INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (BOTÂNICA)

ESTUDOS PALINOLÓGICOS DE PRODUTOS MELIPONÍCOLAS PROVENIENTES DO BAIXO AMAZONAS E DA *CAATINGA* DO NORDESTE DO BRASIL

JAÍLSON SANTOS DE NOVAIS

Manaus, Amazonas
Junho, 2013

JAÍLSON SANTOS DE NOVAIS

ESTUDOS PALINOLÓGICOS DE PRODUTOS MELIPONÍCOLAS PROVENIENTES DO BAIXO AMAZONAS E DA *CAATINGA* DO NORDESTE DO BRASIL

Dra. MARIA LÚCIA ABSY
Orientadora

Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Doutor em CIÊNCIAS BIOLÓGICAS (BOTÂNICA).

Manaus, Amazonas
Junho, 2013

Sinopse:

É apresentada a análise palinológica do conteúdo de potes de mel (57) e pólen (46) armazenados em colônias de *Tetragonisca angustula* (Apidae, Meliponini) no Baixo Amazonas e na *caatinga* do Nordeste do Brasil. Espectros polínicos, dados de concentração polínica e índices ecológicos comparativos são fornecidos.

Palavras-chave: Abelha sem ferrão, mel, melissopalinologia, pólen, *Tetragonisca angustula*

N935 Novais, Jaílson Santos de
Estudos palinológicos de produtos meliponícolas provenientes do Baixo Amazonas e da *caatinga* do Nordeste do Brasil / Jaílson Santos de Novais. --- Manaus : [s.n.], 2013.
xxiii, 201 f. : il. color.

Tese (doutorado) --- INPA, Manaus, 2013.
Orientadora : Maria Lúcia Absy
Área de concentração: Biodiversidade Vegetal da Amazônia

1. *Tetragonisca angustula*. 2. Abelha sem ferrão. 3. Mel. 4. Pólen. 5.Melissopalinologia. I. Título.

CDD 19. ed. 595.799045

BANCA EXAMINADORA DA AULA DE QUALIFICAÇÃO

Dr. Antonio Carlos Marques Souza (INPA)
Dr. Antonio Carlos Webber (UFAM)
Dr. Davi Said Aidar (UFAM)
Dra. Gislene Almeida Carvalho Zilse (INPA)
Dra. Ires Paula de Andrade Miranda (INPA)
Dr. Marcos Vinícius Bastos Garcia (EMBRAPA) *(Suplente)*
Dra. Norma Cecília Rodriguez Bustamante (UFAM) *(Suplente)*

BANCA EXAMINADORA DO TRABALHO DE CONCLUSÃO

Dr. Francisco de Assis Ribeiro dos Santos (UEFS)
Dra. Norma Cecília Rodriguez Bustamante (UFAM)
Dr. Carlos Alberto Cid Ferreira (INPA)
Dra. Ires Paula de Andrade Miranda (INPA)
Dra. Otilene Santos Mattos (UNINILTON LINS)
Dr. Antonio Carlos Marques Souza (INPA) *(Suplente)*
Dr. Paulino Pereira Oliveira (UEFS) *(Suplente)*

Manaus, Amazonas
Junho, 2013

À Nossa Senhora, Mãe da Ternura,

dedico.

Agradecimentos

AGRADECIMENTOS

O Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) concedeu-me bolsa de estudos (processo nº. 143084/2009-7) durante parte do primeiro ano de Doutoramento. Dra Maria Lúcia Absy contribuiu grandemente com a orientação, o estímulo e a gentileza constantes. Dr Francisco de Assis Ribeiro dos Santos tem dispensado a sua amizade e os seus conselhos durante grande parcela da minha vida acadêmica e profissional. Todos os professores e colegas da Pós-Graduação em Botânica do Instituto Nacional de Pesquisas da Amazônia (INPA) contribuíram nas discussões botânicas e descontrações ao longo do curso. As secretárias do Curso foram sempre solícitas no atendimento às demandas apresentadas. Os professores que participaram da banca de qualificação proveram valiosas sugestões ao projeto inicial do Doutorado: Dr Antônio Carlos Marques-Souza (INPA), Dr Antônio Carlos Webber (Universidade Federal do Amazonas, UFAM), Dr Davi Said Aidar (UFAM), Dra Gislene Almeida Carvalho-Zilse (INPA) e Dra Ires Paula de Andrade Miranda (INPA). Dra Favízia Freitas de Oliveira, da Universidade Federal da Bahia, gentilmente tem identificado muitas abelhas sem ferrão encaminhadas ao seu laboratório. Os amigos do Laboratório de Palinologia do INPA, André Rech, Carlos D’Apólito, Cleonice Moura, Isabela Rodrigues, Marcos Ferreira, Natália Sá, Otilene Mattos, Yuri Feitosa e estagiários, calorosamente acolheram-me e alegraram-me na cidade de Manaus. No Laboratório de Micromorfologia Vegetal (LAMIV) da Universidade Estadual de Feira de Santana, coordenado pela Dra Cláudia Elena Carneiro, foi executada grande parte do trabalho desenvolvido na Bahia. No LAMIV há, ainda, antigas e sinceras amizades. De forma especial, agradeço aos palinólogos e amigos baianos MSc Ana Paula Conceição Silva, Dr Francisco de Assis Ribeiro dos Santos, Dr Francisco Hilder Magalhães e Silva, Dra Luciene Cristina Lima e Lima, Biól Marcel Carvalho de Jesus, Dr Marcos da Costa Dórea, Dra Marileide Dias Saba, Dr Paulino Pereira Oliveira, MSc Rita de Cássia Matos dos Santos Araújo, Dr Ricardo Landim Bormann de Borges, MSc Rodolfo França Alves, Biól Tereza Cristina Oliveira Rebouças e MSc Vanessa Ribeiro Matos, e aos demais pós-graduandos e estagiários do LAMIV. Paulino Oliveira é grande parceiro nas discussões, na diversão e nos planos para dominar o mundo (via pólen) em Feira de Santana. Ricardo Landim tem sido amigo e companheiro de congressos ao redor do mundo. O estagiário Bruno Henrique Andrade Silva

deu imprescindível contribuição ao projeto, uma vez que efetuou as coletas mensais de amostras na Bahia, além de ajudar no processamento laboratorial desse material, mesmo com a saúde debilitada. A Empresa Baiana de Desenvolvimento Agrícola (EBDA), por meio da gerência regional em Itaberaba, deu apoio logístico durante as viagens de campo na Bahia. O professor e amigo MSc Carleandro Dias estabeleceu contatos para a obtenção das amostras provenientes da *caatinga*, bem como forneceu amostras a partir de colônias do seu meliponário particular em Itaberaba, BA. Os senhores Alex e Manoel também permitiram coleta de material em seus meliponários. A direção da Escola Agrícola Mãe Jovina, autorizou a coleta de amostras nas dependências da instituição no município Ruy Barbosa, BA. Geancarlo Vidal Gouveia, presidente da Associação de Meliponicultores do Município de Belterra (AMEMBEL), autorizou a coleta de amostras em seu meliponário em Belterra, PA. A Secretaria Municipal de Educação do município de Santarém, PA, e a direção da Escola da Floresta permitiram a coleta de material no meliponário desta escola. A Universidade Federal do Oeste do Pará (UFOPA) forneceu apoio infraestrutural, por meio dos laboratórios de Química, de Ensino de Biologia, de Botânica Taxonômica (em especial à Profa MSc Chieno Suemitsu, conhecedora profunda da Botânica amazônica) e de Tecnologia da Madeira. O Centro de Formação Interdisciplinar (CFI) da UFOPA e os colegas de trabalho colaboraram nas necessidades e compreenderam as dificuldades durante o desenvolvimento desta tese. Os meus estagiários de iniciação científica e monitoria, na UFOPA, auxiliaram em diferentes etapas do trabalho, e provavelmente aguentaram os meus piores momentos de estresse: Alcides Froes Dias Jr., Ângelo Márcio Barbosa Bastos Jr., Arthur Daniel Repolho Valente Sobral, Arthur Iven Tavares Fonseca e Wagner Antonio Tenório Freitas. A Murilo Miranda, pelas conversas via *facebook*. Todos os meus amigos de Manaus (em especial Edgar Alvim, Marcos Ferreira e Isabela Rodrigues), Santarém (em especial Roberto Paiva, Abraão Viana e Ana Garcez), Feira de Santana (em especial Danilo Amorim, Júnior Lima e Leilton Damascena), Amargosa (Heyde e Geanne Brito) e tantos outros cantos me acolheram nas circunstâncias mais diversas e adversas, e eu sou fielmente grato por nossa amizade. Minha família, em especial meus pais – Diodete e Valdemir Novais – e meu irmão – Gean Novais –, me faz experimentar o que é ser feliz na simplicidade. A vocês, o meu profundo, sincero e total obrigado!

E a Deus, pois, sem Ele, todas as linhas acima estariam completamente em branco...

SUB tuum præsidium confugimus,
Sancta Dei Genetrix.

Nostras deprecationes ne despicias in necessitatibus,
sed a periculis cunctis libera nos semper,
Virgo gloriosa et benedicta.
Amen.

