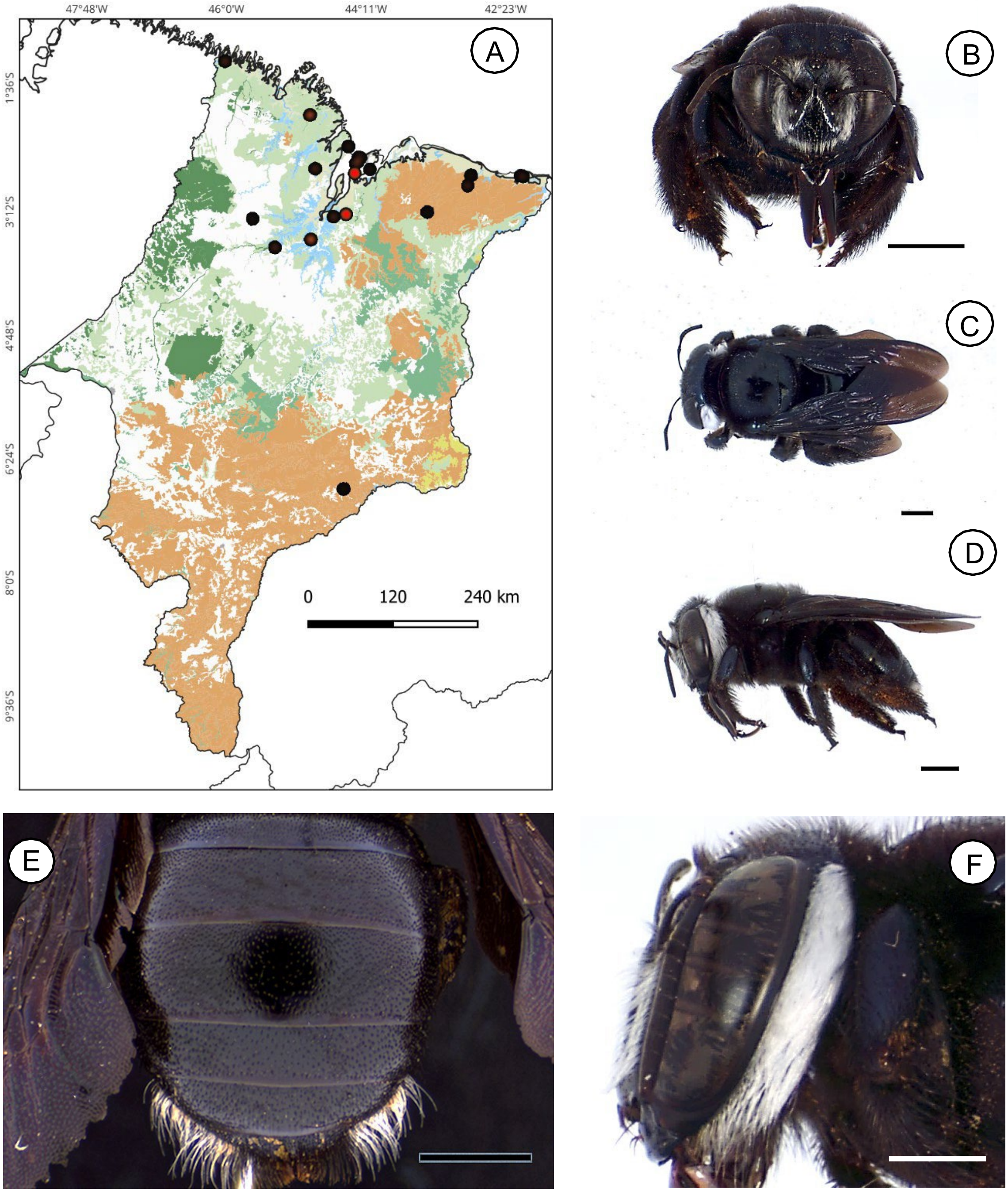

Figure 14: (A) Occurrence records of *Xylocopa* (*Schonnherria*) *muscaria*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Genal area in lateral view. Scale bar: 2 mm.

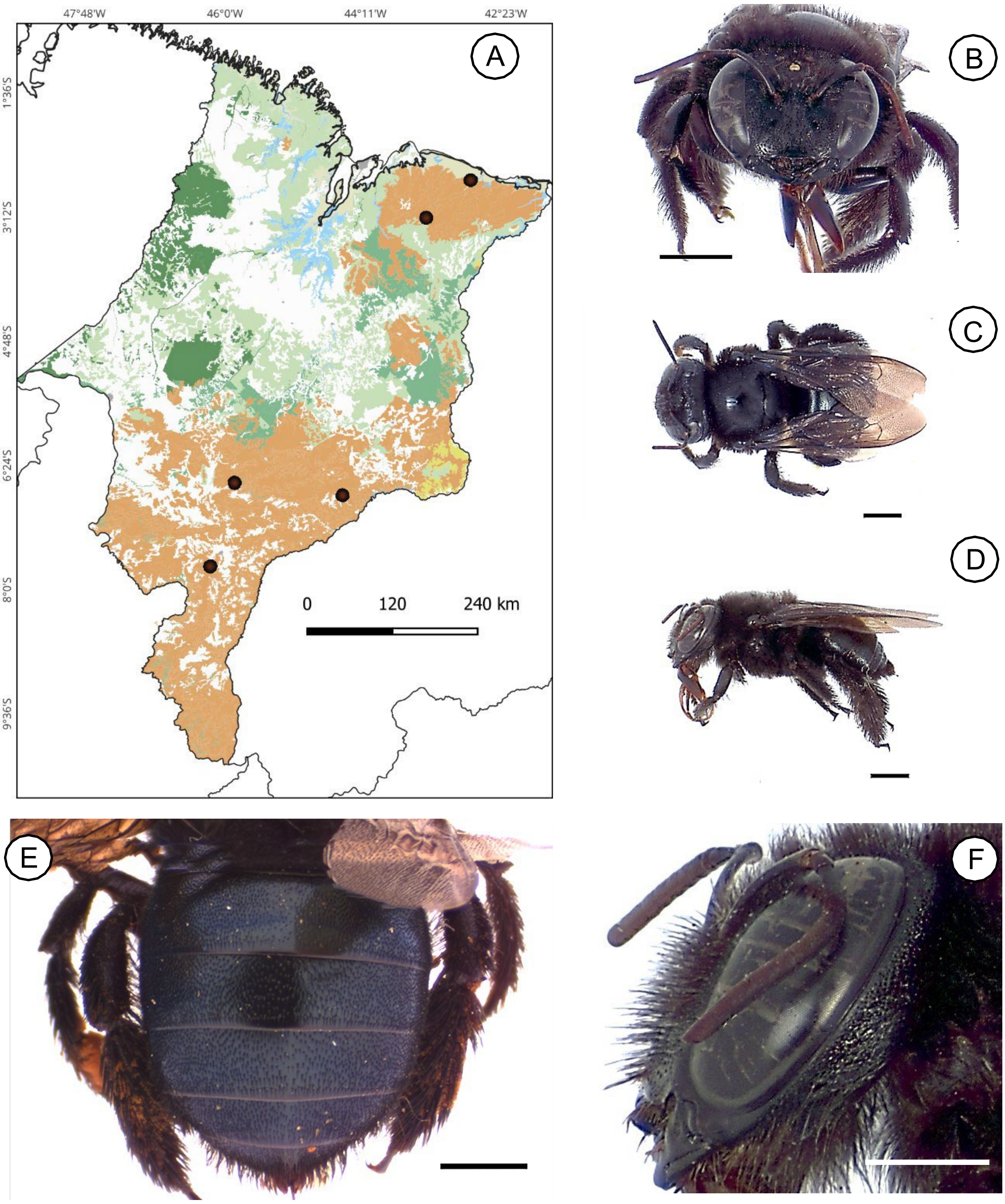

Figure 15: (A) Occurrence records of *Xylocopa* (*Schonnherria*) *subcyanea*, kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Metasoma in dorsal view; (F) Genal area in lateral view. Scale bar: 2 mm.

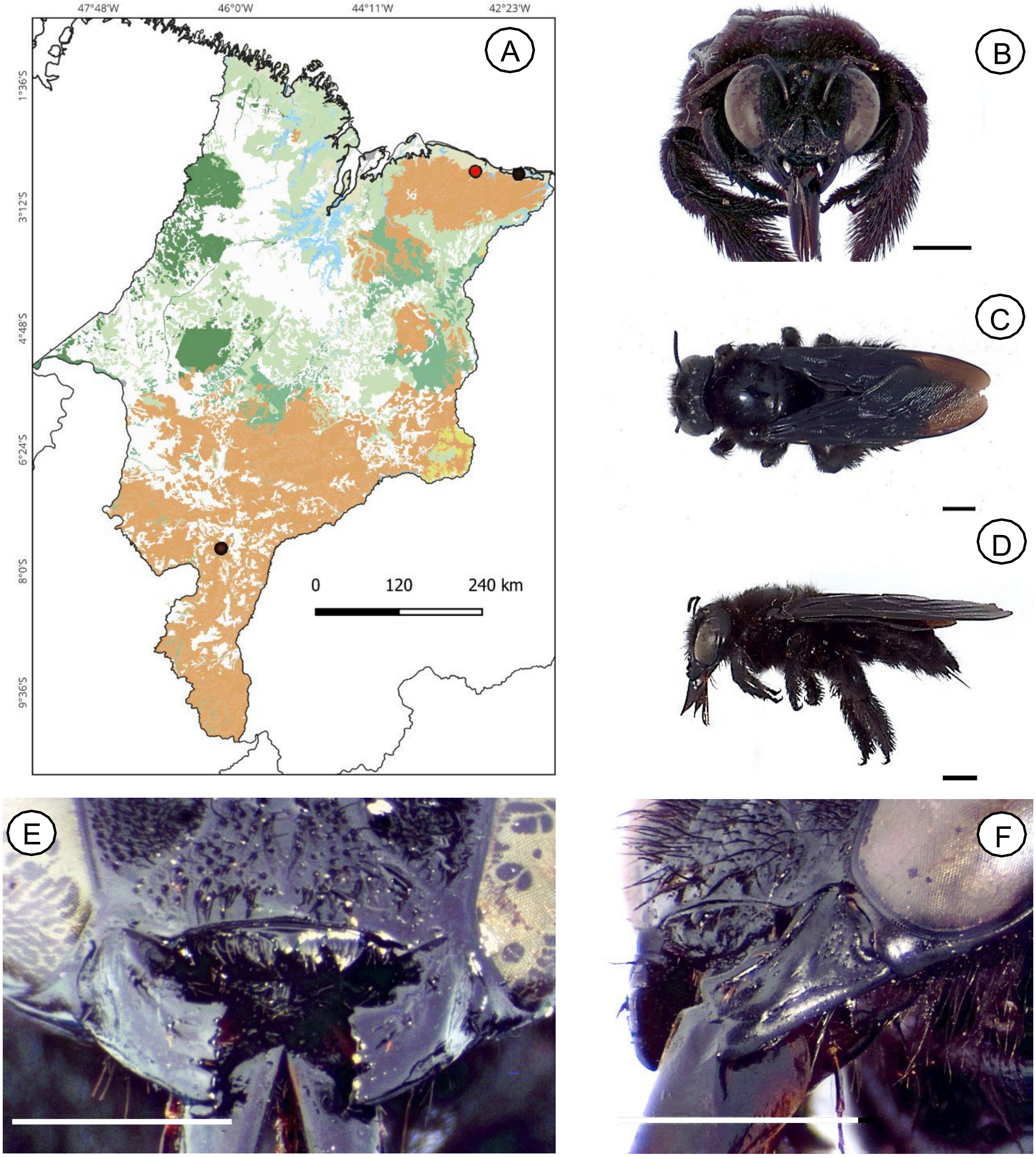

Figure 16: (A) Occurrence records of *Xylocopa* (*Stenoxylocopa*) sp. n., kernel index: red dots = highest density; (B) Frontal view; (C) Dorsal habitus; (D) Lateral habitus; (E) Mandible teeth in frontal view; (F) Mandible teeth in profile. Scale bar: 2 mm.

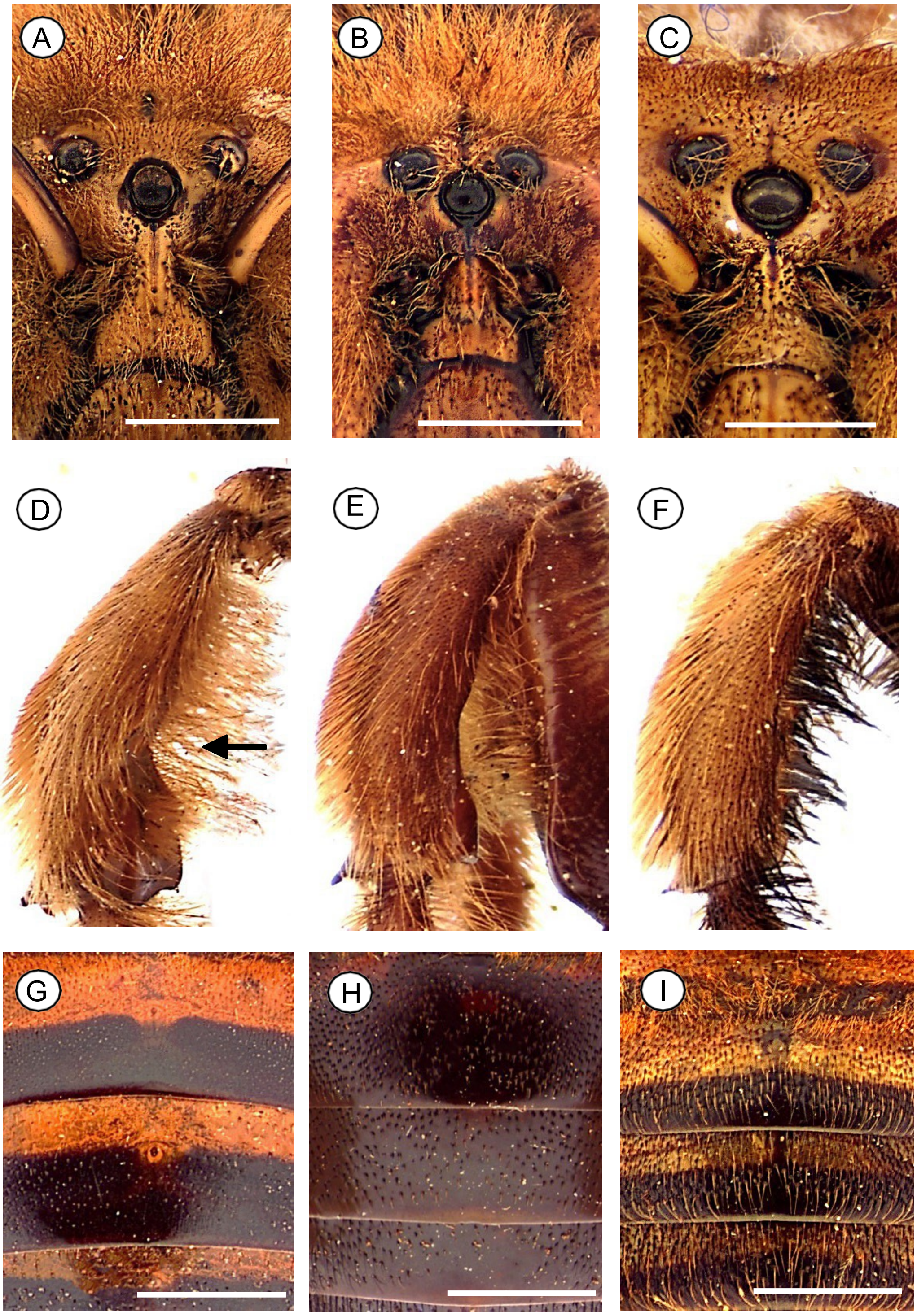

Figure 17: Middle ocellus size of (A) *X. frontalis*, (B) *X. amazonica* and (C) *X. grisescens*; lateral view of posterior tibia of (D) *X. frontalis,* (E) *X. grisescens* and (F) *X. cearensis*; metasoma punctation of (G) *X. frontalis*, (H) *X. amazonica* and (I) *X. cearensis*. Scale bar: 2 mm.

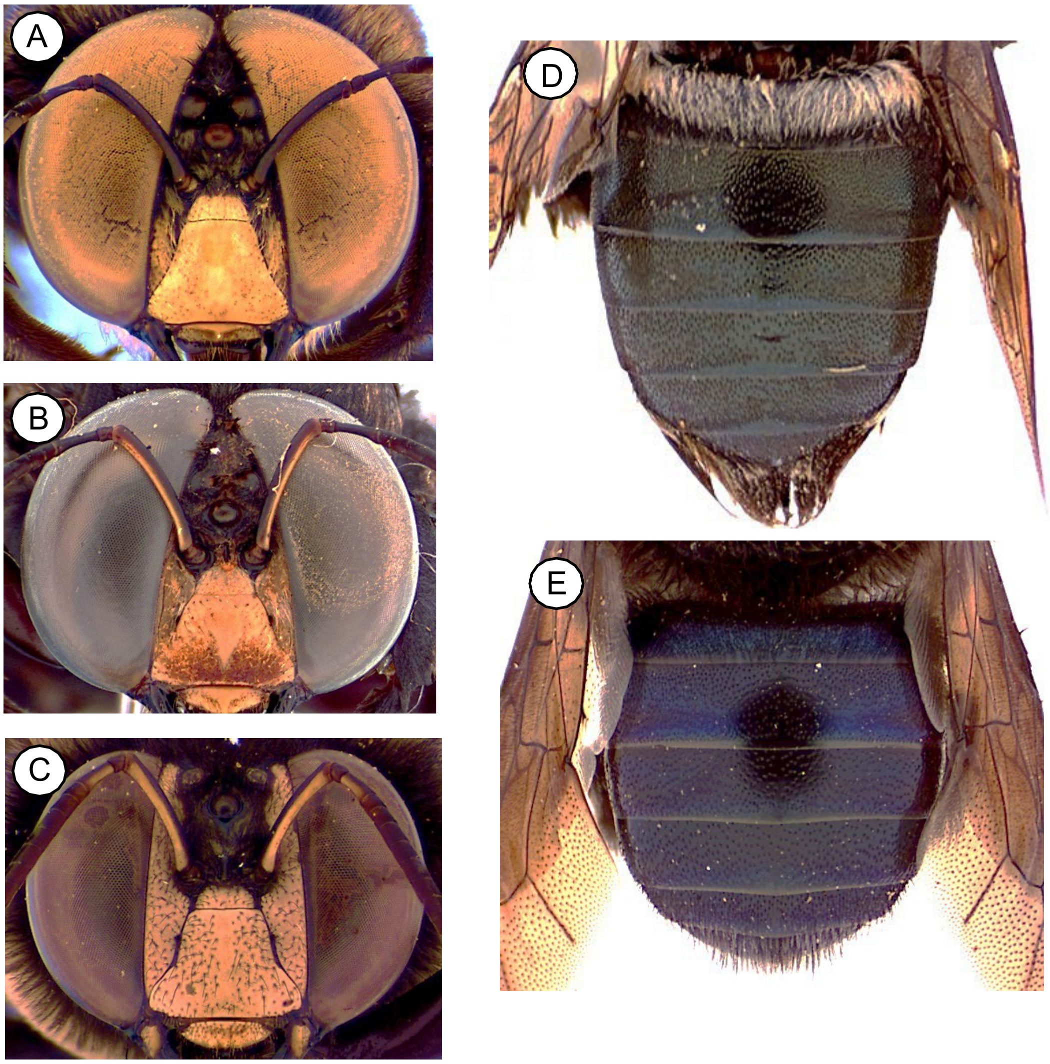

Figure 18: Head details of (A) *X. muscaria*, (B) *X. macrops* and (C) *X. subcyanea*; T1 pubescence of (D) *X. macrops* and (E) *X. muscaria.* Scale bar: 2 mm.