Roman Breviary, Raccolta #333. (S. C. Ind., April 5, 1786; S. P., Dec. 12, 1935)

Resumo

RESUMO

A presente tese teve como objetivo caracterizar, à luz da Palinologia, provisões de mel e pólen de colônias de *Tetragonisca angustula* (Apidae, Meliponini) situadas no Baixo Amazonas e na *caatinga* do Nordeste do Brasil. Foram analisadas 103 amostras (57 de mel e 46 de pólen), coletadas entre setembro 2010 e janeiro 2012 em meliponários no Baixo Amazonas, Pará, e na *caatinga*, Bahia, Brasil. Todas as amostras foram processadas com o emprego da acetólise e posterior identificação botânica e contagem de ao menos 500 grãos de pólen por amostra. Os méis procedentes do Baixo Amazonas caracterizam-se pelos tipos polínicos *Borreria verticillata*, *Byrsonima*, *Cecropia*, *Clidemia*, *Eriope*, *Microtea*, *Myrcia*, *Solanum*, *Tapirira guianensis* e *Warszewiczia coccinea*. Nesse méis, a concentração polínica variou entre 20.000 e 500.000 grãos de pólen em cada 10 g de mel. Os méis da *caatinga* caracterizaram-se pelos tipos polínicos *Heteropterys*, *Mikania*, *Mimosa tenuiflora*, *Myrcia*, *Prosopis juliflora*, *Schinus*, *Senna macranthera*, *Solanum*, *Syagrus coronata* e *Solanum*. Por sua vez, o pólen coletado no Baixo Amazonas destacou-se pelos tipos polínicos *Acalypha*, *Byrsonima*, *Brosimum paraense*, *Borreria verticillata*, *Cecropia*, *Clidemia hirta*, *Davilla kunthii*, *Eriope*, *Lindackeria paludosa*, *Myrcia*, *Schefflera morototoni*, *Tabebuia*, *Tapirira guianensis* e *Vismia guianensis*. Na *caatinga*, os tipos polínicos mais destacados nos potes de pólen foram *Prosopis juliflora* e *Solanum*. *Poincianella pyramidalis* e *Senna macranthera* são indicadores vegetacionais regionais. Considerando-se apenas os tipos polínicos mais representativos (>10%), os méis do Baixo Amazonas e da *caatinga* apresentaram 23 e 16 tipos polínicos, respectivamente, enquanto que as amostras de pólen revelaram 18 e 11 tipos polínicos, respectivamente. A família Fabaceae destacou-se em todas as análises polínicas realizadas, com grande número de tipos polínicos reconhecidos. A amplitude de nicho trófico nos méis foi superior à dos potes de pólen nos dois biomas. A equitabilidade apontou, na maioria das amostras, para um uso homogêneo dos recursos florais por *Tetragonisca angustula*. As análises de cluster apresentaram resultados mais consistentes quando utilizados os espectros polínicos dos méis, agrupando as amostras por região geográfica. Este trabalho representa a primeira contribuição à Melissopalinologia do Baixo Amazonas.

Palavras-chave: Abelha sem ferrão. Melissopalinologia. Mel. Pólen. *Tetragonisca angustula*.

Abstract

ABSTRACT

This thesis is aimed at characterizing, through Palynology, the honey and pollen provisions in colonies of *Tetragonisca angustula* (Apidae, Meliponini) from Amazon and *caatinga* (dryland) regions in Brazil. One-hundred and three samples (57 of honey and 46 of pollen) were collected between September 2010 and January 2012 in meliponaries located in the Lower Amazon region, Pará State, and *caatinga* vegetation in Bahia State, Brazil. All samples were processed through acetolysis. At least 500 pollen grains were identified and counted per sample. *T. angustula*'s honeys from the Lower Amazon region were characterized by the *Borreria verticillata*, *Byrsonima*, *Cecropia*, *Clidemia*, *Eriope*, *Microtea*, *Myrcia*, *Solanum*, *Tapirira guianensis* and *Warszewiczia coccinea* pollen types. In these honeys, the pollen concentration ranged from 20,000 to 500,000 pollen grains per 10 g of honey. Honeys from *caatinga* presented the *Heteropterys*, *Mikania*, *Mimosa tenuiflora*, *Myrcia*, *Prosopis juliflora*, *Schinus*, *Senna macranthera*, *Solanum*, *Syagrus coronata* and *Solanum* pollen types. On the other hand, pollen pots from the Lower Amazon showed the *Acalypha*, *Byrsonima*, *Brosimum paraense*, *Borreria verticillata*, *Cecropia*, *Clidemia hirta*, *Davilla kunthii*, *Eriope*, *Lindackeria paludosa*, *Myrcia*, *Schefflera morototoni*, *Tabebuia*, *Tapirira guianensis* and *Vismia guianensis* pollen types in their composition. The pollen pots from *caatinga* were characterized by the *Prosopis juliflora* and *Solanum* pollen types. Moreover, the *Poincianella pyramidalis* and *Senna macranthera* pollen types were considered indicators of *caatinga* dry vegetation. Regarding the most representative pollen types (>10%), the honeys from the Lower Amazon and *caatinga* revealed 23 and 16 pollen types, respectively. Meanwhile, the pollen pots samples showed 18 and 11 pollen types, respectively. The Fabaceae family stood out in all palynological analyses from both biomes because of its high amount of pollen types. The trophic niche size obtained was higher for the honey pots than for the pollen pots. The evenness points toward homogeneity in the use of floral resources by *Tetragonisca angustula*. For grouping the samples by geographic region, cluster analyses presented more consistent results when pollen spectra of honeys were used. This work represents the first contribution to Melissopalynology of the Lower Amazon region, Pará State, Brazil.

Keywords: Honey. Melissopalynology. Pollen. Stingless bee. *Tetragonisca angustula*.

SUMÁRIO

LISTA DE TABELAS

Capítulo I

Capítulo II

Capítulo III

Capítulo IV

Capítulo V

LISTA DE FIGURAS

Capítulo I

Capítulo II

Capítulo III

Capítulo IV

Capítulo V

1 Introdução Geral

1 INTRODUÇÃO GERAL

Evidências fósseis apontam que a interação entre abelhas e plantas remonta ao período Cretáceo, há cerca de 120 milhões de anos (Poinar Jr. e Danforth, 2006). A grande maioria das plantas depende de agentes polinizadores para concretizar o processo de fertilização. O vento e as abelhas respondem pela maior parcela desse serviço na natureza (Fægri e van der Pijl, 1979; Proctor *et al*., 1996; Michener, 2007), garantindo a manutenção da biodiversidade e a produção de alimentos no planeta (Roubik, 1995; Allen-Wardell *et al*., 1998; Dias *et al*., 1999).

Nas últimas décadas, ameaças à estabilidade e ao equilíbrio das relações planta – polinizador têm suscitado constante debate na comunidade científica, especialmente no sentido de compreender o alcance das consequências decorrentes de ações antrópicas sobre os ecossistemas naturais. Admite-se que fatores como a introdução de espécies exóticas, a crescente supressão de áreas florestadas e a intensificação das atividades agrícolas têm culminado na perda de hábitat e no declínio das populações de polinizadores nativos no planeta, principalmente na região neotropical (Allen-Wardell *et al*., 1998; Dias *et al*., 1999; Freitas *et al*., 2009; Giannini *et al*., 2012).

Para o Brasil, já estão descritas centenas de espécies de abelhas nativas (Apidae, Meliponini) (Silveira et al., 2002), distribuídas ao longo de todos os seis biomas continentais delimitados no país (IBGE, 2004). Dentre estes biomas, a Amazônia e a *caatinga* correspondem em extensão a quase 60% do território nacional (IBGE, 2004). As diferenças especialmente no regime de precipitação pluviométrica entre esses dois biomas resultam em variados mosaicos vegetacionais, aos quais se associa a rica fauna de abelhas. Contudo, o conhecimento acerca da diversidade de meliponíneos e da flora por eles explorada não é uniforme no Brasil, havendo um verdadeiro vazio de informações sobre esses insetos, por exemplo, para a maior parte da Amazônia (Silveira *et al*., 2002; Freitas *et al*., 2009).

Conhecer a flora utilizada pelas abelhas nativas constitui-se um pressuposto elementar para propor ações de conservação da biodiversidade e de mitigação dos efeitos nocivos de ações antrópicas ou naturais que porventura promovam ou contribuam para a diminuição dos polinizadores nos ecossistemas naturais e nos cultivos agrícolas em diferentes regiões brasileiras. Nesse escopo, a Palinologia pode contribuir substancialmente para ampliar a compreensão das relações tróficas, ecológicas e evolutivas entre plantas e abelhas, ao desvendar, por meio do espectro polínico, quais espécies vegetais proveem recursos florais para esses insetos (Barth, 2013; Roubik e Moreno, 2013).

Sendo a maior região de florestas tropicais do planeta, estima-se que na Amazônia existam cerca de 130 espécies de abelhas sem ferrão (Silveira *et al.*, 2002). Contudo, confrontados com essa riqueza de meliponíneos, ainda são poucos os trabalhos melissopalinológicos desenvolvidos com esse grupo de abelhas na região amazônica. Além disso, os estudos existentes concentram-se quase que exclusivamente em áreas da Amazônia Central (*e.g.*, Absy e Kerr, 1977; Absy *et al.*, 1980, 1984; Marques-Souza *et al.*, 1995, 1996, 2002, 2007; Marques-Souza, 1996, 2010; Oliveira *et al.*, 2009; Rech e Absy, 2011a, 2011b), permanecendo as demais regiões ainda desconhecidas sob o ponto de vista melissopalinológico, à exceção dos trabalhos de Kerr *et al.* (1986/1987) e Martins *et al.* (2011), no Maranhão. Essa concentração de trabalhos em poucas áreas geográficas também pode ser observada nos inventários florísticos para a Amazônia (Hopkins, 2007), o que gera lacunas de conhecimento prejudiciais ao uso e manejo adequados da biodiversidade botânica regional.

Em contrapartida, a *caatinga* representa o único bioma genuinamente brasileiro, reconhecida como uma extensa floresta tropical sazonalmente seca, estendendo-se por mais de 800.000 km² e ocorrendo na maior parte da área com clima semiárido no Nordeste brasileiro (Prado, 2003). Apesar disso, apenas nas últimas décadas a flora da *caatinga* tem recebido maior atenção nas publicações científicas (Giulietti *et al.*, 2004), revelando a diversidade vegetal nela encerrada.

No que diz respeito à riqueza de abelhas, são conhecidas 187 espécies para a *caatinga* (Zanella e Martins, 2003), sendo a maior parcela de abelhas nativas sem ferrão (Maia-Silva *et al.*, 2012). Na década de 1990, Freitas (1991) destacou o potencial do bioma *caatinga* para a produção de néctar e pólen com fins de exploração apícola. Entretanto, apenas a partir da década de 2000 começaram a ser executados estudos palinológicos envolvendo meliponíneos nessa região (*e.g.*, Alves *et al.*, 2006; Novais *et al.*, 2006; Lima, 2007; Santana *et al.*, 2011).

Dentre os meliponíneos ocorrentes no Brasil, *Tetragonisca angustula* (Latreille, 1811) representa um dos mais bem distribuídos, sendo reconhecido em 18 estados (Silveira *et al.*, 2002; Camargo e Pedro, 2012). Popularmente conhecida como abelha "jataí", *T. angustula* produz em geral menos de um litro de mel por colônia/ano, sendo esse produto muito apreciado pela qualidade sensorial e por sua aplicação na cura de enfermidades (Iwama e Melhem, 1979). Estudos palinológicos relacionados ao mel e ao pólen transportado ou aprovisionado por essa espécie foram desenvolvidos pontualmente em São Paulo (Iwama e Melhem, 1979; Imperatriz-Fonseca *et al*., 1984; Cortopassi-Laurino e Gelli, 1991; Carvalho *et al*., 1999), Paraná (Cortopassi-Laurino e Gelli, 1991), Bahia (Novais *et al*., 2006; Santana *et al*., 2011) e Rio de Janeiro (Morgado *et al*., 2011; Braga *et al*., 2012).

Contudo, inexistem estudos palinológicos focados em *T. angustula* na região amazônica, bem como estudos comparativos considerando essa espécie nativa em diferentes formações vegetacionais e submetida a diferentes pressões ambientais. Dessa forma, julgamos ser pertinente propor uma análise palinológica de provisões alimentares de *T. angustula* em diferentes áreas situadas em dois dos principais biomas brasileiros, a Amazônia e a *caatinga*, intentando que tais dados subsidiem pesquisas palinoecológicas futuras, ampliando o nosso conhecimento acerca desse meliponíneo no Brasil.

Desta forma, a presente tese estrutura-se em cinco capítulos, todos elaborados em forma de artigo científico. O primeiro capítulo apresenta o espectro e a concentração polínica em méis de *T. angustula* produzidos em duas áreas do Baixo Amazonas, representando a primeira contribuição à Melissopalinologia nesta região da Amazônia. No segundo capítulo, por sua vez, é apresentado o espectro polínico de amostras do pólen aprovisionado por *T. angustula* também no Baixo Amazonas, complementando o primeiro capítulo. No terceiro e no quarto capítulos estão descritos, respectivamente, os espectros polínicos de amostras de mel e pólen estocado por *T. angustula* em duas áreas de *caatinga* no semiárido baiano, no Nordeste do Brasil, ampliando o reduzido conhecimento hoje existente sobre as preferências florais deste meliponíneo em vegetação seca. Por fim, o quinto capítulo concatena comparativamente os dados palinoecológicos obtidos nos quatro capítulos anteriores, considerando os tipos polínicos mais representativos para *T. angustula* no Baixo Amazonas e na *caatinga* baiana. São apresentados ainda os resultados de análises de cluster e discutidos índices ecológicos calculados a partir dos espectros polínicos obtidos.

2 Objetivos

2 OBJETIVOS

Geral:

Caracterizar, sob o ponto de vista palinológico, provisões de mel e pólen estocadas em colônias de *Tetragonisca angustula* em áreas do Baixo Amazonas (Pará) e da *caatinga* nordestina (Bahia), a partir dos tipos polínicos reconhecidos nesses produtos.

Específicos:

a) Determinar os espectros polínicos das amostras estudadas;
b) Identificar os tipos polínicos ou as associações polínicas mais representativas para o mel e para o pólen aprovisionados em cada área de estudo;
c) Acessar a extensão do nicho polínico e o padrão de uso dos recursos florais por *T. angustula*, a partir da aplicação de índices ecológicos;
d) Analisar comparativamente os espectros polínicos gerados para as áreas amazônicas e de *caatinga*, no que diz respeito aos tipos polínicos mais expressivos nestas áreas.

Capítulo I

Novais, J.S. & Absy, M.L. First melissopalynological records in honeys from *Tetragonisca angustula* (Latreille, 1811) in Lower Amazon, Brazil: pollen spectrum and concentration. Submetido ao *Journal of Apicultural Research*

First melissopalynological records in honeys from *Tetragonisca angustula* (Latreille, 1811) in Lower Amazon, Brazil: pollen spectrum and concentration

Summary

We present the first pollen investigation in honeys from *Tetragonisca angustula* (Apidae, Meliponini) in the Lower Amazon region, Pará State, Brazil. The analyses focused on the spectra and pollen concentrations recorded in the honey. We conducted monthly collections between September 2010 and January 2012 in the municipalities of Belterra and Santarém. The samples were acetolysed and the pollen types identified and quantified (500 per sample). *Lycopodium clavatum* L. was used as an exotic marker in the samples. The pollen spectra in the honey from the Belterra and Santarém regions demonstrated 58 and 45 pollen types, respectively. Fabaceae was the most commonly represented plant family in the honey samples from both areas. The main pollen associations observed in the honey include: *Borreria verticillata*, *Byrsonima*, *Eriope*, *Microtea* and *Warszewiczia coccinea* in Belterra and *Byrsonima*, *Cecropia*, *Clidemia hirta*, *Myrcia*, *Solanum paniculatum, Tapirira guianensis* and *W. coccinea* in Santarém. In both municipalities, the mean values of the pollen diversity (Shannon-Weaver, *H'*) and equitability (Pielou, *J'*) indices were 1.6 and 0.6, respectively. Most of the honey from Belterra contained between 20,000 and 100,000 pollen grains/10 g of honey (Group II). In Santarém, most of the samples contained between 100,000 and 500,000 grains/10 g of honey (Group III). *T. angustula* demonstrated polyletic foraging behaviours during the study. The ecological indices point toward uniformity in the use of the available resources in the local flora. The concentration of pollen in the honey samples indicates that these honeys meet the normal, internationally recognised standards.

Keywords: “jataí” bee, entomopalynology, Amazonian honey, melissopalynology, palynological analysis, Brazilian native bee, stingless bee, exotic marker, *Lycopodium clavatum*

Introduction

Recently, the fluctuation in deforestation rates in the Brazilian Amazon has been a focus of the scientific community worldwide (Laurance *et al.*, 2004; Nepstad *et al.*, 2009; FAO, 2010). Between 2000 and 2011, an area of approximately 70,000 km^2 was deforested in the State of Pará (PA) alone, which was the highest rate among the States of the Legal Amazon (Brazilian National Institute for Space Research, known as Instituto Nacional de Pesquisas Espaciais (INPE), 2012). Deforestation in western Pará is related to the expansion of agricultural borders and soybean production in the region (Fearnside, 2001). The intense exploitation of natural resources affects the Amazonian ecosystems, which influences the vegetation cover in the region and the population dynamics of native pollinators, especially stingless bees (Freitas *et al.*, 2009). Rearing these bees through meliponiculture mitigates these ecological effects and contributes to increasing the household income of farmers (beekeepers/meliponiculturists) through the production of honey and other products. If exploited, meliponiculture has the potential to boost the regional economy (Rech and Absy, 2011a).

The sustainability of meliponiculture depends on the availability of the resources required by the bees, which are predominantly nectar and pollen. Therefore, it is essential to know the plant species that contribute to maintaining these insects. However, once the honey plants in a region are identified, how can the contribution of each plant species to the composition of the bee products be determined? Many studies have attempted to answer this and other questions. The most commonly used method is to determine the contribution of each pollen type in the honey samples by establishing frequency classes (Louveaux *et al.*, 1970, 1978). Complementing this method, other studies have estimated the concentration of pollen grains from each plant species in a known amount of honey, adding a marker to the samples (Maurizio, 1976; Moar, 1985; Lutier and Vaissière, 1993; Bryant, 2001; Ramírez-Arriaga *et al.*, 2011). This method has proven useful for detecting the adulteration of commercial honey (Young, 1908; Sorkun and Doğan, 2002); therefore, it can also be used as a tool to regulate the product quality.