CAPÍTULO 2: FLORAL PREFERENCES OF CARPENTER BEES (APIDAE: XYLOCOPINI: *XYLOCOPA*) FROM MARANHÃO, NORTHEAST BRAZIL

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Floral preferences of carpenter bees (Apidae: Xylocopini: *Xylocopa*) from Maranhão, Northeast Brazil

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Abstract

The current study aimed to recognize the floral resources used by bees of the genus *Xylocopa* in transition physiognomies. We compiled the information available from biological collections and analyzed metrics of dystrophic interaction. We listed 2547 records of *Xylocopa* in flowers, across twelve identified bee species. The bees were collected from 109 plant species, belonging to 77 genera and 36 families. An interaction network was constructed based on 193 interactions. In which there was a significant correlation between the abundance of bees collected and the richness of plants visited. The most generalist bees were *X. cearensis* and *X. frontalis*, and the plants with the most records were *Chamaecrista hispidula* and *C. ramosa*. Significant seasonality was observed in the total number of individuals. On the other hand, there was a weak similarity among *Xylocopa* species according to plant species, despite the clear relationship of the bees according to physiognomies. The interaction network proved to be highly nested, indicating a functional partitioning that allows several species to occur in the same environment. The contribution made by the current work for its regional scope stands out, dealing with areas that have distinct characteristics.

Keywords: solitary bees, pollination, plant-pollinator, interaction network, ecotone.

Introduction

Large carpenter bees, also known as mamangava bees, are represented by the genus *Xylocopa* Latreille, 1802 (Michener, 2007). These bees are of medium to large size, usually nest in dead wood, and are characterized by solitary behavior with cooperatively breeding (Gerling et al. 1989; Danforth et al. 2019). The species in this genus are widely distributed around the world, with the greatest diversity found in tropical zones (Hurd & Moure 1963), with approximately 480 species distributed in 31 subgenera (Plant & Paulus 2016; Lucia et al. 2020).

Xylocopa species are dependent on the floral resources and nesting substrates (Hurd 1978; Sazima & Sazima 1989). Their body size, life cycle and long foraging distances make them essential pollinators (Silva et al. 2019; Harano et al. 2023), especially for botanical species that produce large flowers, such as *Bertholletia* spp. (Cavalcante et al. 2023) and *Passiflora* spp. (Barrera et al. 2021).

Because of this service provision, especially with respect to the productive increase in crops with high economic value in Brazil (Giannini et al. 2015), some studies have been conducted to research and conserve large carpenter bees, such as *X. frontalis* and *X. grisescens* (Pereira & Garófalo 2010; Giannini et al. 2020; Araújo et al. 2021; Farias-Silva & Freitas 2021; Costa et al. 2022). These and all other species of the genus, are considered polyletic, meaning that they potentially visit a wide variety of plant species in search of food (Keasar 2010; Lucia et al. 2017; Villamizar et al. 2020).

In Northeast Brazil, several works have identified plant species used by *Xylocopa* in dune and restinga areas (Silva & Martins 1999; Viana et al. 2002; Viana & Kleinert 2006; Albuquerque et al. 2007; Pigozzo et al. 2007; Ramalho & Rosa 2010; Santos et al. 2013; Figueiredo et al. 2013). However, little is known about the use of floral resources in other ecosystems, such as savannas, forests, and, especially, in transitional areas.

The State of Maranhão (MA) is located in the Eastern Amazon, where it is represented by the convergence of the humid vegetation of the ombrophilous forest and the dry and open vegetation of the savanna, characterized by the Brazilian Cerrado. These convergences have created a great diversity of ecosystems, including different types of physiognomies, leading to the region representing a point of biogeographic interest (Eiten 1994).

The records of *Xylocopa* spp. in MA are derived from some structured surveys (Rebêlo 1995; Rêgo et al. 2000; Albuquerque et al. 2007; Oliveira et al. 2010; Gostinski et al. 2016; Neves et al. 2021) and case studies (Oliveira et al. 2016; Pinto et al. 2020), mostly concentrated in coastal areas, and not all report information on the associated plant species. Although other surveys have been carried out in the different physiognomies of MA (Rêgo & Albuquerque 2012), a more comprehensive analysis of the resources exploited by species of the genus *Xylocopa* in these environments is still needed.

Therefore, considering that as well as knowledge of taxonomy and distribution, biotic interactions have been pointed out as an important gap to be filled in ecological research (Giannini et al. 2012; Hortal et al. 2015), the current study aimed to identify the floral resources used by *Xylocopa* species in different physiognomies of MA. As specific objectives, the study aimed to [1] quantify and qualify the interactions exerted by bees; [2] provide general information on the types of resources, habits (vertical stratification), and seasonal patterns involved in the interactions; and [3] analyze the degree of similarity of bees according to the resources used and the physiognomies studied.

Materials and methods

Study area

Maranhão is a northeastern Brazilian state located between 01º01′ – 10º21′ S and 41º48′ – 48º50′ W (IBGE 2012). The topography varies with latitude, with the mid-north characterized by plains and coastal formations, and the mid-south by the presence of plateaus, uplands, and tablelands. The climate varies with longitude, with a tropical hot climate type – Aw (Koeppen 1948), divided into a humid equatorial zone in the western portion; a semi-humid tropical equatorial zone in the central portion; and a semi-arid tropical equatorial zone in the eastern portion (IBGE 2012; NUGEO 2021). The combination of these characteristics is reflected in the direct influence of adjacent biomes (Amazon, Cerrado, and Caatinga), which promote the establishment of different types of vegetation cover or transitional physiognomies (IBGE 2012).

Originally, the Ombrophylous Forest occupied approximately 30.4% of the territory, concentrated in the western part of the state, but in recent decades it has suffered serious impacts due to the agricultural frontier and urban expansion (Martins & Oliveira 2011). Currently, the remnants of primary vegetation characteristic of the Amazon are concentrated in indigenous lands and protected areas (MapBiomas 2022).

The Park Savanna is characterized by shrub vegetation and occupies the entire central-southern part of MA (43.2% of the territory). It consists of the complexity of the Cerrado *stricto sensu*, where it can assume both formations associated with water bodies and humid forest, as well as drier formations. The vegetation has high diversity and environmental heterogeneity (Silva et al. 2008) and is considered fundamental for the maintenance of populations of different animal groups (Barreto 2007). The Steppic Savanna is a variation of this physiognomy that occupies a small area in the east of the state (0.5%) and corresponds to the typical elements of the Caatinga, where the vegetation is resistant to the warmer climate and water deficit (IBGE 2012). The contact areas or enclaves are characterized by the Deciduous Seasonal Forest (10%), which occupies the central-eastern part of the state, where there is a strong presence of Babassu palm trees (*Attalaea speciosa* Mart.) and large discontinuous areas (mosaics) adapted to climatic transitions (Barreto 2019). These elements, combined with the pedological characteristics of the northern coast, make up the Pioneer Formations (4.09%), which can occur under marine (Dunes and Restinga), fluviomarine (Mangroves), and fluvial or lacustrine influence (Flooded Fields) (NUGEO 2021). The typical vegetation of these areas includes a high diversity of herbaceous and liana plants, which are considered important environmental stabilizers, as restingas have been identified as one of the most threatened ecosystems today (Serra et al. 2016; Amorim et al. 2023).

Data collection

Information on the distribution and floral resources of *Xylocopa* spp. was obtained directly from the labels of individuals deposited at the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL – UFMA), where most of the bee records for Maranhão are found (Ferreira et al. 2020). These data were compared with the inventories conducted in the state, which were based on the list of plant species visited by bees. Although some of these inventories were not formally published, the information is available in specialized literature such as technical reports, monographs, dissertations, and thesis (Ferreira et al. 2020). Occasional collections were also considered if they contained information on provenance, date, and associated botanical species.

Records were categorized by phytophysiognomy, according to the classification of the Environmental Information Database (BDiA 2021), with additional information on provenance (municipality), date (collection interval), richness (number of *Xylocopa* species), dominance (*Xylocopa* species with the greatest number of individuals), and relative interaction (observed interactions of *Xylocopa* spp. in relation to the total number of bees).

Some taxonomic inconsistencies were corrected based on the original descriptions of each *Xylocopa* species, through the identification keys proposed by Schlindwein et al. (2003), Marchi & Alves-dos-Santos (2013), Lucia et al. (2014), Lucia et al. (2015), Mawdsley (2018), Villamizar et al. (2020), Mérida-Rivas et al. (2022) and by comparison with the material deposited at the Coleção Entomológica Danúncia Urban, Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, PR (CEDU) and the Coleção de Abelhas da Universidade Federal do Maranhão, São Luís, MA (LEACOL).

The listed plants were classified according to habit, resource, pollination syndrome, and origin, using as a reference: Faegri & van der Pijl (1979) and Almeida et al. (2022) generically, in addition to the online bases RCPol (2013) and Flora do Brasil (2020). The classification system used was APG IV (2016), and the revision and updating of species names was based on the database provided by IPNI (1999).

Data analysis

A bipartite interaction network between bees and visiting plants was constructed using R Core Team software, version 4.2.3 (R development core team 2019), with the bipartite package (Dormann 2020). The following metrics describing a trophic interaction network were calculated: [1] connectance (C), which measures the proportion of observed interactions (IO) to the total possible interactions (IP), where C = IO x 100/IP (Pigozzo & Viana 2010), and [2] average degree (k), which corresponds to the average number of observed interactions as a function of bee (A) and plant (P) richness, where kA = IO/A and kP = IO/P (Blüthgen et al. 2008). To assess the degree of nestedness of the network, the N and NODF (Nestedness metric based on Overlap and Decreasing Fill) indices were calculated using Aninhado software, version 3.0.3 (Guimaraes Jr & Guimaraes 2006). The N index was obtained from the T index (temperature), which is inversely proportional to the degree of nestedness: N =

(100-T)/100. This measure varies from 0 to 1, with values closer to 1 indicating greater nesting and values closer to 0 indicating the opposite (Bascompte et al. 2003). The NODF index, on the other hand, considers the overlapping and decreasing filling of a binary matrix and indicates the number of unexpected presences and absences, with values varying from 0 to 100 (Almeida-Neto et al. 2008). For this calculation, 1000 simulations were performed.

In addition, we evaluated the relationship between the abundance of each bee species and the number of interactions per plant species using an R-squared correlation plot (R^2). The trend line was plotted based on series-logarithmic where it best fits the input data.

To evaluate the seasonality of *Xylocopa* spp. we used the Rayleigh (Z) uniformity test (Zar 1999) to analyze bee activity, based on the date of occurrence of the interactions. In this calculation, the index r is presented as a measure of unimodal clustering on a set of points within a circle. A low value of r indicates that the points are uniformly distributed around the circle, while a high value indicates that the points are clustered in one or more directions, i.e., a seasonal pattern (Morellato et al. 2000). Circular statistics were performed using Oriana - Circular Statistics software, version 4.02 (Kovach 2011a).

The similarity between *Xylocopa* species as a function of plant species used as resources and physiognomies was calculated with the Sorensen index or Coefficient of Association (CA), which is defined as the ratio between twice the number of species common to both samples (c) and the total sum of the number of species in both samples (a + b), where CA = 2c/a + b x 100. This index can range from 0 to 1, where 0 indicates no similarity between the samples and 1 indicates total similarity, i.e. when the two samples share exactly the same species. For this cluster analysis, only binary data (presence and absence) were used to avoid biases caused by uneven sampling in the different physiognomies. The similarity dendrogram was generated using the software MVSP – MultiVariate Statistical Package, version 3.22 (Kovach 2011b).

Results

In total, we listed 2547 records of *Xylocopa* on flowers in Maranhão over a 40–year interval (1982–2022), through 15 structured surveys (77.2% of individuals), seven case studies (20.5%), and 16 occasional collections (2.3%) (Table 1). From these records, we identified three subgenera and 12 bee species: *Xylocopa* (*Neoxylocopa*) *amazonica* Enderlein, 1913; *X.* (*N.*) *aurulenta* (Fabricius, 1804); *X.* (*N.*) *cearensis* Ducke, 1910; *X.* (*N.*) *frontalis* (Olivier, 1789); *X.* (*N.*) *grisescens* Lepeletier, 1841; *X.* (*N.*) *hirsutissima* Maidl, 1912; *X.* (*N.*) *nigrocincta* Smith, 1854; *X.* (*N.*) *transitoria* Pérez, 1901; *X.* (*Schonnherria*) *macrops* Lepeletier, 1841; *X.* (*S.*) *muscaria* (Fabricius, 1775); *X.* (*S.*) *subcyanea* Pérez, 1901; and *X.* (*Stenoxylocopa*) sp., distributed in 23 municipalities. The physiognomies with the highest *Xylocopa* abundance values were Dunes (44.7%) and Restinga (30.6%); and the highest richness values were Park Savanna (75%) and Ombrophylous Forest (58.3%).

Bees were collected visiting 109 plant species, distributed in 77 genera and 36 botanical families (Table 2). The most representative families were Fabaceae (34 spp.), Malvaceae (8 spp.) and Asteraceae and Convolvulaceae (5 spp. each). Another 17 families were represented by only one species. Within this richness, 87% are native plants, of which 9.2% are considered endemic to Brazil, and the others are of exotic origin, naturalized (6.4%) or cultivated (2.7%).

The vertical stratification consisted of herbaceous plants (28.7%), shrubs (27.7%), trees (17.5%), lianas (16.6%), and subshrubs (7.4%). Regarding the availability of the resources offered, almost half of the visited plants offer nectar as the main attraction (49%), followed by pollen (23.1%) and the combination of these two resources (20.3%), while floral oils were offered by only 4.6% of the species. As for the pollination syndromes, most plants present melitophilia as the main system (85.1%), the others present a combination of melitophilia with other pollinating insects (7.4%) and chiropterophily (2.7%).

The interaction network (Figure 1) consisted of 12 bee species and 109 plant species, resulting in 1308 possible interactions, however, only 193 interactions were observed, resulting in a connectance of 14.7%. The generalist bee species were *X. cearensis* (61.5% of all observed plants), *X. frontalis* (37.6%), and *X. nigrocincta* (22%). In contrast, *X. aurulenta* and *X. amazonica* visited only two plant species each, representing only 1.8% of the total. In addition, five other *Xylocopa* species visited less than 10 plant species.

The most visited plants in terms of bee abundance were *Chamaecrista hispidula* (Vahl) H.S.Irwin & Barneby (9.9% of individuals), *Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby (9.2%), and *Passiflora foetida* L. (7.8%); in terms of species richness, the highest values were found for *Chamaecrista ramosa* (50% of species), and *Tecoma stans* (L.) Juss. Ex Kunth, and *Crotalaria retusa* L. (41.6% each).

The average degree of visiting bees to plants (kA) was 16.08 and the average degree of plants to bees (kP) was 1.77. The interaction network showed a high nestedness degree, N = 0.90 and NODF = 36.1. In addition, the correlation graph (Figure 2) showed a clear relationship between the abundance of bee species collected and the number of visited plant species, according to the R^2 value = 0.923.

The seasonality of the bee species is presented with a circular distribution histogram (Figure 3), which showed the low number of species active throughout the year. The Rayleigh test indicated a significant distribution in relation to the total number of individuals (Z = 19.33), with May presenting the average range of interactions. The species with the most significant results were *X. frontalis* (Z = 28.54) and *X. muscaria* (Z = 16.10) (Table 3). The species *X. subcyanea* and *Xylocopa* sp. showed low significance in the Z test due to the limited samples.

The similarity between *Xylocopa* species according to the plant species visited (Figure 4A) showed a 40% similarity between two groups: *X. transitoria* with *X. nigrocincta,* and *X. frontalis* with *X. cearensis*, respectively, while the other species showed 70% or more similarity. Similarity between *Xylocopa* species according to physiognomic forms (Figure 4B) showed that eight of the 12 species had more than 60% similarity, with two well-defined groups (CA = 1): *X. muscaria* with *X. nigrocincta,* and *X. frontalis* with *X. cearensis*. Among species with the highest number of records, *X. muscaria* is the most dissimilar species when we consider the proportion of plants visited per physiognomy.

Discussion

The genus *Xylocopa* is well represented in Maranhão and was present in all surveys previously conducted in this territory, including those that were not included in our analysis due to lack of botanical information (Rebêlo et al. 2003; Rêgo et al. 2007; Ferreira et al. 2019) or due to individuals not being deposited in LEACOL (Ducke 1908; Gottsberger et al. 1988) and which, therefore, could not be verified. However, the distribution of abundance proved to be very uneven, since most of these works were carried out in the northern and northeastern part of MA (Rebêlo et al. 2003), and bee communities in the dunes and restingas areas were dominated by the species *X. cearensis* (Silva et al. 2001; Albuquerque et al. 2007; Oliveira et al. 2010; Gostinski et al. 2016; Neves et al. 2021). The dominance of *X. cearensis* has also been observed in other areas of Brazil with the same phytophysiognomic characteristics (Viana et al. 2002; Silva & Viana 2002; Pigozzo et al. 2007; Ramalho & Rosa 2010; Figueiredo et al. 2013; Silva et al. 2019).

On the other hand, *Xylocopa* richness was slightly higher in park savannas (Rêgo et al. 2007), despite the deficit of systematized sampling in this physiognomy. In this context, occasional or incremental collections play an important role in filling sampling gaps (Huybrechts et al. 2022). In our study, 66% of the richness was concentrated in only 2.3% of the individuals recorded by this method.

Xylocopa species were observed to visit several botanical families with a high proportion of mellitophilous species, including Fabaceae, Malvaceae, and Asteraceae. These families represent a significant part of the diversity of the Brazilian flora (BFG 2021) and are important for maintaining biodiversity and ecosystem functioning (Bawa 1990; Frankie et al. 2005). In the transitional areas of Maranhão, most of the plants visited by *Xylocopa* bees are of native origin, indicating that the historical relationship between native species still prevails over exotic or invasive species, even in areas of high urban occupation (Almeida et al. 2022; Amorim et al. 2023).

However, some exotic plant species can be very attractive, especially to generalist bees, due to mass flower production or the density of individuals that dominate the environment (Silva et al. 2007; Stout & Morales 2009). In our records, *Tecoma stans*, a plant native to Mexico and the southern USA, attracted five of the 12 *Xylocopa* species present in MA. However, three of these species (*X. frontalis*, *X. grisescens*, and *X. nigrocincta*) were found to be nectar robbers in a study of their floral visitors (Silva et al. 2007). On the other hand, for *Crotalaria retusa*, a native Asian plant commonly found in tropical coastal areas (Riet-Correa et al. 2011; Amorim et al. 2023), *X. frontalis* and *X. grisescens* were shown to be effective pollinators (Jacobi et al. 2005).

Among the ten Brazilian native and endemic plants visited by *Xylocopa* in MA, the most representative were *Lepidaploa arenaria* and *Asemeia hirsuta* in dune areas (Albuquerque et al. 2007) and *Cenostigma bracteosum* in restinga. Endemic species are generally adapted to the specific environmental and climatic conditions of their area of occurrence, as well as to the species to which they are related, and often function as key-species in local ecosystems (Martins 2002; Gögler et al. 2009; Miranda et al. 2015).

Another fundamental component in maintaining ecological relationships is environmental heterogeneity, which refers to the diversity of conditions and resources within ecosystems (Palmer & Dixon 1990; Tamme et al. 2010). In the case of plants, variation in floral resources along vertical strata can generate a complementarity effect among local pollinators (Almeida et al. 2022), in some cases avoiding niche overlap (Araújo et al. 2021). In MA, the stratification of resources was variable, and plants with herbaceous and subshrub habits stood out, attracting 47.2% of individuals, mainly among small to medium-sized species, while tree-sized species attracted just under 15% of individuals, regardless of bee size. This same frequency was observed in dune (Gottsberger et al. 1988) and Cerrado (Gottsberger & Silberbauer-Gottsberger 2018) areas, respectively, and overall, this difference may be influenced by the availability and type of resources provided (Almeida et al. 2022).