The use of exotic markers to estimate the concentration of pollen in sediments is a routine technique in palaeopalynology (Benninghof, 1962; Stockmarr, 1971). In general, tablets containing a known volume of a certain marker are added to the test samples, allowing the calculation of the absolute concentration of pollen grains in the sample. A few studies have focused on the use of exotic markers to assess the concentration of pollen grains in honey samples.Most studies have focused on the analysis of honey from *Apis mellifera* L., 1758 (Moar, 1985; Jones and Bryant, 1996; Andrada *et al.*, 1998; Jones and Bryant, 2001; Caccavari and Fagúndez, 2010; Ramírez-Arriaga *et al.*, 2011) and few have been based on honey from stingless bees (Apidae, Meliponini) (Sosa-Nájera *et al.*, 1994; Ramírez-Arriaga and Martínez-Hernández, 2007; Roubik and Moreno, 2009).

In the Brazilian palynological literature, only studies by Lima (2007) and Novais *et al.* (2008) demonstrated the concentration of pollen grains in honey from stingless bees (Bahia State), although Brazil harbours a large number of species that contribute significantly to the maintenance of ecosystems through pollination (Freitas *et al.*, 2009). It is estimated that the Amazon contains approximately 130 species of stingless bees (Silveira *et al.*, 2002), and many of these bees have already been reared for honey production, although the majority of commercialised products come from *A. mellifera*.

In this study, we investigated for the first time the concentration of pollen grains in honey samples from a native stingless bee, *Tetragonisca angustula* (Latreille, 1811) (Apidae, Apinae, Meliponini), in two areas of the Lower Amazon, Pará State, Brazil. We describe the pollen spectra and specify the main pollen associations found in the samples, which reflects the honey plants exploited throughout the year.

Materials and methods

Study municipalities

This study was performed in the municipalities of Belterra and Santarém, Pará State, Brazil (Fig. 1). According to the Köppen classification, the area exhibits the Am (hot and humid) climate type typical of tropical areas. The rainy season occurs between December and May with a peak in April because of the intensification of local effects associated with the presence of the Intertropical Convergence Zone (Albuquerque *et al.*, 2010). The mean annual temperature is approximately 25°C, and the annual rainfall is 1,900 mm (Brazilian Enterprise for Agricultural Research, known as Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), 2012).

Belterra is an area characterised by high plains located on the bank of the Tapajós River and includes several areas of "Indian black earth" (“Terra Preta de Índio”), which is a fertile soil suitable for agriculture. The city of Santarém is located on the southern bank of the Tapajós River at its confluence with the Amazon River and is bordered to the southwest by the municipality of Belterra. Several vegetation groups occur in the region, such as grasslands, alluvial pioneer formations and dense and open tropical forests (Veloso *et al.*, 1991).

Study species: the "jataí" bee

The stingless "jataí" bee *T. angustula* (Fig. 2) is found in most of the Brazilian territories, including the States in the northern region of the country (Amapá, Amazonas, Pará, Rondônia and Roraima), and in other Latin American countries, from Mexico to Argentina (Silveira *et al.*, 2002; Camargo and Pedro, 2012). According to Camargo and Pedro (2012), several species of undescribed stingless bees are included under the name *T. angustula*.

Honey from the "jataí" bee achieves a high market value because of the popular belief in its medicinal and curative (vision and lungs) properties (Iwama and Melhem, 1979). However, "jataí" bee colonies produce less than one litre of honey per year. In the studied areas, the main period for honey harvesting is from October to January. According to Lindauer and Kerr (1960), *T. angustula* hives include between 2,000 and 5,000 individuals.

In Brazil, the palynological study of *T. angustula* honey is limited to the States in the southeastern (Iwama and Melhem, 1979; Cortopassi-Laurino and Gelli, 1991), southern (Cortopassi-Laurino and Gelli, 1991) and northeastern (Novais *et al.*, 2006) regions and is undocumented in the midwestern and northern regions of the country.

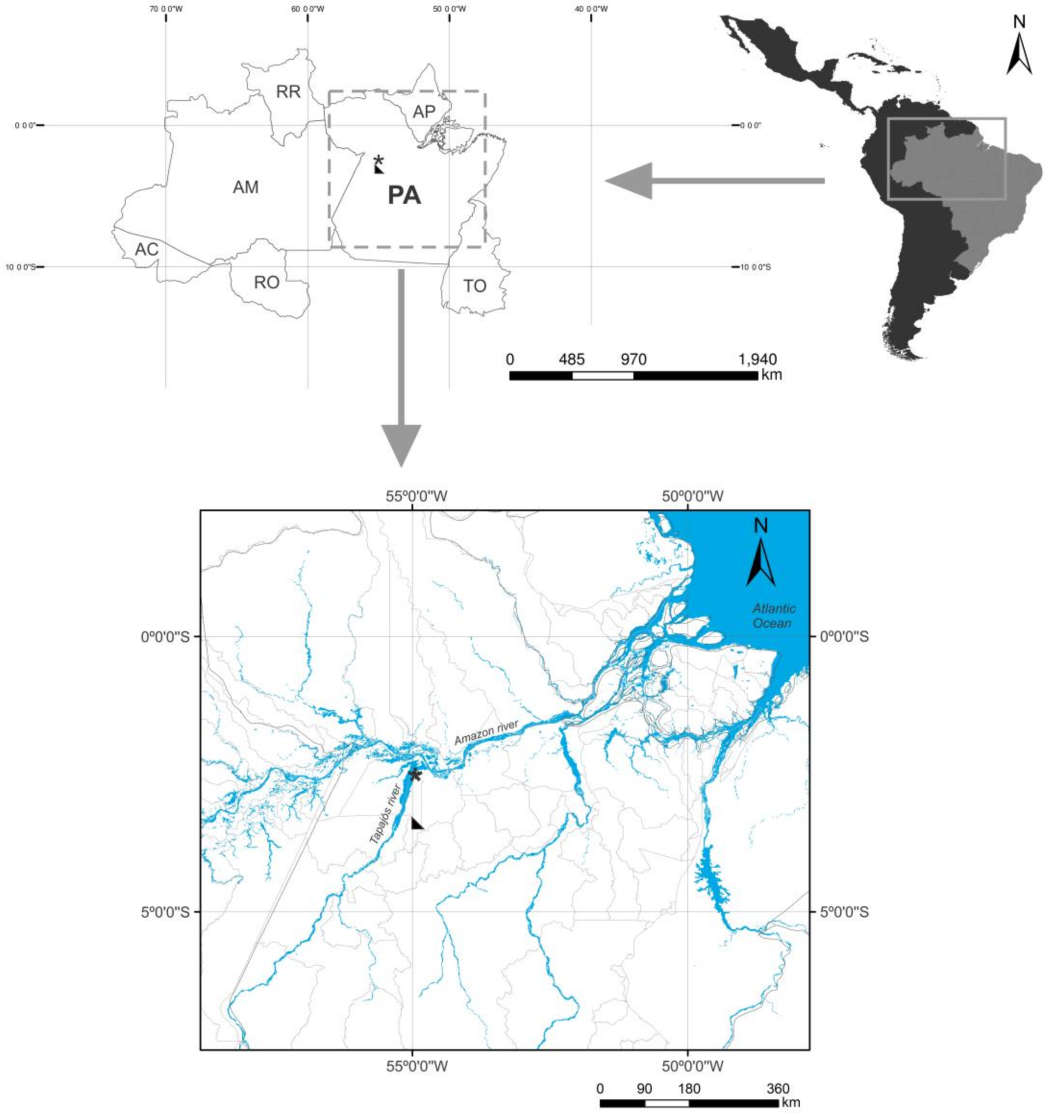


Fig. 1. Map showing all States of the Northern region of Brazil: AC, Acre. AM, Amazonas. AP, Amapá. PA, Pará. RO, Rondônia. RR, Roraima. TO, Tocantins. Study areas in the municipalities of Santarém (*asterisk*) and Belterra (*triangle*), Lower Amazon, PA, Brazil. (*Map: Courtesy of L S Damascena*)

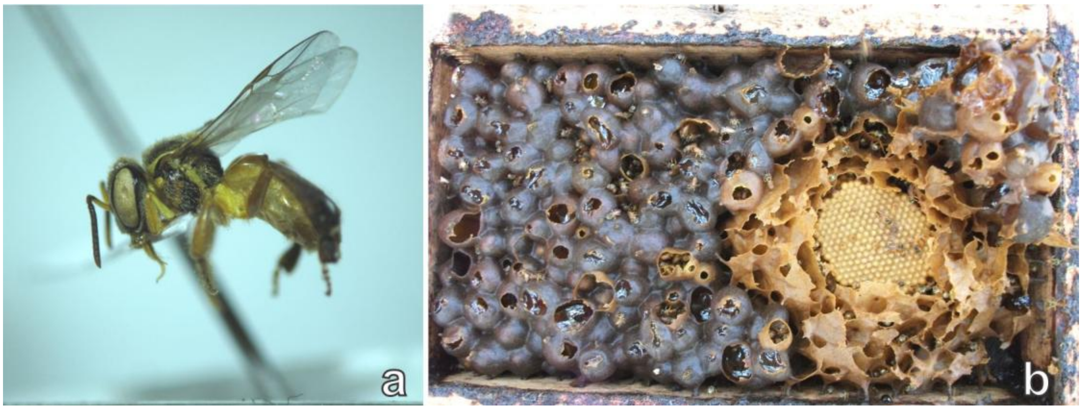


Fig. 2. **a.** *Tetragonisca angustula* (Latreille, 1811), a common stingless bee found in Brazil. **b.** Honeycombs of *T. angustula* from a colony located in the municipality of Belterra, Lower Amazon, Pará, Brazil. *(Photos: a) courtesy of M G Ferreira; b) J S Novais)*

Sample collection and processing

In Belterra, the samples were collected monthly from *T. angustula* (known locally as the "jataí" or " mosquito-amarela") colonies installed in a stingless bee apiary (meliponary) located near the headquarters of the Meliponiculturists Association of the Municipality of Belterra (Associação de Meliponicultores do Município de Belterra (AMEMBEL)) (02°38'07.0"S, 54°55'53.2"W, 126 m.a.s.l.). In Santarém, the monthly samples were obtained from the *T. angustula* colonies maintained at the Forest School (Escola da Floresta) meliponary (02°30'49.3"S, 54°56'07.7"W, 72 m.a.s.l.), an institution supported by the Municipal Department of Education (Secretaria Municipal de Educação, SEMED), which is involved mainly in the development of activities related to environmental education in the local schools.

We collected, processed and palynologically analysed 30 honey samples. Of these, 16 were from Belterra, collected monthly between September 2010 and January 2012 (with the exception of May 2011), and 14 were from Santarém, collected between October 2010 and January 2012 (with the exception of September 2010 and May and December 2011). Monthly collects may provide an overview of nectar/pollen influx into the colonies throughout the year.

Because of the low amount of honey produced by *T. angustula*, samples with 3-4 grams of honey were used in the analysis (Iwama and Melhem, 1979), collected from honey cells into the colonies *in situ* using disposable syringes. The material was stored in acrylic jars that were correctly labelled and sent to the laboratory for standard melissopalynological processing (Louveaux *et al.*, 1978; Iwama and Melhem, 1979). The samples were processed in accordance with the protocol described by Jones and Bryant (2004) for the use of an exotic marker, with modifications, and with the acetolysis procedure described by Erdtman (1960). The laboratory procedures were performed in the Laboratory of Palynology at the National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas State, Brazil), the Laboratory of Plant Micromorphology at the Bahia State University at Feira de Santana (Universidade Estadual de Feira de Santana (UEFS), Feira de Santana, Bahia State, Brazil) and the Laboratory of Chemistry at the Federal University of Western Pará (Universidade Federal do Oeste do Pará (UFOPA), Santarém, Pará State, Brazil).

For each sample, a tablet containing 18,583 spores of *Lycopodium clavatum* was dissolved in a beaker containing 3-5 mL of 10% HCl (Benninghof, 1962; Stockmarr, 1971; Moar, 1985). The honey was added to this solution, and the solution was diluted with ethyl alcohol (ETOH) to minimise the loss of pollen grains during the removal of the supernatant after centrifugation (Jones and Bryant, 2004).

After the acetolysis process, four slides were prepared from each sample using glycerinated gelatin, of which three were stained with safranin. The slides were fixed using paraffin and deposited in the Pollen Library at UFOPA (PUFOPA, Palinoteca da UFOPA) for microscopic analysis.

Microscopic analysis and categorisation

For each sample, at least 500 pollen grains were counted under light microscopy (Vergeron, 1964; Iwama and Melhem, 1979; Moar, 1985). The botanical identification of the pollen types was based on a reference collection of slides from the study areas maintained at the PUFOPA, slides from the pollen library of INPA, as well as through the consultation of specialised guides (Roubik and Moreno, 1991; Carreira *et al.*, 1996) when necessary. Considering the observations of Joosten and de Klerk (2002) and de Klerk and Joosten

(2007), this study adopted the concept of pollen type as a morphological entity, which may include one or more species. Therefore, in this study, the authorship of the botanical species is provided only when there is clear reference to a single taxonomic entity, which is unnecessary when referring to a pollen type, as demonstrated in the tables.

Once the percentage of each pollen type in each honey sample was determined, the following frequency classes were adopted (Louveaux *et al.*, 1978): predominant pollen (p) (>45%), secondary pollen (s) (16-45%), important minor pollen (im) (3-15%) and minor pollen (m) (<3%).

The following categories were adopted to classify the percentage of occurrence of each pollen type over the set of samples, considering only the presence or absence of a particular pollen type per sample: very frequent (>50%), frequent (21-50%), infrequent (10-20%) and rare (<10%) (Jones and Bryant, 1996).

The total concentration of pollen in *X* grams of honey was estimated by counting the *Lycopodium clavatum* spores in the samples (performed in parallel with the counting of 500 pollen grains, as described above), considering the following formula:

TNP-Xgr = (n° of counted pollen × n° of spores added)/(n° of spores counted),

where *TNP-Xgr* represents the total number of pollen grains in *X* grams of honey (Louveaux *et al.*, 1978; Sorkun and Doğan, 2002). Firstly we calculated the pollen concentration for the real weight of each sample and secondly we estimated the pollen concentration in 10 grams (TNP-10gr) by proportion.

From the pollen concentration obtained for each sample, the honey samples were classified as follows: Group I (<20,000), Group II (20,000-100,000), Group III (100,001-500,000), Group IV (500,001-1,000,000) and Group V (>1,000,000) (Maurizio, 1976; Louveaux *et al.*, 1978).

Ecological analysis

The amplitude of the trophic niche for each honey sample was calculated using the Shannon-Weaver diversity index (*H'*) (Ludwig and Reynolds, 1988), which was calculated to indicate the pollen diversity using the following equation: $H' = -\sum_{i}^{n} p_i . \ln p_i$, where p_i is the proportion of each pollen type i found in the sample, given by n_i/N, and where n_i is the number of grains of pollen type i and N is the total number of pollen grains in the sample.

The H' index was complemented by Pielou's evenness index (J') (Pielou, 1977), which indicates the homogeneous or heterogeneous use of a pollen resource by the bees. This index was calculated using the following formula: $J'=H'/H'max$, where $H'max=lnS_e$, and S_e is the total number of pollen types found in the honey sample.

The analyses were performed using the PAST (*PAlaeontological STatistics*) software version 2.16 (Hammer *et al.*, 2001).

Results

Pollen spectra and ecological indices

Belterra

The pollen spectrum of the honey samples from Belterra demonstrated 58 morphologically distinct pollen types related to 29 plant families. In terms of the number of identified pollen types, the most represented were as follows: Fabaceae (15 types); Amaranthaceae, Asteraceae, Euphorbiaceae, Myrtaceae and Rubiaceae (three types each); and Anacardiaceae, Araliaceae, Arecaceae, Bignoniaceae, Lamiaceae and Malpighiaceae (two types each). The other families (17) each exhibited a single pollen type (Table 1). Of the three Fabaceae subfamilies, Papilionoideae stood out in the pollen spectrum with six identified types, *Clathrotropis nitida*, *Cratylia*, *Crotalaria, Desmodium, Zollernia paraensis* and *Zornia*. The pollen types lacking an established botanical affinity occurred in 11 samples and were grouped in an “Undetermined” class.

For the percentage of occurrence in the honey samples, the following pollen types were frequent: *Borreria verticillata* (Rubiaceae) (recorded in 94% of the samples); *Alternanthera* (Amaranthaceae) and *Microtea* (Phytolaccaceae) (each in 88% of the samples); *Schefflera morototoni* (Araliaceae) (in 81% of the samples); *Eriope* (Lamiaceae) and *Warszewiczia coccinea* (Rubiaceae) (each in 69% of the samples); *Emilia fosbergii* (Asteraceae) and *Byrsonima* (Malpighiaceae) (each in 63% of the samples); and *Eupatorium* (in 56% of the samples). In addition, we identified 20 frequent, 9 infrequent and 20 rare pollen types (Table 1 and Fig. 3).

The number of pollen types per sample ranged between 11 and 23 (17 ± s.d. 4 (*n* = 16)). *Byrsonima* was the predominant pollen in three samples representing the months of September, November and December 2011; *Borreria verticillata*, *Cecropia* (Urticaceae), *Diodia* (Rubiaceae) and *Chamaecrista* (Fabaceae/Caesalpinioideae) were each the predominant pollen in one sample from November 2010 and January, February and October 2011, respectively. *B. verticillata* occurred as an secondary pollen in six samples. This class (secondary) also contained the pollen types *Byrsonima*, *Microtea* and *Warszewiczia coccinea* (in three samples); *Eriope* (in two samples); and *Anacardium occidentale* (Anacardiaceae), *Emilia fosbergii* and *Tapirira guianensis* (Anacardiaceae) (in one sample only). Most of the pollen types occurred in minor classes (<16%). The honey sample from February/2011 presented a high amount of *Diodia* (89.53%) and other pollen types included in the minor class only (<3%), suggesting a monofloral honey. All the other samples were classified as polyfloral honeys, although some of these had presented pollen types with frequencies above 45%. This finding alone is not enough to state we have monofloral or bifloral honeys (Molan, 1998). Without studies on floral biology and nectar/pollen production by bee plant species, classifying a sample as monofloral honey may lead us to misleading results.