According to our results, nectariferous plants formed the largest group of species and were visited more uniformly than polliniferous plants. In the latter, a very high visitation frequency was observed, but only in a few plant species, especially in representatives of the genera *Chamaecrista*, *Bixa* and *Senna*. The collection of protein through pollen usually involves some specialization on the part of the pollinating organism (Linsley 1958). In the case of bees, especially solitary bees, the most common strategy is collection by vibration, also known as "buzz pollination" (Buchmann 1983; Vallejo-Marín 2019; Rosi-Denadai et al. 2020).

For some highly generalist carpenter bee species, the offered resource is only optional and seems to be consumed for convenience, according to the degree of local competition (Araújo et al. 2021). The interactions between *Xylocopa* species and plants in the MA were found to be heterogeneous, due to the concentration of many plant species visited by few bees and vice versa. Although this is a regional dataset, this pattern has also been observed in local studies (Pinto et al. 2020; Neves et al. 2021). The asymmetry observed in the interaction network, where five bee species visited more than the average number of plants, was mainly caused by *X. cearensis* and *X. frontalis*. This type of dominance is an expected characteristic of bipartite networks of mutualistic interactions (Pigozzo & Viana 2010; Diniz & Buschini 2015).

According to the correlation of the number of bee individuals per plant species, there is no evidence of specialization in the use of floral resources for any *Xylocopa* species, either by visiting a large number of plant species or by the small number of individuals analyzed, as is the case for *X. amazonica*, *X. subcyanea,* and *X. aurulenta*.

Only when we consider exclusive data from structured surveys can we analyze, for example, the effects generated by seasonal and geographic patterns on some species (Biesmeijer et al. 2005; Teixeira et al. 2007).

Our results revealed that more than half of the *Xylocopa* species in MA reached some level of significance with respect to seasonality. Some species, such as *X. cearensis*, *X. frontalis*, and *X. grisescens*, had regular records throughout the year, indicating possible multivoltinism, when there is overlap between generations (Ramalho et al. 2004), while other species, even those with a reasonable number of records, such as *X. muscaria*, showed a partitioned frequency over the months.

In general, *Xylocopa* species were more frequent between the months of February and June, a period marked by the highest rainfall in the state. This event is probably related to the availability of poricid flowers in coastal regions, also verified by Viana et al. (2002). The pollen supply provided by species of the genus *Chamaecrista* throughout the rainy season corroborates the study of Almeida et al. (2022), in which the authors discuss the temporal relationship of this resource as a complement to the abundant nectariferous species in the dry season.

Considering the *Xylocopa*-plant interactions according to the different types of resources, vertical stratification, and seasonal patterns, low similarity was found among most of the bees, indicating that on average they compete for only 25% of the resources. This is the case even among the most similar species in terms of physiognomy, such as *X. frontalis* and *X. cearensis*, which overlapped strongly in the dunes/restinga environments, and *X. muscaria* and *X. nigrocincta* in the flooded fields.

The nestedness, observed by the significant values of the N and NODF indices, indicates the presence of a functional partitioning, in which the establishment of interactions between the less abundant bee species adjusts to the secondary resources of the most abundant species, thus supporting the permanence of both in the same environment (Bascompte & Jordano 2007; Pigozzo & Viana 2010; Pinto et al. 2020).

Although sampling biases are inherent in the historical data available and should be interpreted with caution, we can conclude from the analysis of the most abundant species that the diversity of floral resources is a crucial factor for *Xylocopa* populations, the transitional areas of the MA can assume an important function as a stronghold for restricted species. The conservation of these natural environments is therefore essential for the protection and conservation of these pollinators.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1. Records of species of the genus *Xylocopa* collected from plants in Maranhão State, deposited at the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL – UFMA). PH – Physiognomies: SS – Steppic Savanna; DS – Deciduous Seasonal Forest; FF – Flooded Fields; *Am – X.* (*Neoxylocopa*) *amazonica, Au – X.* (*N.*) *aurulenta, Ce – X.* (*N.*) *cearensis, Fr – X.* (*N.*) *frontalis, Gr – X.* (*N.*) *grisescens, Hi – X.* (*N.*) *hirsutissima, Ni – X.* (*N.*) *nigrocincta, Tt – X.* (*N.*) *transitoria, Ma – X.* (*Schonnherria*) *macrops, Mu – X.* (*S.*) *muscaria, Su – X.* (*S.*) *subcyanea, St – X.* (*Stenoxylocopa*) sp.; S – richness; D – dominant species: P% – relative frequency of plants visited in surveys; REF – references.

PH		Municipalities	Collectors	Year	S	D	P%	REF
Ombrophylous Forest		Alcântara	Araújo & Gonçalves	1992-1993	2	*Fr*	7.6	1
		Buriticupu	Pereira, C.Q.B.**	1999	1	*Ce*	-	2
		Carutapera	Ferreira, L.A.C.**	2014	3	*Fr*	-	3
		Cururupu	Dos Anjos, J.V.	2015-2016	1	*Fr*	11.1	4
		São Luís	Brenha & Rebêlo	1982-1983	4	*Fr*	15.7	5
			Cruz & Sodré	1999-2000	4	*Mu*	14.8	6
			Apocalypse & Rodrigues	1991-1992	5	*Fr*	15.6	7
			Machado & Botão*	2005	1	*Ce*	-	8
			Ferreira, L.A.C.**	2022	4	*Ce*	-	9
Park Savanna		Balsas	Jesus & Silva	2006-2007	6	*Gr*	-	10
		Barreirinhas	Brito & Mendonça	1991-1992	4	*Fr*	75.0	11
			Serra, B.D.V.*	2005-2006	3	*Fr*	-	12
		Caxias	Pinho, A.N.**	2009	1	*Hi*	-	13
		Chapadinha	Brito & Rêgo**	1994	1	*Am*	-	14
			Barbosa & Pinto**	2011	1	*Ni*	-	15
		Formosa da Serra Negra	Araújo & Brito	2011-2012	2	*Gr*	2.56	16
		Grajaú	Ferreira, L.A.C.**	2022	1	*Fr*	-	17
		São João dos Patos	Ferreira, L.A.C.**	2022	1	*Fr*	-	18
		Urbano Santos	Mendes & Ramos**	2003	2	*Mu*	-	19
			Serra, B.D.V.*	2005-2006	2	*Fr*	-	20
SS		Barão de Grajaú	Ferreira, L.A.C.**	2022	1	*Hi*	-	21
DS		Codó	Ferreira, L.A.C.**	2022	1	*Ce*	-	22
		Colinas	Ferreira, L.A.C.**	2022	1	*Fr*	-	23
		Imperatriz	Ferreira, L.A.C.**	2022	1	*Ce*	-	24
		Timon	Ferreira, L.A.C.**	2022	2	*Hi*	-	25
Pioneer Formations	Dunes	São José de Ribamar	Oliveira & Mendonça	2005-2006	3	*Ce*	66.6	26
			Ferreira, L.A.C.**	2016	2	*Ce*	-	27
			Santana, I.B.P.A.*	2017	2	*Fr*	-	28
		São Luís	Albuquerque & Ferreira	1993-1994	4	*Ce*	63.6	29
	Restinga	Barreirinhas	Gostinski & Carvalho	2009-2010	5	*Ce*	20.3	30
			Silva, F.M.A.*	2009-2010	4	*Fr*	-	31
			Silva, O.**	2011	1	*Su*	-	32
			Oliveira, F.S.*	2015	2	*Ce*	-	33
			Pinto, R.S.*	2017	4	*Ce*	-	34
		Raposa	Souza & Martins	1999-2000	2	*Ce*	46.1	35
		Tutóia	Neves JR & Barros	2017-2018	4	*Ce*	73.6	36
	FF	Anajatuba	Araújo & Carvalho	2008-2009	4	*Ce*	-	37
			Oliveira, F.S.*	2008-2009	4	*Fr*	-	38
		Vitória do Mearim	Ferreira & Santos	1991-1992	5	*Mu*	40.0	39

*Case studies; ** Occasional collections; Publications with botanical data: 5 – Rebêlo (1995); 11 – Albuquerque e Mendonça (1996); 12, 20 – Serra e Drummond (2006); 29 – Albuquerque et al. (2007); 33 – Oliveira et al. (2016); 34 – Pinto et al. (2020); 35 – Silva et al. (2001); 36 – Neves et al. (2021); 38 – Oliveira (2014); 39 – Rêgo et al. (2000); Publications without botanical data:: 10 – Rêgo et al. (2007); 30 – Gostinski et al. (2016); 26 – Oliveira et al. (2010); Unpublished data: 1, 4, 6, 7, 8, 10, 16, 28, 31, 37.

Table 2. Floral resources used by species of the genus *Xylocopa* in Maranhão State, deposited at the Coleção de Abelhas da Universidade Federal do Maranhão (LEACOL – UFMA). Habit: Tr – tree, Sh – shrub, Ss – subshrub, Hb – herbs, Cr – creeper; Resource: Ne – Nectar, Po – Pollen, Ol – Oil; Syndrome: Mel – melitophilia, Psi – psicophilia, Myo – myophilia, Chi – chiropterophily, Orn – ornithophily; Origin: Nv – native, Nz – naturalized, Ct – cultivated; *Xylocopa* species*: Am – X.* (*Neoxylocopa*) *amazonica, Au – X.* (*N.*) *aurulenta, Ce – X.* (*N.*) *cearensis, Fr – X.* (*N.*) *frontalis, Gr – X.* (*N.*) *grisescens, Hi – X.* (*N.*) *hirsutissima, Ni – X.* (*N.*) *nigrocincta, Tr – X.* (*N.*) *transitoria, Ma – X.* (*Schonnherria*) *macrops, Mu – X.* (*S.*) *muscaria, Su – X.* (*S.*) *subcyanea, St – X.* (*Stenoxylocopa*) sp.; REF – references in Table 1.

	CODE / **Family** / *Botanical Species*	Habit	Resource	Syndrome	Origin	*Xylocopa* species												REF
						Am	*Au*	*Ce*	*Fr*	*Gr*	*Hi*	*Ni*	*Tr*	*Ma*	*Mu*	*Su*	*St*	
	Amaranthaceae																	
1	*Alternanthera tenella* Colla	Hb	Po	Mel	Nv			x										26
	Anacardiaceae																	
2	*Anacardium occidentale* L.	Tr	Po+Ne	Mel	Nv			x				x						10, 11, 30, 35, 36
	Apocynaceae																	
3	*Allamanda blanchetii* A.DC.	Sh	Ne	Mel	Nv*			x		x								11
4	*Funastrum clausum* (Jacq.) Schltr.	Cr	Po	Mel+Psi	Nv			x										35
	Asteraceae																	
5	*Centratherum punctatum* Cass.	Hb	Ne	Mel	Nv							x						39
6	*Lepidaploa arenaria* (Mart. ex DC.) H.Rob.	Ss	Ne	Mel	Nv*			x				x						29
7	*Lepidaploa rufogrisea* (A.St.-Hil.) H.Rob.	Sh	Ne	Mel	Nv*			x				x						30, 38
8	*Praxelis kleinioides* (Kunth) Sch. Bip.	Hb	Ne	Mel	Nv				x									6
9	*Tilesia baccata* (L.) Pruski	Sh	Ne	Mel	Nz			x										29
	Bignoniaceae																	
10	*Adenocalymma subincanum* Huber	Cr	Ne	Mel	Nv			x	x									7
11	*Fridericia platyphylla* (Cham.) L.G.Lohmann	Sh	Ne	Mel	Nv			x										29
12	*Tecoma stans* (L.) Juss. Ex Kunth	Sh	Ne	Mel	Nz			x	x		x	x	x					6, 9, 17, 18, 21, 22, 23, 24, 25
	Bixaceae																	
13	*Bixa orellana* L.	Sh	Po	Mel	Nv				x	x		x						4, 6, 20
	Boraginaceae																	
14	*Euploca polyphylla* (Lehm.) J.I.M.Melo & Semir	Hb	Ne	Mel	Nv			x						x				29, 35, 36
15	*Varronia multispicata* (Cham.) Borhidi	Sh	Po+Ne	Mel	Nv*										x			1

Table 2. Continued

	CODE / **Family** / *Botanical Species*	Habit	Resource	Syndrome	Origin	*Xylocopa* species												REF
						Am	*Au*	*Ce*	*Fr*	*Gr*	*Hi*	*Ni*	*Tr*	*Ma*	*Mu*	*Su*	*St*	
	Bromeliaceae																	
16	Bromeliaceae sp.	-	-	-	-												x	10
	Burseraceae																	
17	*Protium heptaphyllum* (Aubl.) Marchand	Sh	Ne	Mel+Chi	Nv			x										29, 35
	Caryocaraceae																	
18	*Caryocar cuneatum* Wittm.	Tr	Po+Ne	Chi+Psi	Nv*			x		x								11
	Chrysobalanaceae																	
19	*Hirtella racemosa* Lam.	Sh	Ne	Psi	Nv										x			6
	Convolvulaceae																	
20	*Ipomoea asarifolia* (Desr.) Roem. & Schult	Hb	Po+Ne	Mel	Nv							x						37
21	*Ipomoea maurandioides* Meisn.	Cr	Po+Ne	Mel	Nv			x										36
22	*Ipomoea mauritiana* Jacq.	Cr	Ne	Mel	Nv			x										29
23	*Ipomoea pes-caprae* (L.) R.Br.	Hb	Ne	Mel	Nv			x										26, 35
24	*Jacquemontia tamnifolia* (L.) Griseb.	Cr	Po+Ne	Mel	Nv			x										36
	Euphorbiaceae																	
25	*Cnidoscolus urens* (L.) Arthur	Hb	Ne	Mel+Psi	Nv			x										26
26	Euphorbiaceae sp.	-	-	-	-											x		19
	Fabaceae																	
27	*Ancistrotropis peduncularis* (Kunth) A. Delgado	Cr	Ne	Mel	Nv			x						x				36
28	*Andira surinamensis* (Bondt) Splitg. ex Amshoff	Tr	Ne	Mel	Nv			x										36
29	*Bauhinia* sp.	Sh	Ne	Mel+Psi	Nz				x									10
30	*Bowdichia* sp.	Tr	Ne	Mel	Nv					x								11
31	*Calopogonium* sp.	Hb	Ne	Mel	Nv			x	x									9
32	*Canavalia rosea* (Sw.) DC.	Cr	Ne	Mel	Nv			x	x				x					26, 29
33	*Canavalia* sp.	Hb	Ne	Mel	Nv				x									36
34	*Cassia* sp.	Tr	Po	Mel	Nv				x	x								11
35	*Cenostigma bracteosum* (Tul.) Gagnon & G.P.Lewis	Tr	Ne	Mel	Nv*			x	x	x		x						30, 31, 38
36	*Centrosema brasilianum* (L.) Benth.	Cr	Ne	Mel	Nv			x										3, 12
37	*Centrosema plumieri* (Turpin ex Pers.) Benth.	Cr	Ne	Mel	Nv				x									10
38	*Centrosema* sp.	Cr	Ne	Mel	Nv			x										28, 29
39	*Chamaecrista diphylla* (L.) Greene	Ss	Po	Mel	Nv										x			39
40	*Chamaecrista hispidula* (Vahl) H.S.Irwin & Barneby	Ss	Po	Mel	Nv			x	x						x			26, 29

Table 2. Continued

CODE / **Family** / *Botanical Species*		Habit	Resource	Syndrome	Origin	*Xylocopa* species												REF
						Am	*Au*	*Ce*	*Fr*	*Gr*	*Hi*	*Ni*	*Tr*	*Ma*	*Mu*	*Su*	*St*	
41	*Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby	Ss	Po	Mel	Nv			x	x	x	x			x		x		10, 35, 36
42	*Crotalaria retusa* L.	Hb	Ne	Mel	Nz		x	x	x	x		x						5, 28, 29, 35, 39
43	*Crotalaria* sp.	Hb	Ne	Mel	Nv				x									1
44	*Dioclea* sp.	Cr	Ne	Mel	Nv				x									4
45	*Dioclea virgata* (Rich.) Amshoff	Cr	Ne	Mel	Nv				x			x	x					5, 7, 39
46	Fabaceae sp.	-	-	-	-			x		x								10, 37
47	*Galactia jussiaeana* Kunth	Ss	Ne	Mel	Nv			x										29
48	*Hymenaea parvifolia* Huber	Tr	Po+Ne	Chi	Nv			x										30
49	*Macroptilium atropurpureum* (Sessé & Moc. ex DC.) Urb.	Cr	Ne	Mel	Nz			x										29
50	*Macroptilium lathyroides* (L.) Urb.	Hb	Ne	Mel	Nv				x									39
51	*Parkia platycephala* Benth.	Tr	Ne	Chi	Nv*					x								11
52	*Pueraria phaseoloides* (Roxb.) Benth.	Hb	Ne	Mel	Nz			x										39
53	*Senna alata* (L.) Roxb.	Sh	Po	Mel	Nv			x	x			x			x			5, 39
54	*Senna latifolia* (G.Mey.) H.S.Irwin & Barneby	Sh	Po	Mel	Nv				x	x								5
55	*Senna obtusifolia* (L.) H.S.Irwin & Barneby	Ss	Po	Mel	Nv			x				x						37, 39
56	*Senna occidentalis* (L.) Link	Sh	Po	Mel	Nv			x										37
57	*Senna reticulata* (Willd.) H.S.Irwin & Barneby	Sh	Po	Mel	Nv				x						x			39
58	*Senna silvestris* (Vell.) H.S.Irwin & Barneby	Sh	Po	Mel	Nv					x								16
59	*Senna* sp.	Sh	Po	Mel	Nv	x			x									4
60	*Vatairea sericea* (Ducke) Ducke	Tr	Po+Ne	Mel	Nv			x	x	x					x			11
	Gentianaceae																	
61	*Coutoubea spicata* Aubl.	Hb	Po	Mel	Nv			x				x	x		x			6, 7
	Humiriaceae																	
62	*Humiria balsamifera* (Aubl.) A.St.-Hil.	Tr	Ne	Mel	Nv				x									30
63	*Humiria balsamifera* var. *floribunda* (Mart.) Cuatrec.	Tr	Ne	Mel	Nv			x	x	x		x						34
	Hypericaceae																	
64	*Vismia guianensis* (Aubl.) Choisy	Sh	Po+Ne	Mel	Nv										x			1
	Lamiaceae																	
65	*Marsypianthes chamaedrys* (Vahl) Kuntze	Hb	Ne	Mel	Nv			x										29
66	*Mesosphaerum suaveolens* (L.) Kuntze	Hb	Ne	Mel	Nv										x			39
	Lecythidaceae																	

Table 2. Continued

CODE / **Family** / *Botanical Species*		Habit	Resource	Syndrome	Origin	*Xylocopa* species												REF
						Am	*Au*	*Ce*	*Fr*	*Gr*	*Hi*	*Ni*	*Tr*	*Ma*	*Mu*	*Su*	*St*	
67	*Gustavia augusta* L.	Tr	Po	Mel	Nv			x										29
	Loganiaceae																	
68	*Spigelia anthelmia* L.	Hb	Po+Ne	Mel	Nv			x										36
	Loranthaceae																	
69	*Phthirusa* sp.	Hb	Ne	Mel	Nv			x										2,
70	*Psittacanthus robustus* (Mart.) Mart.	Hb	Ne	Orn+Chi	Nv				x									16, 30
	Lythraceae																	
71	*Cuphea mimuloides* Cham. & Schltdl.	Hb	Ne	Mel	Nv			x									x	30
72	*Cuphea* sp.	Hb	Ne	Mel	Nv			x			x							13, 30
	Malpighiaceae																	
73	*Banisteriopsis nummifera* (A.Juss.) B.Gates	Cr	Po+Ol	Mel	Nv										x			7
74	*Byrsonima crassifolia* (L.) Kunth	Tr	Po+Ol	Mel	Nv			x				x	x					6, 36
75	*Malpighia glabra* L.	Tr	Po+Ol	Mel	Ct				x									37
	Malvaceae																	
76	*Eriotheca globosa* (Aubl.) A.Robyns	Tr	Po+Ne	Mel	Nv				x	x		x						5
77	*Eschweilera decolorans* Sandwith	Tr	Ne	Mel	Nv			x	x									11
78	*Gossypium* L.	Sh	Po+Ne	Mel	Nv											x		32
79	*Hibiscus sabdariffa* L.	Sh	Po+Ne	Mel	Nz			x										8
80	Malvaceae sp.	-	-	-	-		x					x			x			39
81	*Pavonia cancellata* (L.) Cav.	Hb	Po+Ne	Mel	Nv										x			39
82	*Sida acuta* Burm.f.	Ss	Po+Ne	Mel	Nv				x									4
83	*Sida* sp.	Ss	Po+Ne	Mel	Nv							x	x					6
	Melastomataceae																	
84	*Comolia villosa* (Aubl.) Triana	Sh	Po	Mel	Nv			x										30
85	*Mouriri acutiflora* Naudin	Tr	Po+Ol	Mel	Nv			x	x			x			x			30, 37, 39
86	*Mouriri guianensis* Aubl.	Sh	Po+Ol	Mel	Nv			x		x								33
	Myrtaceae																	39
87	*Myrtus* sp.	Sh	Ne	Mel+Myo	Ct						x							10
	Ochnaceae																	
88	*Ouratea hexasperma* (A.St.-Hil.) Baill.	Tr	Po	Mel	Nv			x	x	x					x			11, 36
89	*Ouratea racemiformis* Ule	Tr	Po	Mel	Nv*			x	x			x	x		x			6, 30
90	*Ouratea semiserrata* (Mart. & Nees) Engl.	Sh	Po	Mel	Nv*	x												14
91	*Ouratea* sp.	Sh	Po	Mel	Nv							x			x			15, 19

Table 2. Continued

CODE /	**Family** / *Botanical Species*	Habit	Resource	Syndrome	Origin	*Xylocopa* species												REF
						Am	*Au*	*Ce*	*Fr*	*Gr*	*Hi*	*Ni*	*Tr*	*Ma*	*Mu*	*Su*	*St*	
	Oxalidaceae																	
92	*Oxalis juruensis* Diels	Sh	Po+Ne	Mel	Nv										x			39
	Passifloraceae																	
93	*Passiflora acuminata* DC.	Cr	Ne	Mel	Nv							x						37
94	*Passiflora edulis* Sims	Cr	Ne	Mel	Nv				x									3
95	*Passiflora foetida* L.	Cr	Ne	Mel	Nv			x	x									26, 29
96	*Passiflora* sp.	Cr	Ne	Mel	Nv			x	x									27, 35
	Polygalaceae																	
97	*Asemeia hirsuta* (A.St.-Hil. & Moq.) J.F.B.Pastore & J.R.Abbott	Hb	Ne	Mel	Nv*			x										29
	Rubiaceae																	
98	*Borreria verticillata* (L.) G.Mey.	Hb	Po+Ne	Mel+Psi	Nv			x	x					x	x			4, 7, 29, 35, 36
99	*Diodia* sp.	Hb	Ne	-	-			x										28
100	*Mitracarpus* sp.	Hb	Po+Ne	Mel+Psi	Nv			x										35
	Sapindaceae																	
101	*Pseudima frutescens* (Aubl.) Radlk.	Sh	Ne	Mel	Nv			x										29
	Sapotaceae																	
102	*Manilkara* sp.	Sh	Ne	Mel	Nv			x										36
	Solanaceae																	
103	*Solanum jamaicense* Mill.	Sh	Po	Mel	Nv			x	x						x			37
104	*Solanum nudum* Dunal	Sh	Po	Mel	Nv			x	x									29
105	*Solanum subinerme* Jacq.	Sh	Po	Mel	Nv			x				x						5
	Talinaceae																	
106	*Talinum* sp.	Hb	Po	Mel	Nv			x										26
	Turneraceae																	
107	*Piriqueta cistoides* (L.) Griseb.	Hb	Po+Ne	Mel	Nv			x	x			x						26, 30, 35, 38
108	*Turnera melochioides* Cambess.	Hb	Po+Ne	Mel	Nv			x										29, 36
109	*Turnera ulmifolia* L.	Hb	Po+Ne	Mel	Ct				x									37
	Total interactions	**n**				2	2	67	41	17	4	24	7	4	20	3	2	
		%				1.8	1.8	61.5	37.6	15.6	3.7	22	6.4	3.7	18.3	2.8	1.8	

*endemic species to the Brazilian territory according to Flora do Brasil (2020)

Table 3. Rayleigh test of uniformity (Z) applied to *Xylocopa* species recorded from plants in Maranhão State, Brazil.

Xylocopa species	Mean vector (μ)	Month	Length of mean vector (R)	Rayleigh test (Z)
Total number	122.801°	May	0.087	19.33**
X. amazonica	261.738°	September	0.789	2.489
X. aurulenta	118.898°	April	0.912	3.325*
X. cearensis	136.835°	May	0.044	3.323*
X. frontalis	99.448°	April	0.226	28.54**
X. grisescens	100.182°	April	0.09	0.434
X. hirsutissima	67.631°	March	0.563	2.221
X. nigrocincta	127.848°	May	0.249	6.401*
X. transitoria	163.713°	June	0.549	3.310*
X. macrops	49.792°	February	0.739	3.273*
X. muscaria	226.117°	August	0.463	16.109**
X. subcyanea	135°	May	0.337	0.341
X. sp.	45°	February	0.337	0.341

*$p < 0.05$; **$p < 0.001$.

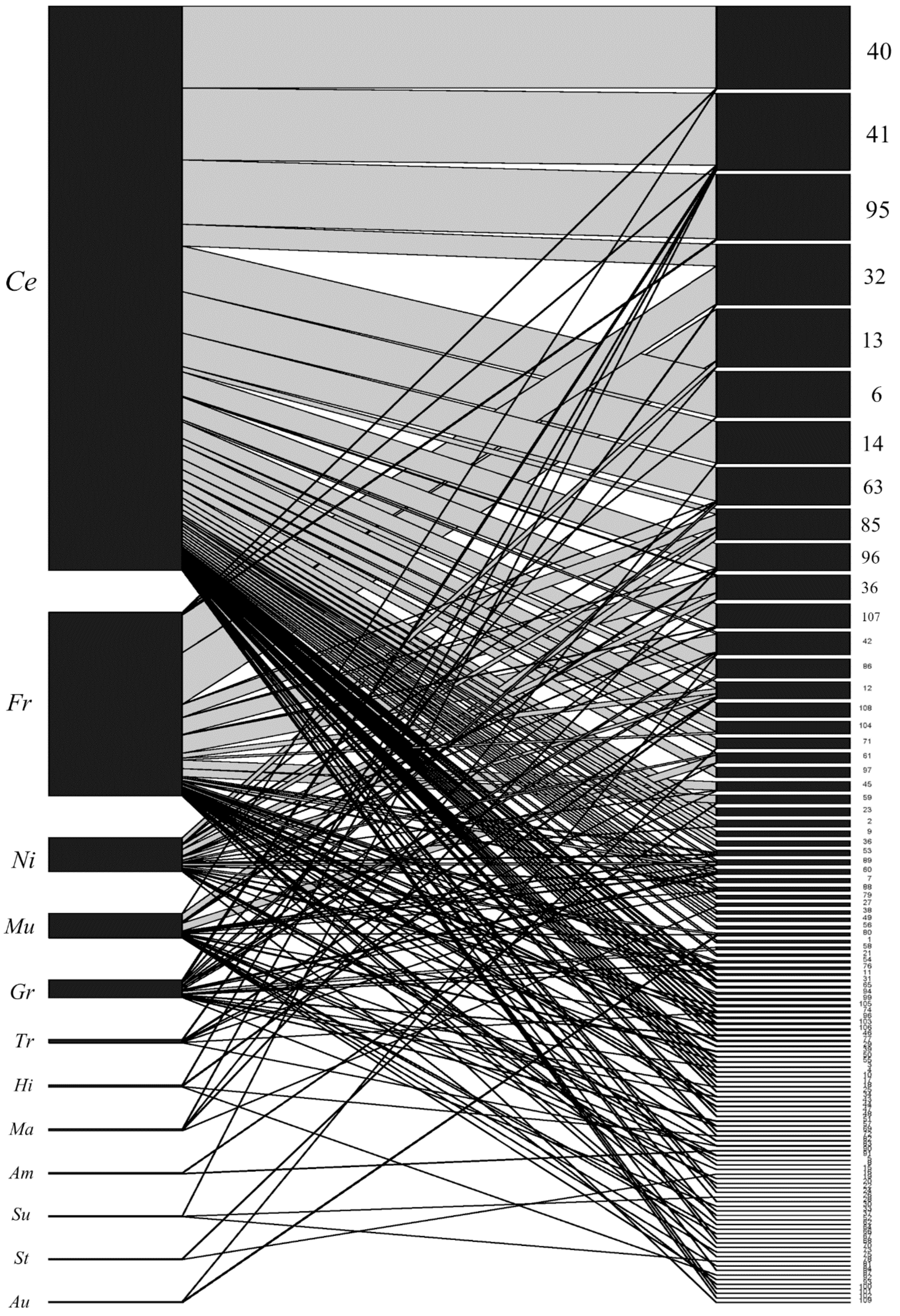
Figure Captions

Figure 1. Bipartite interaction network: interactions between *Xylocopa* species (left) and plants (right) in transition areas of MA. The vectors represent the interactions between these species. The thickness of the vectors is proportional to the relative abundance of the visiting bees.

Figure 2. Relation between the number of individuals and the species of plants visited by *Xylocopa* spp. recorded in Maranhão State, Brazil. Species abbreviations in Table 2.

Figure 3. Circular distribution histogram of *Xylocopa* species collected from plants in Maranhão State, Brazil. The standard deviation is represented by the line at the top of the vector.

Figure 4. Sorensen similarity between (A) *Xylocopa* species according to plants visited and (B) *Xylocopa* species according to physiognomies in MA, Brazil.


Ce
Fr
Ni
Mu
Gr
Tr
Hi
Ma
Am
Su
St
Au
40
41
95
32
13
6
14
63
85
96
36
107
42
86
12
108
104
71
61
97
45
59
23
2
9
36
53
89
60
7
88
79
27
38
49
56
80
1
58
21
54
76
11
31
65
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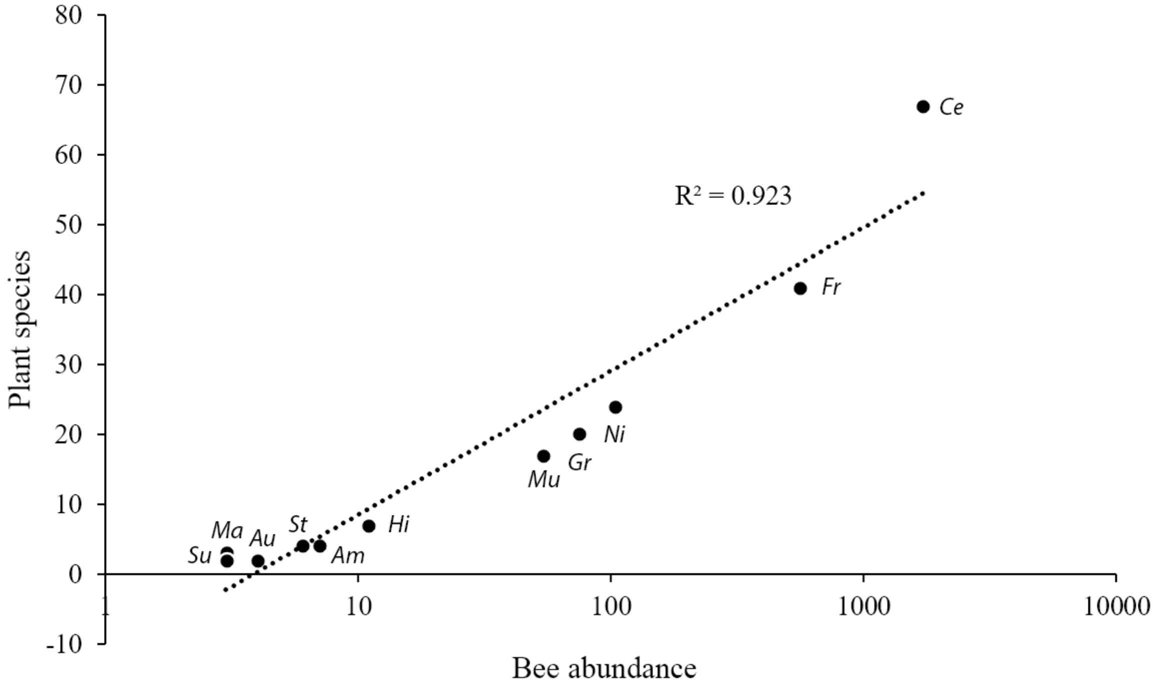
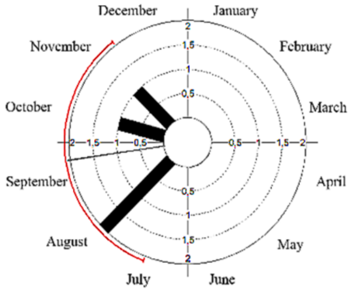
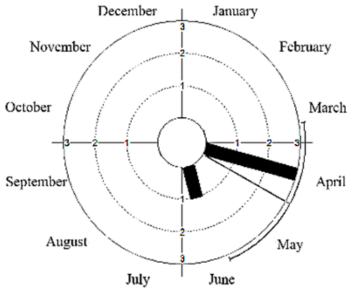
50
55
3
4
10
100
101
102
109


Plant species
Bee abundance
80
70
60
50
40
30
20
10
0
-10
1
10
100
1000
10000
R² = 0.923
Ce
Fr
Ni
Gr
Mu
Hi
St
Am
Au
Ma
Su

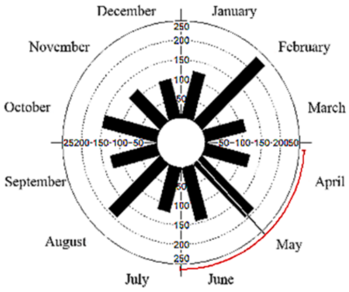
Xylocopa amazonica



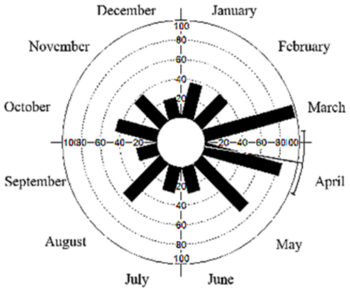
Xylocopa aurulenta



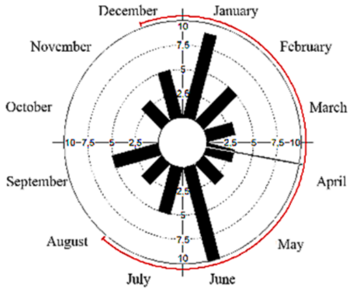
Xylocopa cearensis



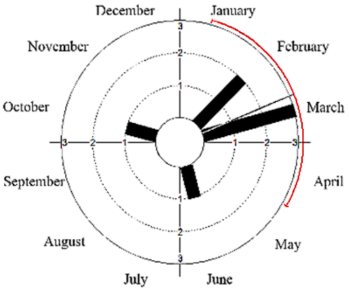
Xylocopa frontalis



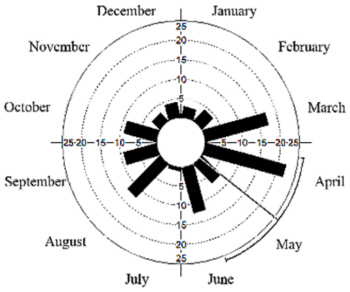
Xylocopa grisescens



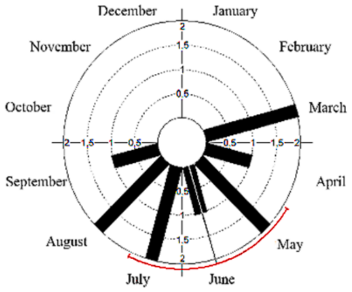
Xylocopa hirsutissima



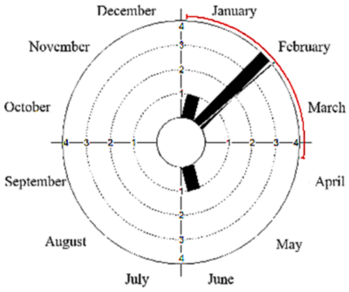
Xylocopa nigrocincta



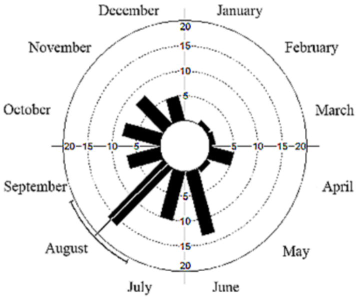
Xylocopa transitoria



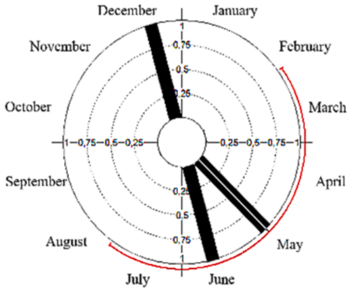
Xylocopa macrops



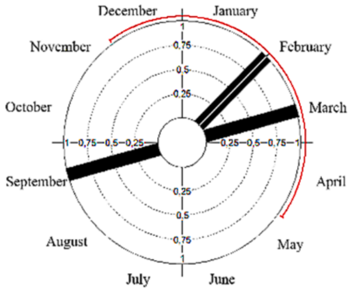
Xylocopa muscaria

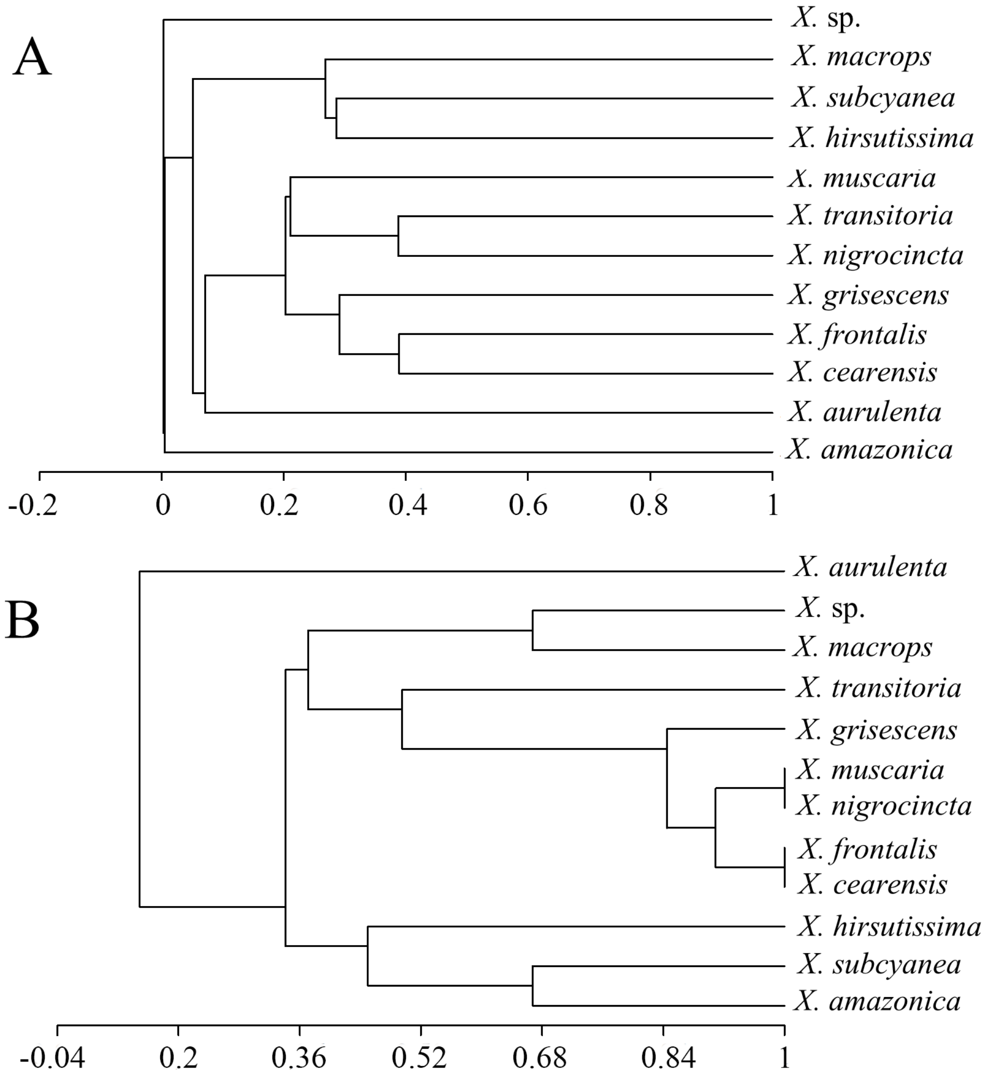


Xylocopa subcyanea



Xylocopa (*St.*) sp.