Thus, two pollen associations characterised the composition of the pollen spectrum in the honey samples from Belterra. The first association (*i*) corresponds to the pollen types recorded as the predominant and/or secondary pollen in two or more samples: *Borreria verticillata* - *Byrsonima* - *Eriope* - *Microtea* - *Warszewiczia coccinea*. The second pollen association (*ii*) indicates secondary or predominant pollen types in just one sample: *Anacardium occidentale* - *Cecropia* - *Chamaecrista* - *Diodia* - *Emilia fosbergii* - *Tapirira guianensis*.

The pollen niche size derived from the Shannon-Weaver diversity index (H') ranged from 0.6 (February 2011) to 2.1 (October and December 2010 and April and June 2011), with a mean value of 1.6 ± s.d. 0.5 (*n* = 16). Pielou’s evenness index (J') varied between 0.2 (February 2011) and 0.7 (October and December 2010 and April, June and August 2011), with a mean value of 0.6 ± s.d. 0.1 (*n* = 16), indicating an initial tendency toward homogeneity in the use of resources (Table 1 and Fig. 4).

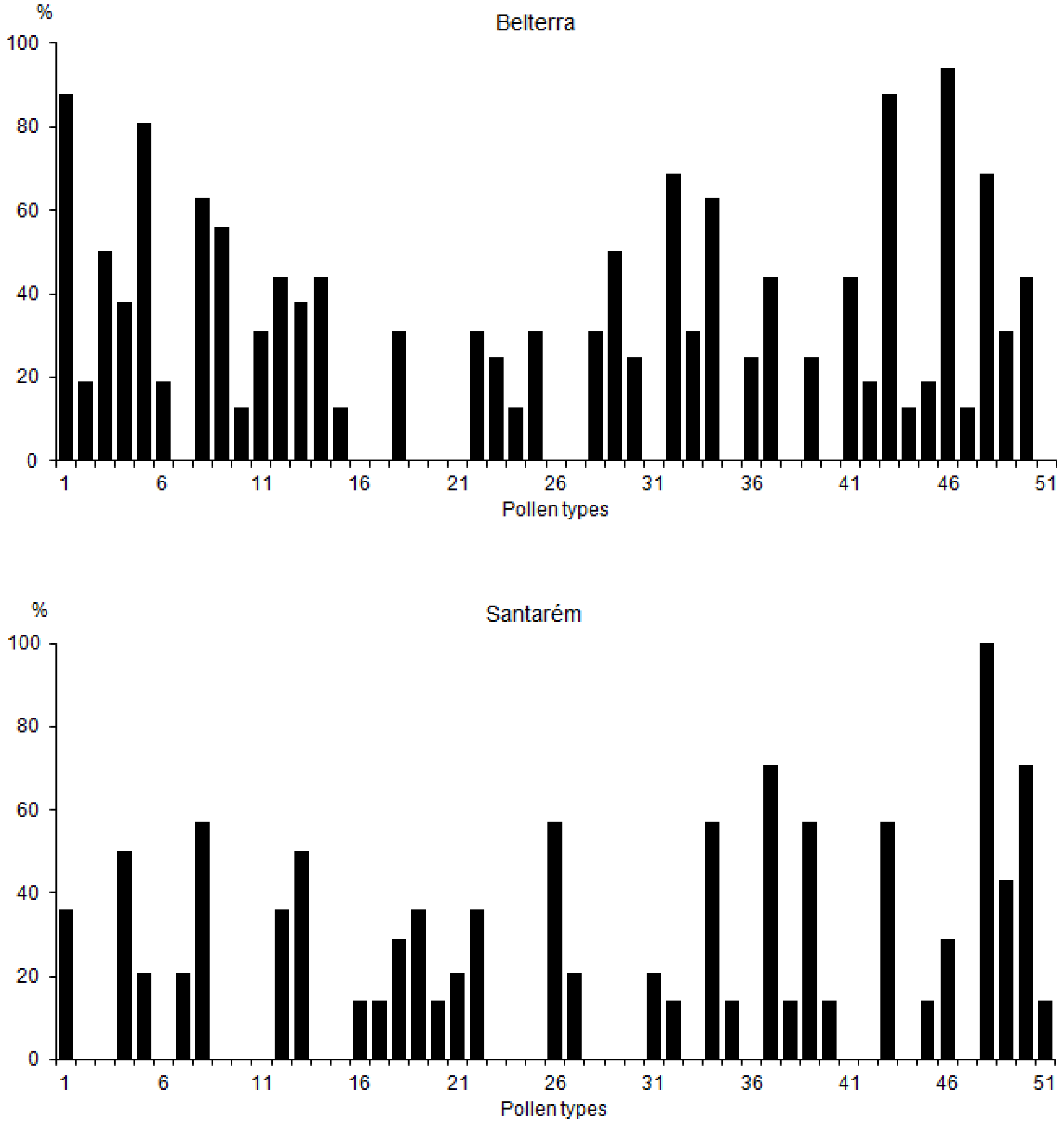


Fig. 3. Percentage occurrence (>10%) of pollen types (1-51) in honey samples from *Tetragonisca angustula* (Latreille, 1811) collected in Belterra and Santarém, Lower Amazon, Brazil: AMARANTHACEAE 1. *Alternanthera*, 2. *Amaranthus viridis*; ANACARDIACEAE 3. *Anacardium occidentale*, 4. *Tapirira guianensis*; ARALIACEAE 5. *Schefflera morototoni*; ARECACEAE 6. *Astrocaryum aculeatum*; ARECACEAE 7. *Attalea speciosa*; ASTERACEAE 8. *Emilia fosbergii*, 9. *Eupatorium*, 10. *Vernonia*; BIGNONIACEAE 11. Bignoniaceae type, 12. *Tabebuia*; BURSERACEAE 13. *Protium*; EUPHORBIACEAE 14. *Croton*, 15. *Dalechampia*, 16. Euphorbiaceae type; FABACEAE 17. Fabaceae type; FABACEAE/CAESALPINIOIDEAE 18. *Chamaecrista*, 19. *Copaifera*, 20. *Schizolobium*, 21.

Sclerolobium paniculatum, 22. *Senna*; FABACEAE/MIMOSOIDEAE 23. *Inga*, 24. *Mimosa arenosa*, 25. *Mimosa pudica*, 26. *Stryphnodendron*; FABACEAE/PAPILIONOIDEAE 27. *Clathrothropis nitida*, 28. *Cratylia*, 29. *Desmodium*, 30. *Zornia*; LACISTEMATACEAE 31. *Lacistema*; LAMIACEAE 32. *Hyptis*; MALPIGHIACEAE 33. Malpighiaceae type, 34. *Byrsonima*; MALVACEAE 35. *Ceiba*, 36. *Waltheria*; MELASTOMATACEAE 37. *Clidemia hirta*; MORACEAE 38. *Brosimum*; MYRTACEAE 39. *Myrcia*, 40. *Syzygium malaccense*; PASSIFLORACEAE 41. *Turnera ulmifolia*; PHYLLANTHACEAE 42. *Phyllanthus*; PHYTOLACCACEAE 43. *Microtea*; PLANTAGINACEAE 44. *Scoparia dulcis*; POACEAE 45. Poaceae Type I; RUBIACEAE 46. *Borreria verticillata*, 47. *Diodia*, 48. *Warszewiczia coccinea*; SOLANACEAE 49. *Solanum paniculatum*; URTICACEAE 50. *Cecropia*; VERBENACEAE 51. *Lippia*.