A
X. sp.
X. macrops
X. subcyanea
X. hirsutissima
X. muscaria
X. transitoria
X. nigrocincta
X. grisescens
X. frontalis
X. cearensis
X. aurulenta
X. amazonica
-0.2
0
0.2
0.4
0.6
0.8
1
B
X. aurulenta
X. sp.
X. macrops
X. transitoria
X. grisescens
X. muscaria
X. nigrocincta
X. frontalis
X. cearensis
X. hirsutissima
X. subcyanea
X. amazonica
-0.04
0.2
0.36
0.52
0.68
0.84
1

CAPÍTULO 3: DISTRIBUTION PATTERNS OF LARGE CARPENTER BEES (APIDAE: XYLOCOPINI: *XYLOCOPA*) IN TRANSITION AREAS OF EASTERN AMAZON UNDER FUTURE CLIMATE CHANGE SCENARIOS

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Distribution patterns of large carpenter bees (Apidae: Xylocopini: *Xylocopa*) in transition areas of eastern Amazon under future climate change scenarios

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Abstract. Carpenter bees are important crop pollinators in Brazil and are under threat from anthropogenic activities. We aim to predict the impact of climate change on twelve *Xylocopa* species previously recorded in transitional areas of three major biomes in the Brazil, Amazon rainforest, Cerrado and Caatinga (state of Maranhão, northeast Brazil). We used species distribution models, forecasting the impact of climate change for the period 2041–2060. The models revealed that ten out of the twelve *Xylocopa* species that occur in this region will face a potential decrease in their occurrence areas, due to the negative impact of climate change on habitat suitability. Species occurring only on rainforests will be the most affected. *Xylocopa aurulenta* is expected to potentially lose its entire area of occurrence in Maranhão, even in the optimistic scenario, while *X. amazonica* will potentially suffer a reduction of up to 95% of its distribution. On the other hand, our models showed that two species will benefit in future scenarios. *Xylocopa hirsutissima* will increase about 23% of the total area of Maranhão, while *X. grisescens* will expand over more than half of its area, covering more than 80% of Maranhão in all scenarios. Nevertheless, *X. frontalis* will probably still be the species with the largest distribution in region. We observed that, although *Xylocopa* species have uneven distributions, most species are concentrated in the northern areas of the state and most of these areas are legally protected. Other areas of future suitability include the Cerrado in the southern part of the state and the intermediate transition areas in the central region. These areas require special attention, and we propose the implementation of management plans and friendly agricultural practices be implemented to ensure the availability of resources and, ultimately, the conservation of these pollinators.

Key words: Maranhão, predictive models, climate suitability, global warming, crop pollinators.

Introduction

Bees are crucial to ecosystems, serving as the primary pollinators in natural and agricultural environments (Klein et al. 2007). They play a vital role in worldwide crop production by relying on pollen to feed their larvae, ensuring consistency and fidelity in their floral visits (Ollerton et al. 2011; Garibaldi et al. 2013; Kennedy et al. 2013; Alves-dos-Santos et al. 2016).

Carpenter bees, represented by the genus *Xylocopa* Latreille, 1802, are a group of solitary bees of generally robust in size that nest in substrates associated with wood, such as trunks and dead trees (Hurd 1978; Sazima and Sazima 1989). It is a diverse genus, with more than 470 species described in 31 subgenera (Michener 2007; Plant and Paulus 2016), and widely distributed throughout the world, predominantly occupying tropical regions with high temperatures and diverse environments (Hurd and Moure 1963; Silveira et al. 2002).

In Brazil, this genus are important crop pollinators (Giannini et al. 2015, 2020a), but despite this, most *Xylocopa* species, are not well known (Silveira et al. 2002; Mawdsley 2018). Fundamental information such as plant-bee interactions (Pigozzo and Viana 2010; Yamamoto et al. 2012; Ferreira et al. 2023), geographic distribution (Schlindwein et al. 2003; Silva et al. 2009; Marchi and Alves-dos-Santos 2013), and even taxonomic knowledge (Zanella and Silva 2010; Melo 2016, 2023) are scarce, limiting more in-depth studies and contributing to the overall biodiversity crisis (Wilson 1985). The unprecedented loss of species richness could destabilize ecosystems and cause irreversible problems for the planet (Lovejoy and Nobre 2018; White et al. 2020). There are three main causes of this problem: (1) the habitat destruction; (2) introduction of invasive species and (3) climate change, all resulting from anthropogenic activities (Prakash and Verma 2022).

Recent studies have attributed the increase in average global temperature to changes in the phenology of botanical species (Piao et al. 2019), and consequently to the desynchronization of their pollinators (Schenk et al. 2018; Freimuth et al. 2022). In addition, spatial distribution (Marshall et al. 2018), which can alter the dynamics of local ecosystems, with increased competition for resources (Montalva et al. 2023) and cases of increased susceptibility to the occurrence of invasive species (Acosta et al. 2016; Nascimento et al. 2022) were also reported. Extreme events are expected to be increasingly frequent and intense. We are already facing an increase in global temperature, estimated to be 1.5 to 4.4ºC higher than current averages by 2100 due to greenhouse gas emissions (IPCC – Intergovernmental Panel of Climate Change, 2021).

The global decline in bee populations is currently attributed to anthropogenic impacts, including climate change (Sánchez-Bayo and Wyckhuys 2019; Zattara and Aizen 2021; Lima et al. 2022), and represents a significant threat to safeguard food security (Potts et al. 2016; Giannini et al. 2020a). In Brazil, estimates suggest that the majority of crop pollinators will face reductions in their areas of occurrence (Giannini et al. 2012). In Cerrado biome, where knowledge of pollinators is inversely proportional to degradation rates, passion fruit pollinators could decline by up to 90% (Giannini et al. 2013). And recently, in the first predictive study of bees in the Brazilian Amazon, it was observed that the species will lose suitable habitats in areas of rainforest (Giannini et al. 2020b).

Given the need to anticipate the consequences of these catastrophic scenarios, the use of Species Distribution Modeling (SDM) has been useful and is consistent (Elith et al. 2006; Elith and Leathwick 2009; Valavi et al. 2021). Essentially, SDM delineates the interrelationship among environmental variables of the suitable habitats of a target species (Phillips et al. 2006). Its primary objective is to establish the range of tolerance levels, guaranteeing the sustainability of populations within these defined limits in the long term (Oliveira et al. 2019).

In performing these procedures, certain algorithms offer significant benefits when working with species that have sampling deficits (Phillips et al. 2006). This is particularly relevant in tropical areas, where high biodiversity can pose challenges to comprehensive data collection. Due to the complexity of tropical ecosystems, logistical limitations, and the sheer variety of species present, datasets are often incomplete or sparse (Oliveira et al. 2016; Carvalho et al. 2023).

Data concerning *Xylocopa* species in the lower latitudes of Brazil has predominantly been derived from sporadic collections and historical expeditions (Ducke 1908, 1910). It wasn't until the late 1980s that systematic surveys began to gain traction, marking a significant turning point in the comprehensive understanding of these species in the region (Pereira et al. 2021). However, reviewing and digitizing this information into public data is necessary for climate modeling studies (Canhos et al. 2015, 2022).

Taking this into consideration, a comprehensive review (Ferreira et al. 2024) was undertaken for the *Xylocopa* species on an ecotonal region where the Amazon rainforest, Cerrado (Park Savanna) and Caatinga (Steppic Savanna) Brazilian biomes intersect

(Maranhão state). This study included 20 structured surveys, each one with monthly surveys, for at least one year. In addition, researchers conducted six case studies that focused on the floral visitors of specific plants, that resulted on new records for *Xylocopa* species.

We aim here to predict the impact of climate change on twelve *Xylocopa* species previously recorded in transitional areas of three biomes in the Brazil, Amazon rainforest, Caatinga and Cerrado (state of Maranhão, northeast Brazil). Specifically, we aim: (1) to analyze the potential changes in the distributional areas of *Xylocopa* species and (2) to indicate the priority areas for the conservation of these species.

Material and methods

Study area

The study focuses on a region that hosts diverse vegetation types and transitional landscapes as a result of the convergence of three primary biomes (Amazon, Cerrado, and Caatinga) in the Maranhão State (northeastern Brazil). The area has 329.651 km^2 and is located between 01º01′ to 10º21′ S and 41º48′ to 48º50′ W (Fig 1A). The vegetation cover is heterogeneous, characterized by remnants of ombrophilous forest in the west, park savanna covering the center-south, steppic savanna in the east, and pioneer formations adapted to marine, fluvial and lake influence in the north. The contact areas are formed by physiognomic interpenetrations and large discontinuous areas (BDiA 2021).

The study area has a warm tropical climate type – Aw (Koeppen 1948), and the climatic variation follows a longitudinal pattern combining with the vegetal physiognomies. It is divided into a humid equatorial zone in the western portion; a semi-humid tropical zone in the central portion; and a semi-arid tropical zone in the eastern portion (Fig 1A) (IBGE, 2002). The average temperature shows little variation throughout the year (17.5 ºC – 29.5 ºC) but is slightly warmer in continental regions (Fig 1B). During the dry season, the maximum temperature typically hovers at around 32ºC, but recently it was recorded at over 40ºC (Cerqueira 2023), as a result to the impact of the current El Niño event (Bennett et al. 2023).

This region has two well-defined seasons, varying from east to west respectively: six dry months with average annual precipitation of 700 – 1.000 mm and eight rainy months with precipitation of 2.500 – 2.900 mm (Fig 1C). Humidity is high especially along the coast and decreases in the central and southeast areas, ranging from 85 – 70%

an annual average (Fig 1D). The central areas are characterized by extreme events of prolonged droughts and short periods of torrential rains, classifying these areas as potentially climatically aggressive (Filho 2014).

Occurrence data acquisition

We based our study on the list of *Xylocopa* species recorded in the Maranhão state in a previous study (Ferreira et al. 2024), which counted twelve species distributed in three subgenera: *Neoxylocopa* (*X. amazonica* Enderlein; *X. aurulenta* Fabricius; *X. cearensis* Ducke; *X. frontalis* Olivier; *X. grisescens* Lepeletier; *X. hirsutissima* Maidl, *X. nigrocincta* Smith; *X. transitoria* Pérez); *Schonnherria* (*X. macrops* Lepeletier; *X. muscaria* Fabricius; *X. subcyanea* Pérez) and *Stenoxylocopa* (*X.* sp). This study presents the most complete occurrence data for the Maranhão and was obtained from the following collections: Coleção de Abelhas da Universidade Federal do Maranhão – UFMA, São Luís, MA (LEACOL), Coleção do Laboratório de Ecologia e Sistemática de Insetos Polinizadores e Predadores, UFMA, São Luís, MA (LESPP), Coleção Zoológica do Maranhão, UEMA, Caxias, MA (CZMA), Museu Paraense Emílio Goeldi (MPEG), Belém, PA (MPEG) and Coleção Entomológica Danúncia Urban, UNILA, Foz do Iguaçu, PR (CEDU).

Records of the complete distribution area of *Xylocopa* bees, apart from Maranhão, were obtained from the main public biodiversity data providers: Global Biodiversity Information Facility – GBIF (doi.org/10.15468/dl.ezbew4) and Specieslink (specieslink.net/search/download/20231010141931-0007074). The DarwinCore-formatted dataset has undergone filters to exclude incomplete or inconsistent information. Occurrence data was compared with information available in systematic catalogs (Hurd 1978; Moure and Melo 2023). From the GBIF, we excluded the data extracted from the citizen science platform iNaturalist because it is a group that is difficult to identify through photographs (especially males and melanic females).

The collections that providing most of the data followed by the specialists who identified the species, were: American Museum of Natural History (AMNH), John Ascher; Snow Entomological Collection (SEMC), Robert Brooks; National Museum of Natural History (USNM), Paul Hurd Jr. The latter institution also includes photographs of the dorsal habitus of the individuals that can be examined and compared. The Brazilian collections with the most occurrence records of the selected species (with the exception of above mentioned) include: Coleção Entomológica do Departamento de Sistemática e

Ecologia (UFPB), Fernando Zanella (UNILA); Museu de Zoologia (USP), Pe. Moure (UFPR) and Coleção Entomológica do Laboratório de Abelhas (UFC), Favízia Oliveira (UFBA). In addition, data from specialized literature was included, especially taxonomic and systematic studies (Lucia et al. 2014, 2015; Mawdsley 2018; Villamizar et al. 2020; Mérida-Rivas et al. 2022). The list of occurrence records can be accessed at Supplementary Material A.

Climatic data acquisition

Climate layers for the current scenario (baseline) were extracted from WordClim 2.1 database (worldclim.org/data/worldclim21.html) (Fick and Hijmans 2017). We obtained 19 bioclimatic layers and altitude with a 2.5 minutes arc resolution (cell size ~5 km^2) that define mean climate data for 1970–2000. We used VIF (Variance Inflation Factor) collinearity test (Zuur 2009) using R v.4.3.2 (R development core team 2019) to remove the least-correlated layers, minimizing noise and ensuring the models robustness (Aguirre-Gutiérrez et al. 2013; Tourne et al. 2019). The following layers were selected: Altitude (ALT), Mean Diurnal Range (BIO 02), Isothermality (BIO 03), Temperature Seasonality (BIO 04), Temperature Annual Range (BIO 07), Mean Temperature of Driest Quarter (BIO 09), Annual Precipitation (BIO 12), Precipitation of Wettest Month (BIO 13), Precipitation of Driest Month (BIO 14), Precipitation Seasonality (BIO 15), Precipitation of Warmest Quarter (BIO 18) and Precipitation of Coldest Quarter (BIO 19).

Climate layers for the future scenarios were also extracted from WorldClim 2.1 and resulted from the Coupled Model Intercomparison Project Phase 6 (CMIP6) considering future projections (Eyring et al. 2016). The climate information was represented through global circulation models (GCM) and Shared Socio-economic Pathways (SSPs) considering the general trends presented in the latest IPCC report (IPCC – Intergovernmental Panel of Climate Change, 2021). We chose the GCM HadGEM3-GC31-LL from the Hadley Center, UK (Roberts 2017), which has been used in modeling studies and demonstrated good simulation performance (Jackson et al. 2022; Li et al. 2023). We used two scenarios, SSP245 and SSP585 considered optimistic and pessimistic scenario respectively, for the period 2041–2060. This medium-term scenarios are more suitable for supporting management and conservation plans (Giannini et al. 2017, 2020b; Martínez-López et al. 2021).

Species distribution modeling

To perform SDM, we used the Biomod2 package v. 4.2-4 (Thuiller et al. 2023) in R (R development core team, 2019). Modeling relied on two algorithms: Maximum entropy (MAXENT) which uses entropy to estimate the probability of occurrence of a species in a location (Phillips et al. 2006), and Generalized linear model (GLM) which uses a linear relation between variables and the response, creating a linked function to adjust the distribution probability (McCullagh and Nelder 1989). The use of these algorithms is justified by their robustness (mainly for restricted occurrence records) and their frequency use which has generated increasing validation (Giannini et al. 2020b; Kaky et al. 2020; Zhang et al. 2021; Ahmadi et al. 2023).

With the unavailability of true absence data for the selected species, we generated five datasets of pseudo-absences containing ten times the number of presence data randomly distributed (Barbet-Massin et al. 2012). The modeling procedure was based on randomly partitioned 80% of the data for training and 20% for evaluation, this random process was repeated ten times, in order to obtain a significant number of replications (Kindt 2018). As a result, we obtained 300 models per species, considering the current scenario and two future scenarios.

The generated models were evaluated using the True Skill Statistic (TSS), which measures sensitivity (presence accuracy rate) and specificity (pseudo-absences accuracy rate). Their values range between -1 to 1, indicating null and high prediction accuracy respectively (Allouche et al. 2006). Therefore, in this study we consider a cutoff threshold equal to 0.7, to discard low-quality models and filter only the most consistent ones (Hijmans 2012).

Ensemble forecast and suitability estimates

After performing the distribution modelling, a weighted consensus method (ensemble forecast) was used. This procedure combines the filtered models from the distribution modeling into a unique and more robust result (Acosta et al. 2016). We used a function available in the Biomod2 to generate ensemble forecast for each species/scenario based mean of probabilities over the selected models (Thuiller et al. 2023). Subsequently, the models were binarized according to the modeling cutoff threshold (0.7), in order to facilitate comparison with the rates of gain and loss in future projections (Lira et al. 2020).

Finally, we combined (stacked) the final binary model of the current scenario with the final model of each future scenario to calculate the proportional change in the size of the occurrence in the study area. We calculated Σ current area and Σ future area in proportion to the total study area, and then the total balance of suitability areas was obtained using the following formula: [(Σ future area - Σ current area) ÷ Σ current area] $*$ 100. All spatial analyses, area classifications in the binary models and final visual representations were produced in ArcMap 10.5 (ESRI 2015).

Results

The final occurrences dataset was composed of 2349 records for twelve species, which generated models that were considered accurate with an overall average of TSS = 0.806, Sensitivity = 88.131 and Specificity = 87.699 (Tab 2). The Maxent algorithm performed slightly better than GLM for most species. Among the climatic layers, the Isothermality (BIO 03) had the highest responsiveness while Precipitation of Warmest Quarter (BIO 18) had the lowest (Tab 2).

According to models under current conditions, we observed different sizes of climate suitability between *Xylocopa* species. The species with higher potential distribution area in Maranhão state were *X. frontalis* (91.9%) followed by *X. amazonica* (68.3%) and *X. grisescens* (56.8%). Small potential distributional area was obtained for *X. macrops* (10.9%), *X.* sp. (17.7%) and *X. aurulenta* (20.4%) (Tab 1).

The models projected under future conditions revealed that ten out of the twelve *Xylocopa* species will be affected by reductions in their areas of occurrence. *Xylocopa aurulenta* is expected to potentially lose its entire area of occurrence in Maranhão, even in the optimistic scenario (Fig 2B). Another species with a high potential loss of occurrence area is *X. amazonica*, losing between 72.3% and 95.3% of its range (Fig 2A).

In general, *Xylocopa* species potentially affected will have considerably different responses depending on the SSP scenario. On average, these species will loss 41.2% of suitable areas in the optimistic scenario and 65% in the pessimistic scenario. Some species as *X. nigrocincta* and *X. subcyanea* exhibit a potential difference of 40 and 50% on the future distributional area considering both scenarios (Tab 1).

On the other hand, even with a slight reduction, *X. frontalis* will remain widely distributed in Maranhão (Fig 2D), in addition, two other species will benefit in future scenarios. *Xylocopa hirsutissima* will maintain its current range and will potentially increase it, expanding its current distribution area nearly on 23%, mainly in the southern region of Maranhão state (Fig 2F). *Xylocopa grisescens* will potentially lose only 2% of its current distribution under future scenarios. However, its future distribution will potentially expand more than half of its current area, covering more than 80% of Maranhão state in all scenarios (Fig 2E).

Although *Xylocopa* species have uneven distributions, most species were recorded predominantly in the northern areas of the Maranhão state, possibly associated with spatial sampling biases. However, the species *X. hirsutissima* and *X. subcyanea* compensate for the suitable areas in the central region (Fig 2F–K).