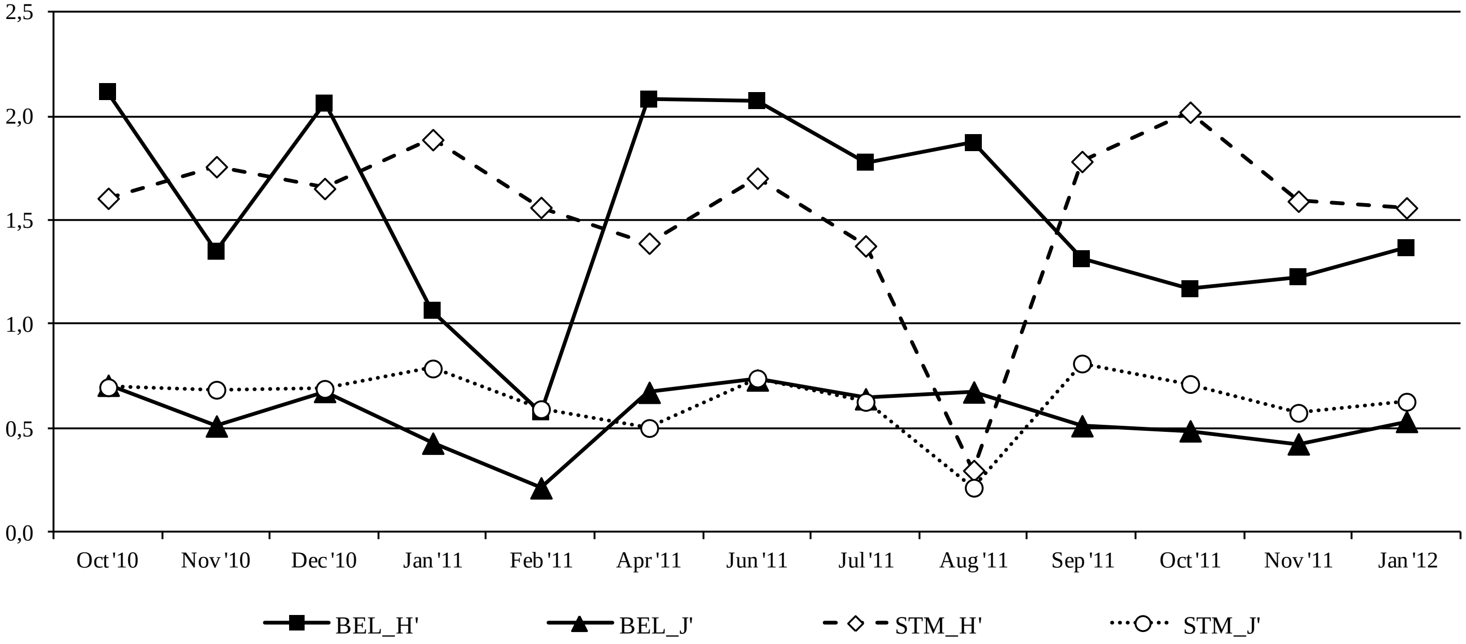


Fig. 4. Comparison of the Shannon-Weaver diversity index (*H'*) and Pielou’s evenness index (*J'*) for the same period in the municipalities of Belterra (BEL) and Santarém (STM), Lower Amazon, Pará, Brazil, calculated from the pollen spectra of honeys collected from *Tetragonisca angustula* (Latreille, 1811) in these areas (only the months during which honey was collected in both study areas were considered).

Table 1. Pollen spectrum, percentage and classes of occurrence, diversity and evenness indexes in honey samples from *Tetragonisca angustula* (Latreille, 1811) collected in the municipality of Belterra, Lower Amazon, Pará, Brazil.

Plant Family	Pollen Type	Sep, 2010	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Apr, 2011	May, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Dec, 2011	Jan, 2012	PO(a) (%)	CO(b)
Achariaceae	*Lindackeria paludosa*	−	−	−	im(c)	−	−	−	−	−	−	−	−	−	−	−	−	6	R
Amaranthaceae	*Alternanthera*	im	im	m	m	m	m	m	m	im	m	m	im	−	m	−	m	88	VF
	Amaranthus viridis	−	−	−	−	−	−	m	m	m	−	−	−	−	−	−	−	19	I
	Gomphrena	m	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	6	R
Anacardiaceae	*Anacardium occidentale*	m	im	−	m	−	−	m	−	im	im	s	m	−	−	−	−	50	F
	Tapirira guianensis	m	m	s	im	−	−	−	−	−	−	−	m	m	−	−	−	38	F
Araliaceae	*Schefflera morototoni*	im	im	m	im	−	m	im	im	m	m	−	−	m	m	m	m	81	VF
Arecaceae	*Astrocaryum aculeatum*	−	m	−	−	−	−	m	−	−	−	−	m	−	−	−	−	19	I
	Elaeis	−	−	−	−	−	−	−	m	−	−	−	−	−	−	−	−	6	R
Asteraceae	*Emilia fosbergii*	im	m	m	m	im	m	−	im	im	s	m	−	−	−	−	−	63	VF
	Eupatorium	m	m	m	−	−	m	m	−	−	−	−	−	m	m	m	im	56	VF
	Vernonia	m	−	−	−	−	−	−	−	−	−	−	−	−	m	−	−	13	I
Bignoniaceae	Bignoniaceae type	im	m	m	−	m	m	−	−	−	−	−	−	−	−	−	−	31	F
	Tabebuia	−	m	−	−	−	−	−	im	im	m	im	im	m	−	−	−	44	F
Burseraceae	*Protium*	−	−	−	m	−	−	m	−	m	−	m	−	m	im	−	−	38	F
Convolvulaceae	Convolvulaceae type	−	−	−	−	−	m	−	−	−	−	−	−	−	−	−	−	6	R
Euphorbiaceae	*Alchornea triplinervia*	−	−	−	−	−	−	m	−	−	−	−	−	−	−	−	−	6	R
	Croton	−	−	−	m	−	−	−	−	−	m	im	m	−	m	m	m	44	F
	Dalechampia	m	−	−	−	−	−	−	−	−	m	−	−	−	−	−	−	13	I
Fabaceae - C	*Chamaecrista*	−	−	−	−	m	m	−	−	−	−	−	−	p	im	im	−	31	F
(Caesalpinioideae)	*Copaifera*	−	−	−	−	−	−	−	m	−	−	−	−	−	−	−	−	6	R
	Schizolobium	−	−	−	m	−	−	−	−	−	−	−	−	−	−	−	−	6	R

Table 1 (continuation)

Plant Family	Pollen Type	Sep, 2010	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Apr, 2011	May, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Dec, 2011	Jan, 2012	PO[(a)] (%)	CO[(b)]
	Senna	m	m	–	m	–	–	–	–	m	–	–	m	–	–	–	–	31	F
Fabaceae - M (Mimosoideae)	*Inga*	m	m	–	–	–	m	–	m	–	–	–	–	–	–	–	–	25	F
	Mimosa arenosa	–	–	m	–	–	–	–	–	–	–	m	–	–	–	–	–	13	I
	Mimosa lewisii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	m	6	R
	Mimosa pudica	m	m	–	–	–	–	m	m	m	–	–	–	–	–	–	–	31	F
	Stryphnodendron	–	–	–	–	–	–	–	–	–	–	–	m	–	–	–	–	6	R
Fabaceae - P (Papilionoideae)	*Cratylia*	–	–	–	–	–	–	–	m	m	m	–	–	–	m	m	–	31	F
	Crotalaria	–	–	–	–	–	–	–	–	–	–	m	–	–	–	–	–	6	R
	Clathrotropis nitida	–	–	–	m	–	–	–	–	–	–	–	–	–	–	–	–	6	R
	Desmodium	–	m	–	–	–	m	m	m	–	–	m	–	–	m	m	m	50	F
	Zollernia paraensis	m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	R
	Zornia	–	–	–	–	–	m	m	–	m	–	m	–	–	–	–	–	25	F
Gentianaceae	*Schultesia*	–	–	–	–	–	–	–	m	–	–	–	–	–	–	–	–	6	R
Hypericaceae	*Clusia odorata*	–	–	–	–	–	–	m	–	–	–	–	–	–	–	–	–	6	R
Lamiaceae	*Eriope*	–	m	m	–	m	m	im	im	s	s	m	m	–	m	–	–	69	VF
	Salvia	–	–	–	–	–	–	–	–	–	–	–	–	–	m	–	–	6	R
Malpighiaceae	Malpighiaceae type	m	m	–	m	–	–	–	–	–	–	–	–	m	–	m	–	31	F
	Byrsonima	–	im	–	–	–	–	im	m	im	–	s	p	s	p	p	s	63	VF
Malvaceae	*Waltheria*	–	–	–	–	m	–	–	m	m	–	–	–	–	m	–	–	25	F
Melastomataceae	*Clidemia hirta*	m	–	–	m	m	m	m	–	–	m	m	–	–	–	–	–	44	F
Meliaceae	*Trichilia hirta*	–	–	–	m	–	–	–	–	–	–	–	–	–	–	–	–	6	R
Myrtaceae	*Myrcia*	–	–	m	im	m	–	–	m	–	–	–	–	–	–	–	–	25	F
	Eucalyptus	–	–	–	–	–	–	im	–	–	–	–	–	–	–	–	–	6	R

Table 1 (continuation)

Plant Family	Pollen Type	Sep, 2010	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Apr, 2011	May, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Dec, 2011	Jan, 2012	PO[(a)] (%)	CO[(b)]
	Syzygium malaccense	–	–	–	–	–	–	–	m	–	–	–	–	–	–	–	–	6	R
Passifloraceae	*Turnera ulmifolia*	–	–	m	–	–	–	m	m	–	–	–	–	m	m	m	m	44	F
Phyllanthaceae	*Phyllanthus*	–	–	–	–	m	–	–	m	–	m	–	–	–	–	–	–	19	I
Phytolaccaceae	*Microtea*	im	s	m	im	im	m	im	s	im	s	–	m	–	m	m	m	88	VF
Piperaceae	*Piper*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	im	6	R
Plantaginaceae	*Scoparia dulcis*	–	–	–	–	–	m	im	–	–	–	–	–	–	–	–	–	13	I
Poaceae	Poaceae type	–	m	–	m	–	–	–	–	–	m	–	–	–	–	–	–	19	I
Rubiaceae	*Borreria verticillata*	im	s	m	im	p	–	s	s	im	im	im	s	im	im	s	s	94	VF
	Diodia	–	–	–	–	m	p	–	–	–	–	–	–	–	–	–	–	13	I
	Warszewiczia coccinea	s	s	im	s	–	–	–	im	m	m	m	m	–	m	–	m	69	VF
Solanaceae	*Solanum paniculatum*	–	–	–	m	–	–	m	–	–	–	–	–	–	m	m	m	31	F
Urticaceae	*Cecropia*	m	–	p	im	–	–	m	m	–	–	m	–	m	–	–	–	44	F
Verbenaceae	*Lippia*	–	–	–	–	–	–	–	–	–	m	–	–	–	–	–	–	6	R
Undetermined		im	im	m	m	im	–	–	m	–	im	s	m	m	–	–	s	69	VF
$H'^{(d)}$		1,9	2,1	1,3	2,1	1,1	0,6	2,1	1,9	2,1	1,8	1,9	1,3	1,2	1,2	1,0	1,4	–	–
$J'^{(e)}$		0,6	0,7	0,5	0,7	0,4	0,2	0,7	0,6	0,7	0,6	0,7	0,5	0,5	0,4	0,4	0,5	–	–