According to the forecast combining all *Xylocopa* species, we found that eight species overlap in the north region of the study area (Fig 3). Some species will become less susceptible in these areas and shift towards the southern regions.

In general terms, the Amazon biome, in the west portion of study area, probably will lose its climate suitability for all the species studied. In contrast to the Cerrado biome and the dry transition areas characteristic of the Caatinga biome (north and central areas) that will probably become more attractive to the species. Coastal areas, to a lesser extent, will remain suitable for at least half of the *Xylocopa* species found in the studied area.

Discussion

This study addresses the potential impact of climate change on the future distribution of *Xylocopa* species in transition areas of eastern Amazon. Our results reflected the richness and distribution patterns of *Xylocopa* species under current and future climate conditions.

Under current conditions, *X. frontalis* is the most widely susceptible species, covering almost the entire state of Maranhão. This was to be expected, as it is distributed throughout South and Central America, with many occurrences in different types of environments (Lucia et al. 2014; Mérida-Rivas et al. 2022). In Maranhão, *X frontalis* has the highest number occurrence points, since it has been recorded in all the surveys already conducted (Ferreira et al. 2024).

On the other hand, *X. amazonica*, despite having few occurrences, also has a large area of suitability, with almost 70% of the total area of the state. This species is not only restricted to the Amazon basin (Silva et al. 2009) and their under-sampling is probably associated with a taxonomic impediment (Engel et al. 2021). Other two species (*X. aurulenta* and *X. grisescens*) are clearly contrasting, the former occupying forested areas of the Amazon basin, while the latter mainly open areas, present in transition regions, Cerrado and Caatinga of the northeast. *Xylocopa macrops* had the smallest range of suitability in Maranhão, restricted to the coast and small isolated areas in the south. This species presents the unclear distribution pattern (probably another taxonomic limiting factor), occurring predominantly in southern Brazil and northern Argentina, but has some widespread records in the interior of Brazil, including in the Amazon basin (Schlindwein et al. 2003; Lucia et al. 2015; Moure and Melo 2023).

Potential changes in the distributional areas of Xylocopa species under climate change

Our models for future scenarios indicate the potential reduction in the distribution area of ten *Xylocopa* species, showing that those restricted to Amazon forests will likely be the most affected. Most records of *X. aurulenta* are concentrated in the 1990s (Rebêlo et al. 2003), in places that were conducive to its survival, was rediscovered 10 years ago in areas on the extreme northwestern border (Ferreira et al. 2019), and will potentially completely lose its areas of occurrence in Maranhão over the next 20 years. *Xylocopa amazonica*, which currently has high suitability, could continue to be under sampled if new surveys are not conducted, as it will also be drastically affected.

We observed that some of the species with the highest proportion of potential losses are generally less studied. There is a scarcity of knowledge, for example, about bee-plant interactions of *X. aurulenta*, *X. amazonica*, *X. subcyanea*, *X. macrops* and *X.* sp. in the transitional areas mentioned (Ferreira et al. 2023). As with most bee species in the Amazon, the lack of basic information about their resources is worrying, because it makes it difficult to understand the degree of threat they will face (Giannini et al. 2020b). Since even the restricted areas that will be suitable for bees in the future may not be suitable for the plants that subsidize their food sources (Kuhlmann et al. 2012; Giannini et al. 2013).

As expected, the intensity of the losses faced by the species will be proportional to the scenarios, so we can direct optimistic expectations towards 25% fewer losses for most of these species. Nevertheless, international policy efforts are not keeping pace with short- and medium-term temperature trends (O'Neill 2022), that way, the pessimistic scenario has been considered the closest to reality (Kemp et al. 2022), based on the indices presented in the indices presented in the latest IPCC AR6 assessment (2021). Under these circumstances, the trend for most *Xylocopa* species will be one of intermittent decline, even those that are currently more climatically adjusted (Farias-Silva and Freitas 2021).

Two species showed a different result. Our models showed the *X. grisescens* and *X. hirsutissima* will potentially double their areas of occurrence in Maranhão. This expansion is probably due to the increase in temperature of currently humid regions, which will result in drier (Maia et al. 2020) and more homogeneous environments (Giannini et al. 2020b). Despite this, a climate modeling study carried out previously indicated *X. hirsutissima* as one of the species most negatively affected by climate change in the Cerrado (Giannini et al. 2013). In the same study, *X. grisescens* also showed potential losses, but with less intensity.

In general, some loss rates were partially offset by increases in areas in other directions. The shift in their geographic distribution will occur in a north-south direction. The loss of suitability in the Amazon region of Maranhão is aggravated by the fact that, in addition to the climatic factor, the rate of environmental degradation is increasing to alarming levels (Silva Junior et al. 2020). Considered as an important component of transition areas, this forest environment could perhaps allow the occurrence of other species restricted to the Amazon basin. For example, *X. viridis* probably occurred at the extreme edge of the eastern Amazon at the beginning of the century (Ducke 1908), and over time its range became more restricted. Today, its easternmost occurrence is limited to the state of Pará, and it continues to decline (Mawdsley 2018; Giannini et al. 2020b).

From all the *Xylocopa* species recorded in the Amazon basin (Mawdsley 2018), only 41% are found in Maranhão, and these are the species with the widest distribution. On the other hand, 80% of the species recorded in the Caatinga (Silva et al. 2009) are found in the state. In view of this, our results suggest that Maranhão will have more characteristics associated with the Brazilian semi-arid region.

Priority areas for the conservation of Xylocopa species analyzed

In the future, certain areas where *Xylocopa* species can thrive are protected, such as the Lençóis Maranhenses National Park and Environmental Protection Areas (APA) located on the northern coast (in addition to the Restingas' Integral Protection) and the Mirador State Park and Chapada das Mesas National Park located in the southern region. However, the connection between these two regions is composed of vast discontinuous and fragmented areas under pressure from the agricultural and urban frontier (Bastos et al. 2019). These ecotone areas are complex and will be fundamental to the movements of these species in the future.

Management plans for agricultural practices could potentially be implemented in these regions. One approach could involve utilizing plant species identified by Ferreira et al. (2023) while considering floral resources, pollinator preferences, and seasonality. This would ensure resources are available throughout the year and reduce the competition generated by niche overlaps (Araújo et al. 2021). Other conservation aspects of these pollinators, proposed for species in the Brazilian Cerrado (Giannini et al. 2013), can also be applied here. These include considering the availability of nesting substrates (dead trees, logs, stumps, and wood in general) near managed areas, or provide artificial nesting boxes (Freitas and Oliveira Filho 2003) and trap nest as solitary bee hotels (Pereira and Garófalo 2010; Ribeiro and Gaglianone 2021).

Caveats and future steps

Even after accounting for sampling limitations in southern Maranhão, the models were found to be suitable, for the majority of species, in the northern portion of the state. Filling in distribution gaps could enhance the reliability of the results. Conducting new surveys in regions where information is scarce, such as the far south and west of the state, would be beneficial. A possible way of increasing our comprehensive knowledge of these pollinators would be to encourage citizen-science recordings (Theobald et al. 2015), especially from places that are difficult to access.

In addition to climate predictions, it is necessary to consider details regarding the ecological niche of the species, such as insect-plant interaction networks and habitat changes, especially considering the heterogeneous characteristics of transition areas, given the high rates of environmental degradation (MapBiomas 2022). These findings can be used to spread awareness among the general public and particularly to guide conservation strategies for decision-makers through public policies.

Conclusions

This study presents the expected effects of climate change on the distribution of *Xylocopa* species in the Eastern Amazon. Most species are likely to suffer a reduction in their range, especially those that have restricted habitats in humid forests, such as *X. aurulenta*, which may completely lose its range in Maranhão. On the other hand, *X. grisescens* and *X. hirsutissima* may expand their range as temperatures rise. *Xylocopa frontalis* will probably still be the species with the largest distribution area and is considered to be an important pollinator of various plant species. These findings are highly significant for the conservation of *Xylocopa* species in the Eastern Amazon and it is essential to identify and protect the areas that will remain suitable for these species in the future. We identified three areas of future suitability, which include the coastal areas, which will serve as sanctuaries for most species, the Cerrado located in the southern part of the state and the intermediate transition areas in the central region. These areas require special attention, and it is suggested that management plans and friendly agricultural practices be implemented to ensure the availability of resources and, ultimately, the conservation of these pollinators.

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Table 1. *Xylocopa* species climate suitability, current and future scenarios in Maranhão. All values in percentages. (*Σ* Ca) Current area; (*Σ* Fa) Future area; (+/-) Rates of loss (-) or gain (+); *Xylocopa* species*: Am – X.* (*Neoxylocopa*) *amazonica, Au – X.* (*N.*) *aurulenta, Ce – X.* (*N.*) *cearensis, Fr – X.* (*N.*) *frontalis, Gr – X.* (*N.*) *grisescens, Hi – X.* (*N.*) *hirsutissima, Ni – X.* (*N.*) *nigrocincta, Tr – X.* (*N.*) *transitoria, Ma – X.* (*Schonnherria*) *macrops, Mu – X.* (*S.*) *muscaria, Su – X.* (*S.*) *subcyanea, St – X.* (*Stenoxylocopa*) sp.

Xylocopa species	*Σ* Ca	2041-2060							
		SSP 245				SSP 585			
		Gain	Loss	*Σ* Fa	+/-	Gain	Loss	*Σ* Fa	+/-
Am	68.3	10.4	59.7	18.9	**-72.3**	2.10	67.2	3.17	**-95.3**
Au	20.4	–	20.4	–	**-100**	–	20.4	–	**-100**
Ce	51.1	0.92	19.8	32.2	**-36.9**	0.03	29.7	14.5	**-67.1**
Fr	91.9	0.35	12.9	79.3	**-13.7**	0.41	23.2	68.3	**-25.6**
Gr	56.8	31.0	1.44	86.4	**52.1**	25.3	2.46	82.2	**44.7**
Hi	45.2	21.0	–	66.2	**46.4**	25.0	–	70.2	**55.3**
Ni	41.8	14.5	22.5	33.8	**-19.1**	4.60	35.1	11.3	**-72.9**
Tr	28.1	0.45	11.4	17.1	**-39.1**	–	16.6	11.5	**-59.0**
Ma	10.9	6.04	10.8	6.07	**-44.3**	3.42	10.9	3.42	**-68.6**
Mu	53.7	25.1	26.8	38.5	**-28.3**	11.2	25.6	23.4	**-56.4**
Su	43.1	14.1	21.4	35.6	**-17.4**	5.96	32.7	16.1	**-62.6**
St	17.7	0.74	8.11	10.3	**-41.8**	0.50	8.04	10.1	**-42.9**

Table 2. Statistical analyses of model quality, mean evaluation scores and variables importance. Climatic variables: ↑ = more explanatory; ↓ = less explanatory; BIO 02 = Mean Diurnal Range; BIO 03 = Isothermality; BIO 07 = Temperature Annual Range; BIO 09 = Mean Temperature of Driest Quarter; BIO 12 = Annual Precipitation; BIO 14 = Precipitation of Driest Month; BIO 15 = Precipitation Seasonality; BIO 18 = Precipitation of Warmest Quarter; BIO 19 = Precipitation of Coldest Quarter.

Xylocopa species	Evaluation scores			Variables importance	
	TSS	Sensitivity	Specificity	↑	↓
Am	0.896	95.652	93.913	BIO 04	BIO 15
Au	0.755	83.505	91.925	BIO 14	BIO 09
Ce	0.803	92.152	84.223	BIO 19	BIO 03
Fr	0.882	89.573	83.127	BIO 03	BIO 18
Gr	0.749	85.185	89.691	BIO 07	BIO 15
Hi	0.814	96.610	84.788	BIO 03	BIO 19
Ni	0.711	82.143	80.503	BIO 12	BIO 07
Tr	0.840	95.238	88.793	BIO 07	BIO 18
Ma	0.719	85.600	77.206	BIO 03	BIO 18
Mu	0.707	77.510	84.805	BIO 07	BIO 14
Su	0.801	86.275	93.755	BIO 03	BIO 09
St	0.997	100.00	99.667	BIO 14	BIO 02

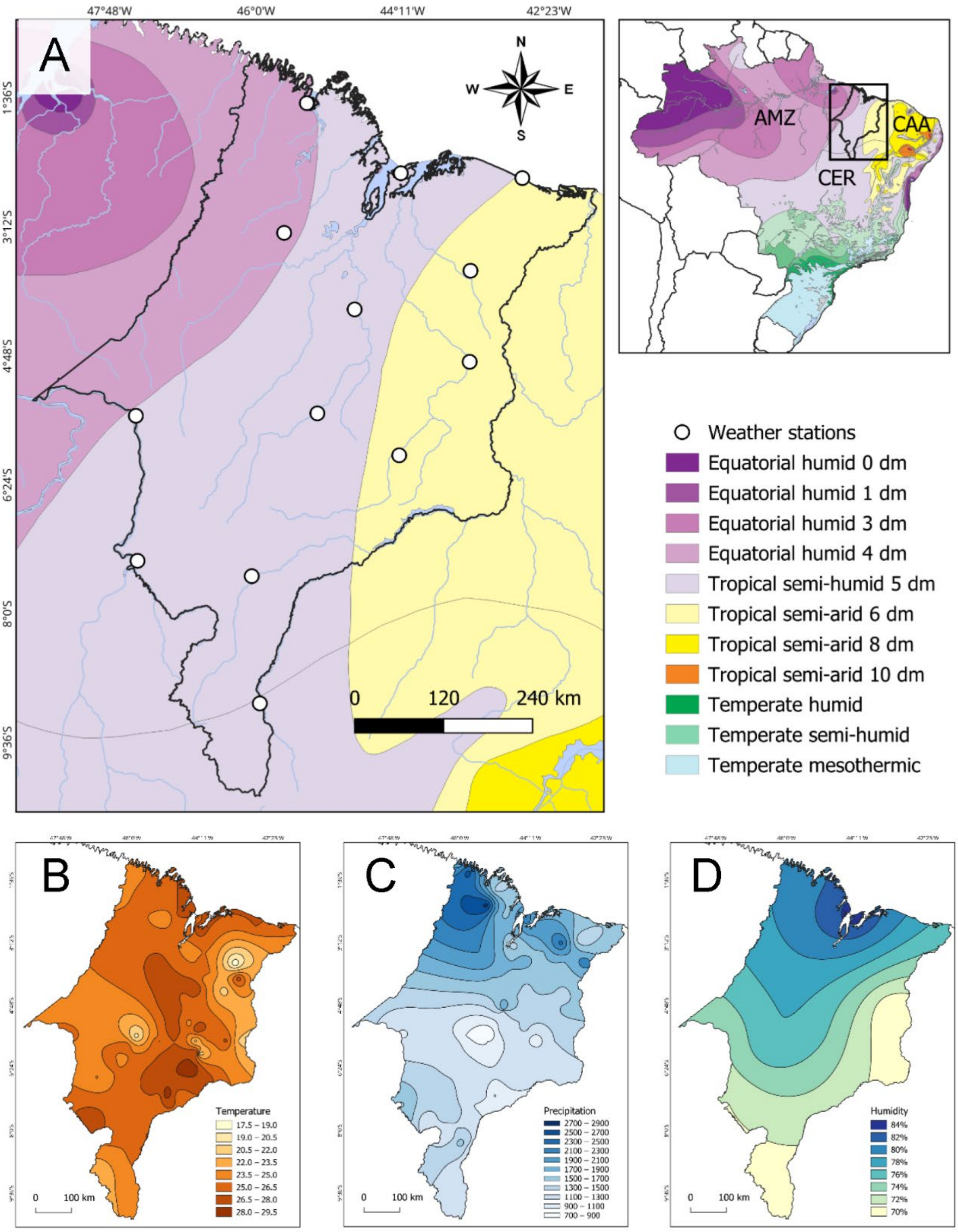
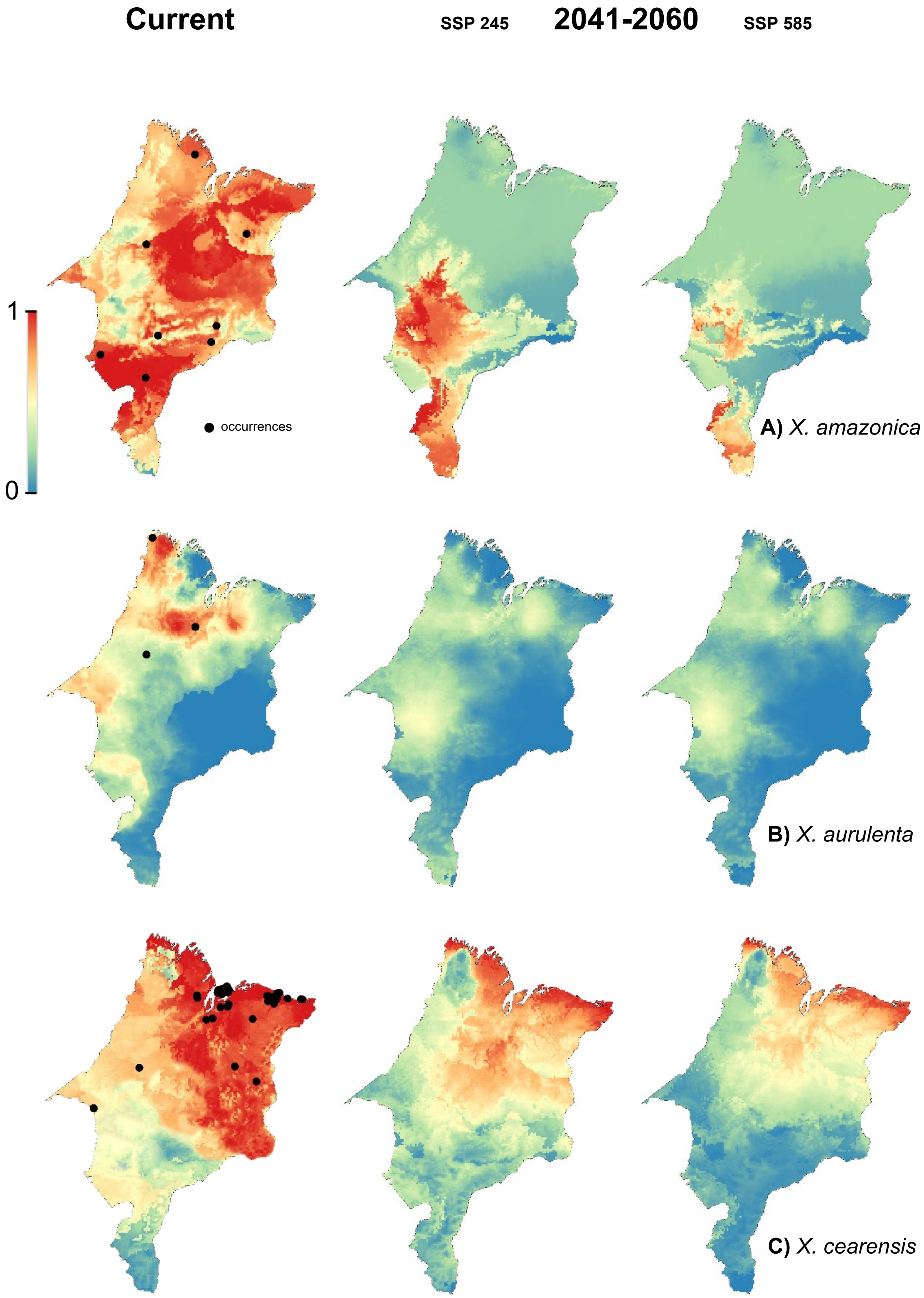
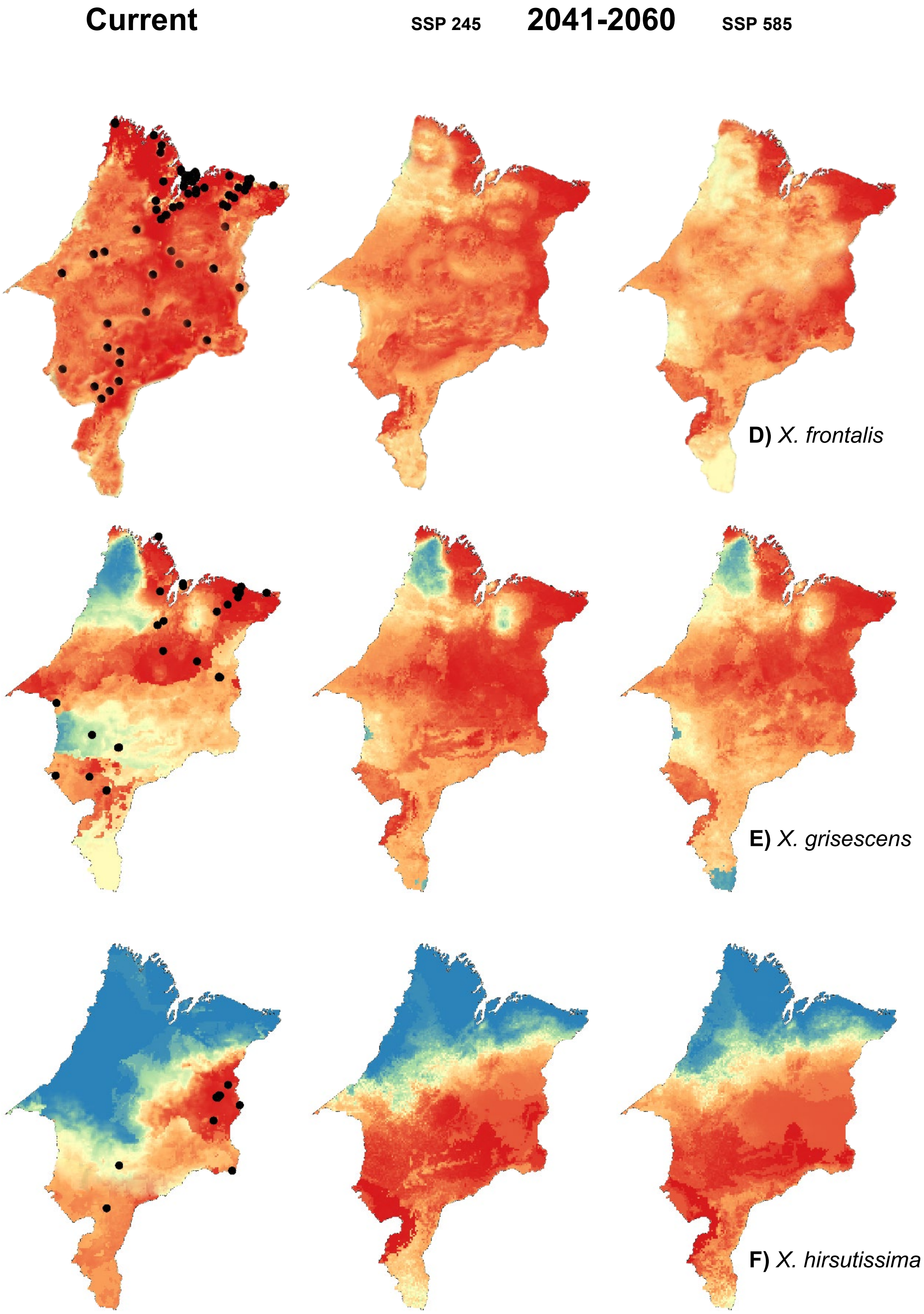
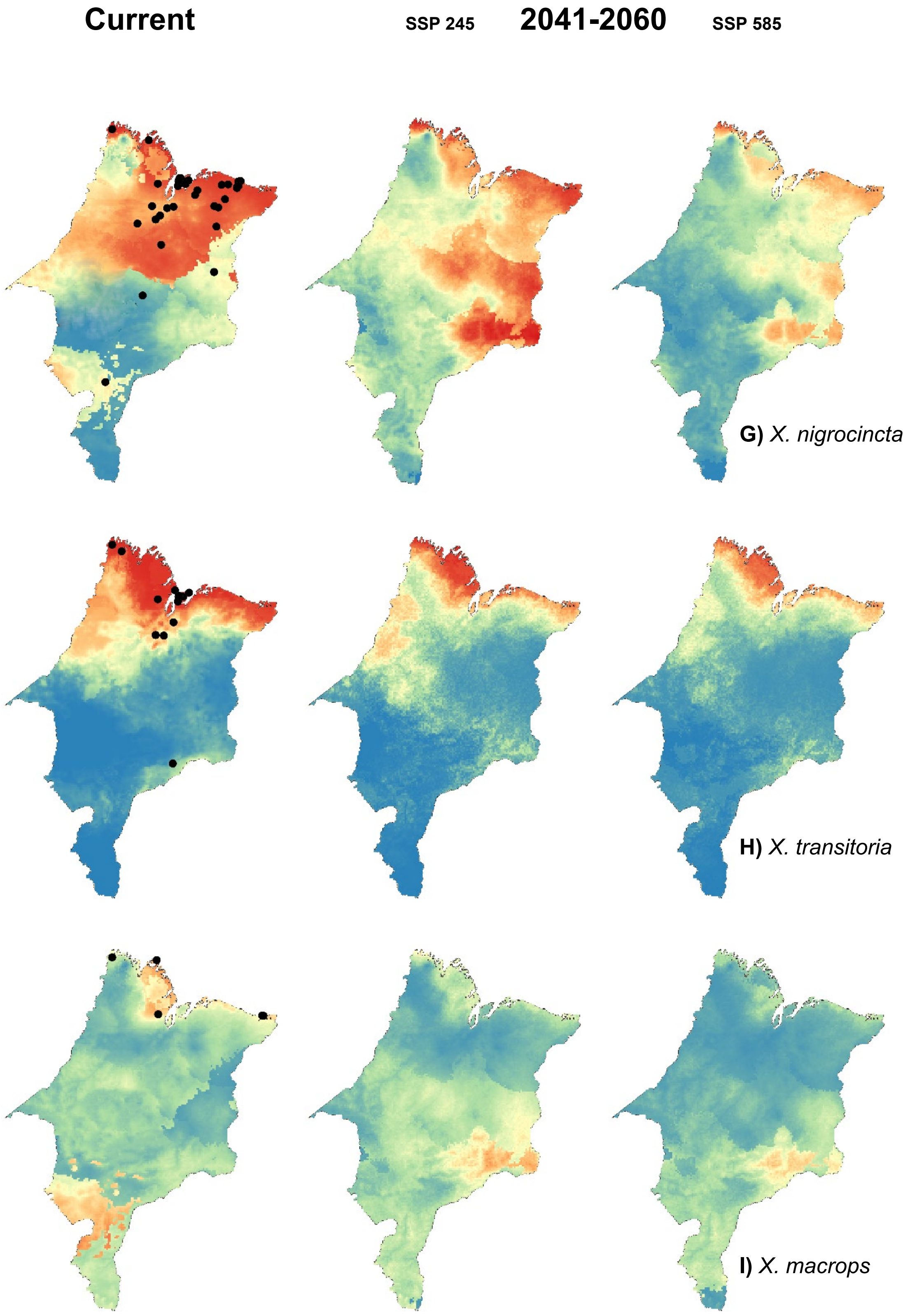


Figure 1. **A**) Climate typologies and the arrangement of regional weather stations in the Maranhão state. The Amazon Biome (AMZ) are mainly under the influence of the Equatorial humid climate, while the Cerrado area (CER) under the influence of Semi-humid and scattered spots of Caatinga (CAA) under Semi-arid climate (See Ferreira et al. 2024). The color gradients are divided by the number of dry months (dm). Source: IBGE, 2002; **B**) Average annual temperature (Cº); **C**) Average annual precipitation (mm); **D**) Average annual humidity (%). Source: UEMA/NUGEO, 2009.


Current
SSP 245
2041-2060
SSP 585
1
0
● occurrences
A) X. amazonica
B) X. aurulenta
C) X. cearensis


Current
SSP 245
2041-2060
SSP 585
D) *X. frontalis*
E) *X. grisescens*
F) *X. hirsutissima*


Current
SSP 245
2041-2060
SSP 585
G) *X. nigrocincta*
H) *X. transitoria*
I) *X. macrops*

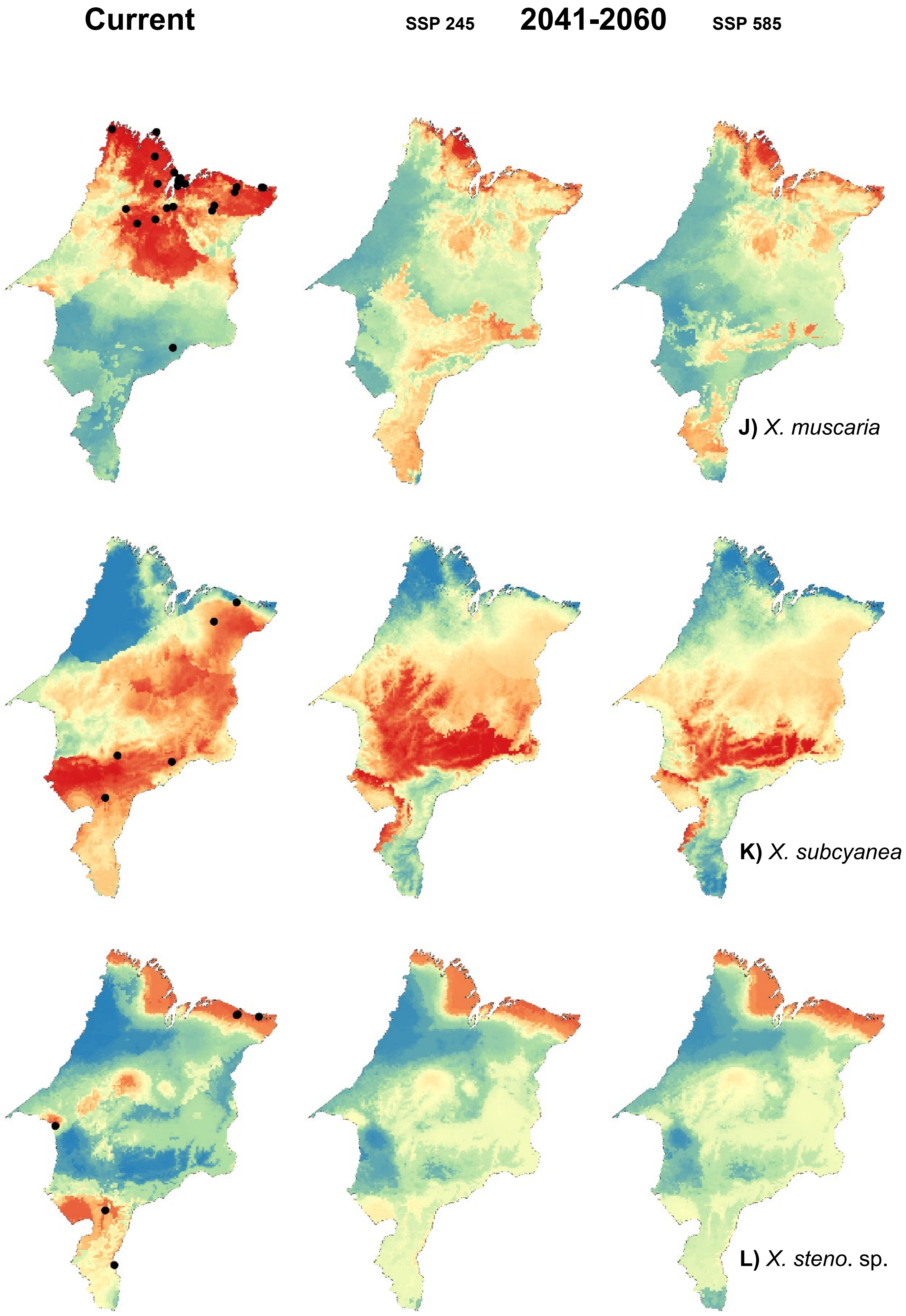


Figure 2. Current and future ranges for the *Xylocopa* species under optimistic (SSP 245) and pessimistic (SSP 585) scenario. Color gradients are proportional to the occurrence probability of each species: 1 = suitability; 0 = unsuitability.

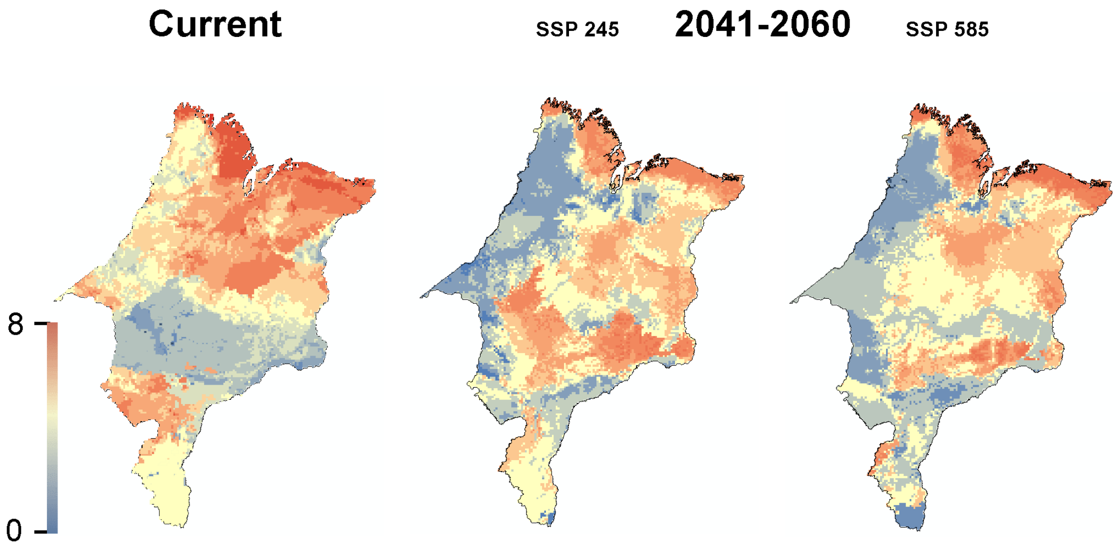


Figure 3. Overlapping current and future ranges for the *Xylocopa* richness from Maranhão state under optimistic (SSP 245) and pessimistic (SSP 585) scenarios.

4. DISCUSSÃO INTEGRADORA

Neste estudo buscamos contribuir para o entendimento da diversidade, distribuição e ecologia das abelhas do gênero *Xylocopa* no estado do Maranhão. Ao longo de três capítulos, exploramos aspectos relacionados à taxonomia, padrões de distribuição, interações alimentares e impactos das mudanças climáticas sobre essas espécies. Além disso, direcionamos estratégias de conservação considerando os cenários atuais e futuros mais realistas.

No primeiro capítulo, identificamos 12 espécies distribuídas em três subgêneros (*Neoxylocopa*, *Schonnherria* e *Stenoxylocopa*), destacando a importância das áreas de transição e a complexidade da distribuição em um estado caracterizado pela confluência de três grandes biomas brasileiros (Amazônia, Cerrado e Caatinga). Os padrões de distribuição observados indicaram uma associação entre a antropização e a expansão de espécies adaptadas a ambientes abertos, por outro lado, espécies restritas às áreas florestadas podem ser mais afetadas. Estes indícios, no entanto, foram tratados com cautela, devido aos vieses amostrais inerentes aos levantamentos realizados no estado, que, em sua maioria concentrou-se na porção norte e nordeste.

A ausência de algumas espécies previamente observadas sugere que elas podem estar ameaçadas ou extintas localmente. Isso destaca a necessidade de confirmação e a importância de futuras pesquisas para compreender melhor a dinâmica dessas populações. Além disso, o registro de uma nova espécie (*Stenoxylocopa*) ressalta a relevância da pesquisa taxonômica para a compreensão integral da biodiversidade, fornecendo subsídios básicos para estudos mais aprofundados.

No segundo capítulo, reforçamos o generalismo alimentar já conhecido do gênero *Xylocopa*. As espécies analisadas visitaram uma ampla gama de espécies botânicas e promoveram o compartilhamento de parte destes recursos. Foi observado um particionamento funcional nas interações destas abelhas, sugerindo estratégias adaptativas que possibilitam a coexistência de espécies generalistas e menos generalistas no mesmo ambiente. No geral, as espécies botânicas mais atrativas foram *Chamaecrista hispidula* e *C. ramosa* como fornecedoras de pólen e *Passiflora foetida* e *Canavalia rosea* como fontes de néctar. A rede de interação se mostrou diferente conforme a fitofisionomia analisada, mas no geral, foram dominadas por pelo menos duas espécies de abelhas (*X. cearensis* e *X. frontalis*).

Em escala regional foi possível identificar espécies típicas tanto do nordeste semiárido, quanto da bacia amazônica, garantindo, portanto, recursos variados necessários para a manutenção da diversidade de polinizadores no Maranhão.

No terceiro capítulo, examinamos os potenciais efeitos das mudanças climáticas na distribuição das espécies de *Xylocopa* nesta região limítrofe da Amazônia Oriental. As projeções indicaram prováveis alterações para a maioria das espécies. Espera-se, por exemplo, que *X. aurulenta* perca potencialmente toda a sua área de ocorrência no Maranhão, mesmo no cenário mais otimista. Outra espécie com alto potencial de perda de área de ocorrência é *X. amazonica*, perdendo entre 72,3% e 95,3% de sua distribuição. Apenas duas espécies (*X. hirsutissima* e *X. subcyanea*), aparentemente, tendem a expandir suas áreas de adequabilidade. O contraste ambiental entre essas espécies é expressivo nos modelos projetados para o futuro. De acordo com as representações climáticas, as espécies adaptadas a ambientes úmidos, como florestas ombrófilas, podem enfrentar desafios significativos para sobreviver. Isso ocorre porque as espécies associadas a áreas mais secas e com características savânicas tendem a ganhar espaço em curto e médio prazo.

Apesar dos cenários de mudanças, há pelo menos uma espécie com padrão de distribuição constante. *Xylocopa frontalis* é a espécie com maior distribuição, sendo amostrada em praticamente todos os pontos de coleta, o que já era esperado, uma vez que essa espécie ocorre em grande parte da América do Sul e Central. As projeções evidenciam uma adequabilidade ambiental muito alta, independente da fitofisionomia, e mesmo considerando o pior dos cenários, ela provavelmente continuará a dominar toda a região.

Quanto à riqueza total, os modelos finais e sobrepostos identificaram pelo menos três áreas com potencial de adequabilidade no futuro. Estas incluem as áreas costeiras, que funcionarão como santuários para a maioria das espécies, o Cerrado no sul-sudeste do estado e as áreas intermediárias de transição na região centro-leste. Constituem-se de pontos focais prioritários para conservação, os quais são apenas parcialmente protegidos. A região central é caracterizada por áreas ecotonais complexas que serão fundamentais para os movimentos destas espécies no futuro, no entanto, é composta por vastas áreas descontínuas e fragmentadas sob forte pressão da fronteira agrícola e urbana.

Sugere-se, portanto, uma atenção especial nesta região, através, por exemplo, da implementação de planos de gestão para práticas agrícolas amigáveis, com a utilização preferencial das espécies botânicas mais atrativas, identificadas no segundo capítulo. Além disso, é necessário considerar a disponibilidade de substratos de nidificação (árvores mortas, troncos, tocos e madeira em geral) perto das áreas manejadas, ou o fornecimento de caixas de nidificação artificiais e ninhos-armadilha adaptados nos chamados “hotéis de abelhas”. Em última análise, considera-se como ideal a delimitação legal dessas áreas, levando em conta as condições e recursos mencionados neste trabalho.

5. CONSIDERAÇÕES FINAIS

Apresentamos aqui o primeiro estudo sistemático sobre as abelhas carpinteiras do gênero *Xylocopa* em áreas de transição da Amazônia Oriental. A diversidade do gênero no estado do Maranhão abrange diversas fisionomias, com espécies associadas a áreas secas e abertas, como *X. cearensis*, *X. grisescens* e *X. hirsutissima*, e outras pertencentes a ambientes de floresta úmida, como *X. aurulenta* e *X. transitoria*. Adicionalmente, espécies amplamente distribuídas, como *X. frontalis*, *X. muscaria* e *X. nigrocincta*, incrementam a composição dessa riqueza.

Apesar das limitações impostas pelo processo de amostragem em locais de difícil acesso, os resultados deste trabalho possuem alta representatividade espacial. Assim, identificamos as áreas prioritárias para a conservação dessas espécies, além de suas preferencias fitofisionômicas e alimentares. Estas são informações valiosas no sentido mais amplo de entendimento do nicho ecológico do grupo, especialmente se tratando de áreas de transição caracterizadas por elevados índices de degradação ambiental.

Esperamos que as chaves de identificação e ilustrações fornecidas sirvam como estímulo e facilitador para futuros inventários na região. Recomendamos a realização de novas expedições, especialmente, no sul e oeste do Maranhão, onde os níveis de ocupação e uso da terra são inversamente proporcionais ao conhecimento básico sobre a maioria das espécies.

A lista de espécies botânicas apresentada poderá servir como orientação para planos de manejo, recuperação de áreas degradadas e até mesmo no aprimoramento das práticas agrícolas de subsistência. Incentivamos ativamente a participação da comunidade em projetos de ciência cidadã, especialmente em locais de difícil acesso, a fim de enriquecer o conhecimento com novos registros e relatos sobre esses importantes polinizadores.

Por fim, os modelos climáticos foram atenciosamente desenvolvidos por meio de mapas didáticos de fácil compreensão, com o propósito claro de guiar, de forma predecessora, planejamentos e estudos da área ambiental. Destacamos, portanto, a relevância dessas descobertas como alicerce informativo para moldar políticas públicas direcionadas às estratégias de conservação. Além disso, ressaltamos o potencial desses resultados em sensibilizar não apenas a comunidade acadêmica e técnicos analistas, mas também o público em geral. Assim, em última análise, cooperamos para a valorização e conservação da biodiversidade maranhense.

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ANEXOS

Anexo 1: Normas da Zootaxa (Capítulo 1)

Aim and scope

Zootaxa is a peer-reviewed international journal for rapid publication of high quality papers on any aspect of systematic zoology, with a preference for large taxonomic works such as monographs and revisions. *Zootaxa* considers papers on all animal taxa, both living and fossil, and especially encourages descriptions of new taxa. All types of taxonomic papers are considered, including theories and methods of systematics and phylogeny, taxonomic monographs, revisions and reviews, catalogues/checklists, biographies and bibliographies, identification guides, analysis of characters, phylogenetic relationships and zoogeographical patterns of distribution, descriptions of taxa, and nomenclature. Open access publishing option is strongly encouraged for authors with research grants and other funds. For those without grants/funds, all accepted manuscripts will be published but access is secured for subscribers only. All manuscripts will be subjected to peer review before acceptance. *Zootaxa* aims to publish each paper within one month after the acceptance by editors.

Based on length, two categories of papers are considered.

1) **Research article**

Research articles are significant papers of four or more printed pages reporting original research. Papers between 4 and 59 printed pages are published in multi-paper issues of 60, 64 or 68 pages. Monographs (60 or more pages) are individually issued and bound, with ISBNs.

Zootaxa encourages large comprehensive taxonomic works. There is no upper limit on the length of manuscripts, although authors are advised to break monographs of over 1000 pages into a multi-volume contribution simply because books over 1000 pages are difficult to bind and too heavy to hold.

Very short manuscripts with isolated descriptions of a single species are generally discouraged, especially for taxa with large number of undescribed species. These short manuscripts may be returned to authors without consideration. Short papers on species of economic, environmental or phylogenetic importance may be accepted at the discretion of editors, who will generally encourage and advise authors to add value to the paper by providing more information (e.g. checklist of or key to species of the genus, biological information......). Short papers of 4 or 5 pages accepted for publication may be shortened for publication in the Correspondence section.

2) **Correspondence**

High quality and important short manuscripts of normally 1 to 4 pages are considered to fill blank pages in multi-paper issues. Zootaxa publishes the following six types of correspondence:

- opinions and views on current issues of interests to systematic zoologists (e.g.Zootaxa 1577: 1-2)
- commentary on or additions/corrections to papers previously published in *Zootaxa*(e.g. Zootaxa 1494: 67-68)
- obituary in memory of deceased systematic zoologists (e.g. Zootaxa 545: 67-68)
- taxonomic/nomenclatural notes of importance
- book reviews meant to introduce readers to new or rare taxonomic monographs (interested authors/publishers must write to subject editors before submitting books for review; editors then prepare the book review or invite colleagues to prepare the review; unsolicited reviews are not published)
- and short papers converted from manuscripts submitted as research articles but are too short to qualify as formal research articles.

These short contributions should have no more than **20 references** and its **total length should not exceed four printed pages (except editorials).** Neither an abstract nor a list of key words should be included; major headings (Introduction, Material and methods...) should NOT be used, except for new taxon heading and references. A typical correspondence should consist of (1) a short and concise title, (2) author name and address (email address), (3) a series of paragraphs of the main text,and (4) a list of references if any. For correspondence of 3 or 4 pages, the first or last paragraph may be a summary.

Commentaries on published papers are intended for scholarly exchange of different views or interpretations of published data and should not contain personal attack; authors of concerned papers may be invited to reply to comments on their papers.

Special issues

Special issues with collected papers such as a Festschrift (see Zootaxa 1325 and Zootaxa 1599) within the scope of the journal are occasionally published. Guest editors should send the proposal to the chief editor for approval and instructions. Although guest editors for special issues are responsible for organising the peer review of papers collected within these issues, they must follow Zootaxa's style, stardard and peer review procedures. If any papers by the guest editors are to be included in the special issue, then these papers must be handled by editors/colleagues other than the editor(s) involved. Special issues must be 60 or more pages. Normally funding is required to offset part of the production cost. Author payment for open access is strongly encouraged. Reprints can be ordered for the entire issue or for individual papers.

Preparation of manuscripts

1) *General.* All papers must be in English. Authors whose native language is not English are encouraged to have their manuscripts read by a native English-speaking colleague before submission. Nomenclature must be in agreement with the International Code of Zoological Nomenclature (4th edition 1999), which came into force on 1 January 2000. Author(s) of species name must be provided when the scientific name of any animal species is first mentioned (the year of publication needs not be given; if you give it, then provide a full reference of this in the reference list). Authors of plant species names need not be given. Metric systems should be used. If possible, use the common font Times New Roman and use

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3) The **name(s) of all authors** of the paper must be given and should be typed in the upper case (e.g. ADAM SMITH, BRIAN SMITH & CAROL SMITH). The address of each author should be given in *italics* each starting a separate line. E-mail address(es) should be provided if available.

4) The **abstract** should be concise and informative. Any new names or new combinations proposed in the paper should be mentioned. Abstracts in other languages may also be included in addition to English abstract. The abstract should be followed by a list of**key words**that are not present in the title. Abstract and key words are not needed in short correspondence.

5) The arrangement of the **main text** varies with different types of papers (a taxonomic revision, an analysis of characters and phylogeny, a catalogue etc.), but should usually start with an **introduction** and end with a list of **references**. References should be cited in the text as Smith (1999), Smith & Smith (2000) or Smith *et al.* (2001) (3 or more authors), or alternatively in a parenthesis (Smith 1999; Smith & Smith 2000; Smith *et al*. 2001). All literature cited in the text must be listed in the references in the following format (see a sample page here in PDF).

A) **Journal paper**:
Smith, A. (1999) Title of the paper. *Title of the journal in full*, volume number, issue number if possible & page range.

B) **Book chapter**:
Smith, A. & Smith, B. (2000) Title of the Chapter. *In*: Smith, A, Smith, B. & Smith, C. (Eds), *Title of Book*. Publisher name and location, pp. x–y.

C) **Book**:
Smith, A., Smith, B. & Smith, C. (2001) *Title of Book*. Publisher name and location, xyz pp.

D) **Internet resources**
Author (2002) Title of website, database or other resources, Publisher name and location (if indicated), number of pages (if known). Available from: http://xxx.xxx.xxx/ (Date of access).

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2 Leg II longer than leg I ... Genus B
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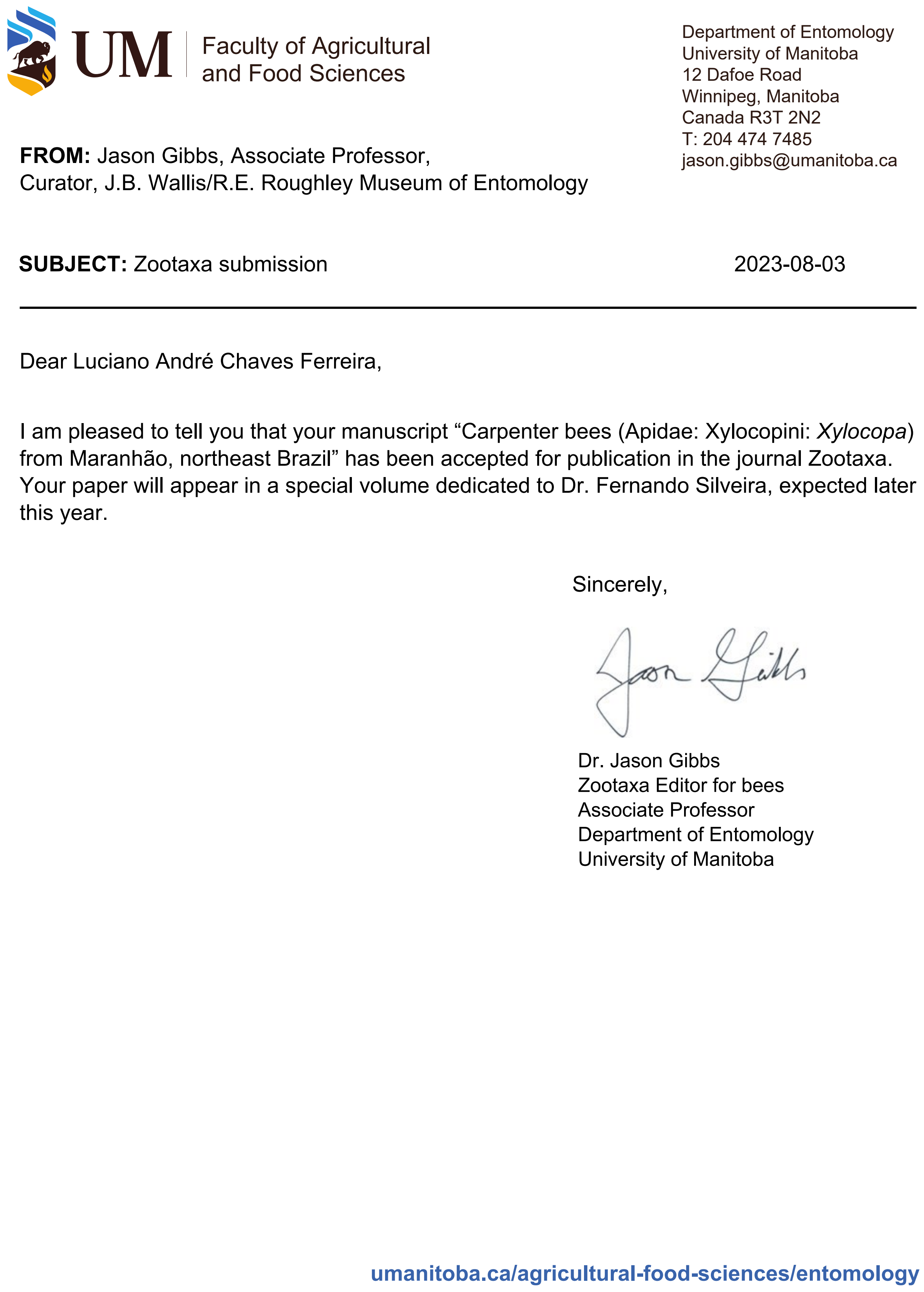

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FROM: Jason Gibbs, Associate Professor,
Curator, J.B. Wallis/R.E. Roughley Museum of Entomology

SUBJECT: Zootaxa submission 2023-08-03

Dear Luciano André Chaves Ferreira,

I am pleased to tell you that your manuscript “Carpenter bees (Apidae: Xylocopini: *Xylocopa*) from Maranhão, northeast Brazil” has been accepted for publication in the journal Zootaxa. Your paper will appear in a special volume dedicated to Dr. Fernando Silveira, expected later this year.

Sincerely,

Jason Gibbs

Dr. Jason Gibbs
Zootaxa Editor for bees
Associate Professor
Department of Entomology
University of Manitoba

Anexo 3: Capa do 1º artigo (Zootaxa)

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Carpenter bees (Apidae: Xylocopini: *Xylocopa*) from Maranhão, Northeast Brazil

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Abstract

We present a list of *Xylocopa* Latreille species that occur in Maranhão State, a region where several physiognomic formations characteristic of the Amazon, Cerrado, and Caatinga biomes overlap. The information was compiled through numerous surveys conducted in this territory, in addition to direct consultation in scientific collections, which have many unpublished records. Twelve species belonging to three subgenera were documented: *Xylocopa* (*Neoxylocopa*) *amazonica* Enderlein, 1913, *X.* (*N.*) *aurulenta* (Fabricius, 1804), *X.* (*N.*) *cearensis* Ducke, 1910, *X.* (*N.*) *frontalis* (Olivier, 1789), *X.* (*N.*) *grisescens* Lepeletier, 1841, *X.* (*N.*) *hirsutissima* Maidl, 1912, *X.* (*N.*) *nigrocincta* Smith, 1854, *X.* (*N.*) *transitoria* Pérez, 1901, *X.* (*Schonnherria*) *macrops* Lepeletier, 1841, *X.* (*S.*) *muscaria* (Fabricius, 1775), *X.* (*S.*) *subcyanea* Pérez, 1901 and *X.* (*Stenoxylocopa*) sp. Of these, two species are reported as first records for Maranhão (*X. hirsutissima* and *X. subcyanea*), one for Brazil (*X. transitoria*), and one for science (*X.* (*Stenoxylocopa*) sp.—not yet published).

Key words: Anthophila, biogeography, conservation, diversity, systematics

Introduction

The genus *Xylocopa* Latreille, 1802 consists of usually quite large bees widely distributed on all continents; however, they are more diverse in the old world and more abundant in tropical and subtropical regions where temperatures are higher (Hurd 1978; Michener 2007). *Xylocopa* comprises approximately 400 species, distributed in 31 subgenera, although there are estimates of up to 700 extant species (Silveira *et al.* 2002). Thus, this group is considered one of the largest evolutionary lineages of bees (Hurd & Moure 1963; Plant & Paulus 2016).

Xylocopa bees are popularly known as carpenter bees, as females make their nests in dead wood, twigs, or bamboo cavities, with the exception of the subgenus *Proxylocopa*, which nests in the soil (Hurd & Moure 1963). Some species are strictly solitary and may form aggregate nests (Sakagami & Laroca 1971; Pereira & Garófalo 2010), while others have facultatively social habits, in which females usually live together in the same nest but at different reproductive stages (Hogendoorn & Velthuis 1993; Richards 2011; Duff *et al.* 2023).

In general, carpenter bees are remarkably robust, reaching over 30 mm in length. For this reason, these bees can overcome the resistance of strong winds and can fly long distances, reaching radii of more than 10 km in search of food (Gerling *et al.* 1989). During this routed, flowers of various species can be visited, because these bees are polylectic and thus act as effective pollinators of many species of native and cultivated plants (Roubik 1995). Perhaps the best-known example is their role in passion fruit production, as, due to their morphometric adaptations,

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Anexo 4: Normas da Studies on Neotropical Fauna and Environment (Capítulo 2)

About the Journal

Studies on Neotropical Fauna and Environment is an international, peer-reviewed journal publishing high-quality, original research. Please see the journal's Aims & Scope for information about its focus and peer-review policy.

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STUDIES ON NEOTROPICAL FAUNA AND ENVIRONMENT
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Floral preferences of carpenter bees (Apidae: Xylocopini: *Xylocopa*) from Maranhão, Northeast Brazil

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ABSTRACT

The current study aimed to recognize the floral resources used by bees of the genus *Xylocopa* in transition physiognomies. We compiled the information available from biological collections and analyzed metrics of dystrophic interaction. We listed 2547 records of *Xylocopa* in flowers, across twelve identified bee species. The bees were collected from 109 plant species, belonging to 77 genera and 36 families. An interaction network was constructed based on 193 interactions. In which there was a significant correlation between the abundance of bees collected and the richness of plants visited. The most generalist bees were *X. cearensis* and *X. frontalis*, and the plants with the most records were *Chamaecrista hispidula* and *C. ramosa*. Significant seasonality was observed in the total number of individuals. On the other hand, there was a weak similarity among *Xylocopa* species according to plant species, despite the clear relationship of the bees according to physiognomies. The interaction network proved to be highly nested, indicating a functional partitioning that allows several species to occur in the same environment. The contribution made by the current work for its regional scope stands out, dealing with areas that have distinct characteristics.

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KEYWORDS
Solitary bees; pollination; plant-pollinator; interaction network; ecotone

Introduction

Large carpenter bees, also known as mamangava bees, are represented by the genus *Xylocopa* Latreille, 1802 (Michener 2007). These bees are of medium to large size, usually nest in dead wood, and are characterized by solitary behavior with cooperatively breeding (Gerling et al. 1989; Danforth et al. 2019). The species in this genus are widely distributed around the world, with the greatest diversity found in tropical zones (Hurd & Moure 1963), with approximately 480 species distributed in 31 subgenera (Plant & Paulus 2016; Lucia et al. 2020).

Xylocopa species are dependent on the floral resources and nesting substrates (Hurd 1978; Sazima & Sazima 1989). Their body size, life cycle and long foraging distances make them essential pollinators (Silva et al. 2019; Harano & Hrncir 2023), especially for botanical species that produce large flowers, such as *Bertholletia* spp (Cavalcante et al. 2023) and *Passiflora* spp (Barrera et al. 2021).

Because of this service provision, especially with respect to the productive increase in crops with high economic value in Brazil (Giannini et al. 2015), some studies have been conducted to research and conserve large carpenter bees, such as *X. frontalis* and *X. grisescens* (Pereira & Garófalo 2010; Giannini et al. 2020; Araújo et al. 2021; Farias-Silva & Freitas 2021; Costa et al. 2022). These and all other species of the genus, are considered polyletic, meaning that they potentially visit a wide variety of plant species in search of food (Keasar 2010; Lucia et al. 2017; Villamizar et al. 2020).

In Northeast Brazil, several works have identified plant species used by *Xylocopa* in dune and restinga areas (Silva & Martins 1999; Viana et al. 2002; Viana & Kleinert 2006; Albuquerque et al. 2007; Pigozzo et al. 2007; Ramalho & Rosa 2010; Santos et al. 2013; Figueiredo et al. 2013). However, little is known about the use of floral resources in other ecosystems, such as savannas, forests, and, especially, in transitional areas.

The State of Maranhão (MA) is located in the Eastern Amazon, where it is represented by the convergence of the humid vegetation of the ombrophilous forest and the dry and open vegetation of the savanna,

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Gullan, P. J. & Cranston, P. S. (2005). *The insects - an outline of entomology*. Oxford: Blackwell Publishing.

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Kiss, J., Komaromi, J., Bayar, K., Edwards, C. R. & Hatala-Zseller, I. (2005). Western corn rootworm (*Diabrotica firgifera virgifera LeConte*) amid crop rotation systems in Europe. In S. Vidal, U. Kuhlmann & R. Edwards (Eds.), *Western corn rootworm: ecology and management* (pp. 189–220). Wallingford, United Kingdom: CABI Publisher.

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Websites

Estes, R. (2004). *2004 Evaluations of Rootworm Control Products*. [Text article]. Retrieved from http://bulletin.ipm.illinois.edu/print.php?id=182

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