[(a)]PO: Percentage of Occurrence. [(b)]Classes of Occurrence (CO): R, rare (<10%); I, infrequent (10 - 20%); F, frequent (21 - 50%); VF, very frequent (>50%). [(c)]Frequency classes: p, predominant pollen (>45%); s, secondary pollen (16 - 45%); im, important minor pollen (3 - 15%); m, minor pollen (<3%). [(d)]*H'*, Shannon-Weaver Diversity Index; [(e)]*J'*, Pielou's Index.

Santarém

The honey samples originating from Santarém demonstrated the presence of 45 pollen types, representing 29 families. Fabaceae was the most frequently recorded family of pollen types identified (13), followed by the Arecaceae, Bignoniaceae, Malpighiaceae and Myrtaceae families, each with two pollen types. The remaining families (24) contributed only one pollen type to the spectrum (Table 2). Among the Fabaceae subfamilies, Caesalpinioideae exhibited the largest number of pollen types (six): *Bauhinia*, *Chamaecrista*, *Copaifera*, *Schizolobium*, *Sclerolobium paniculatum* and *Senna*. The pollen types from the "Undetermined" class occurred in six samples.

The pollen types with a greater than 50% occurrence in the samples (very frequent) were: *Warszewiczia coccinea* (Rubiaceae) (100%), *Cecropia* (Urticaceae) and *Clidemia hirta* (Melastomataceae) (71% each), *Byrsonima* (Malpighiaceae), *Emilia fosbergii* (Asteraceae), *Microtea* (Phytolaccaceae), *Myrcia* (Myrtaceae) and *Stryphnodendron* (Fabaceae/Mimosoideae) (57% each). Additionally, the spectrum revealed 15 frequent, 9 infrequent and 14 rare pollen types (Table 2).

The number of pollen types identified for each honey sample varied between 4 and 18 (13 ± s.d. 4 (n = 14)). *Clidemia hirta* occurred as the predominant pollen in three samples in February, April and November 2011. Each of the pollen types *Cecropia* (Urticaceae), *Warszewiczia coccinea*, *Solanum paniculatum* (Solanaceae) and *Byrsonima* occurred as the predominant pollen in only one sample in October 2010, July and August 2011 and January 2012. The following occurred as secondary pollens: *Clidemia hirta* (five samples); *Cecropia* (three samples); *Myrcia*, *W. coccinea* and *Tapirira guianensis* (Anacardiaceae) (two samples each); and *Byrsonima*, *Clathrotropis nitida* (Fabaceae/Papilionoideae), *Microtea*, *Protium* (Burseraceae), *Senna* and *S. paniculatum* (one sample each). Most pollen types identified occurred in minor classes (<16%), similar to the results obtained for the Belterra honey samples. All honeys from Santarém were classified as polyfloral due to the reasons stressed previously. One honey sample from August/2011 showed a high amount of *Solanum paniculatum* (93.39%), suggesting a monofloral honey, however, this plant species is predominantly polliniferous.

Using the same standard adopted for Belterra, the data demonstrated two main pollen associations for the Santarém honey: (*i*) *Byrsonima* - *Cecropia* - *Clidemia hirta* - *Myrcia* - *Solanum paniculatum* - *Tapirira guianensis* - *Warszewiczia coccinea*; (*ii*) *Clathrothopis nitida* - *Microtea* - *Protium* - *Senna*.

The H' index ranged from 0.3 (August 2011) to 2.0 (March and October 2011), with a mean of 1.6 ± s.d. 0.4 (*n* = 14). The evenness index (J') ranged from 0.2 (August 2011) to 0.8 (January and September 2011) (Table 2 and Fig. 4). The mean Pielou's evenness index (J') for the Santarém honey spectrum was 0.6 ± s.d. 0.1 (*n* = 14), the same value obtained for Belterra, which also indicated a tendency toward the homogeneous use of the pollen resources available in the area.

Pollen concentration in ten grams of honey

The pollen concentration indicates the estimated total number of pollen grains per ten grams of honey (TNP-10gr). In the samples from the municipality of Belterra, the TNP-10gr ranged between 19,388 (Group I) and 950,347 (Group IV). Most of the honeys obtained from this study area were Group II (12 samples) and two samples were Group III, corresponding to September 2010 and November 2011. Groups I and IV contained only one sample each, corresponding to April and June 2011, respectively (Table 3).

The TNP-10gr obtained for the honey from Santarém ranged from 12,491 (Group I) to 787,072 (Group IV). There were two samples classified as Group I (June and September 2011), three samples classified as Group II (March, July and October 2011), six samples classified as Group III (October 2010, January, February, August and November 2011 and January 2012) and three samples classified as Group IV (November and December 2010 and April 2011) (Table 3).

None of the samples analysed in this study were classified as Group V (>1,000,000). In both areas studied, greater variation in the recorded frequency classes (m, im, s and p) of pollen types was observed in the samples from the concentration Groups II and III. When concentration groups were compared among themselves and by location, the important minor pollen class predominated in terms of the number of records in the samples. The set of samples from Santarém (Group I) differed because most of the records were in the minor pollen class (Fig. 5).

Table 2. Pollen spectrum, percentage and classes of occurrence, diversity and evenness indexes in honey samples from *Tetragonisca angustula* (Latreille, 1811) collected in Santarém, Lower Amazon, Pará, Brazil. PO: Percentage of Occurrence. Classes of Occurrence (CO): R, rare (<10%); I, infrequent (10 - 20%); F, frequent (21 - 50%); VF, very frequent (>50%). Frequency classes: p, predominant pollen (>45%); s, secondary pollen (16 - 45%); im, important minor pollen (3 - 15%); m, minor pollen (<3%). *H'*, Shannon-Weaver Diversity Index; *J'*, Pielou's Index.

Plant Family	Pollen Type	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Mar, 2011	Apr, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Jan, 2012	PO (%)	CO
Acanthaceae	Acanthaceae type	–	–	–	–	–	–	–	–	im	–	–	–	–	–	7	R
Achariaceae	*Lindackeria paludosa*	–	–	–	–	–	–	–	–	–	–	–	–	m	–	7	R
Amaranthaceae	*Alternanthera*	–	–	–	–	–	m	m	–	–	–	im	m	m	–	36	F
Anacardiaceae	*Tapirira guianensis*	m	s	s	m	m	m	m	–	–	–	–	–	–	–	50	F
Araliaceae	*Schefflera morototoni*	–	–	–	–	–	–	m	–	–	–	m	m	–	–	21	F
Arecaceae	*Attalea speciosa*	–	–	–	–	–	–	–	–	m	–	–	m	–	m	21	F
	Mauritia flexuosa	–	–	–	–	–	–	–	–	–	–	–	–	m	–	7	R
Asteraceae	*Emilia fosbergii*	–	m	m	im	m	m	m	–	m	–	–	–	im	–	57	VF
Bignoniaceae	*Tabebuia*	–	–	–	–	–	m	m	–	–	m	im	im	–	–	36	F
	Bignoniaceae type	–	–	–	–	–	–	–	–	–	–	–	im	–	–	7	R
Bixaceae	*Bixa orellana*	–	–	–	–	m	–	–	–	–	–	–	–	–	–	7	R
Burseraceae	*Protium*	–	–	m	–	im	im	m	s	m	–	–	–	m	–	50	F
Euphorbiaceae	Euphorbiaceae type	–	–	–	–	–	–	–	–	–	–	–	–	m	im	14	I
Fabaceae	Fabaceae type 1	im	im	–	–	–	–	–	–	–	–	–	–	–	–	14	I
	Fabaceae type 2	–	im	–	–	–	–	–	–	–	–	–	–	–	–	7	R
Fabaceae - C (Caesalpinioideae)	*Bauhinia*	–	–	–	–	–	–	–	–	–	–	–	m	–	–	7	R
	Chamaecrista	–	–	–	im	im	m	–	–	–	–	–	m	–	–	29	F
	Copaifera	–	–	m	m	m	m	m	–	–	–	–	–	–	–	36	F

Table 2 (Continuation)

Plant Family	Pollen Type	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Mar, 2011	Apr, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Jan, 2012	PO (%)	CO
	Schizolobium	–	m	im	–	–	–	–	–	–	–	–	–	–	–	14	I
	Sclerolobium paniculatum	im	im	m	–	–	–	–	–	–	–	–	–	–	–	21	F
	Senna	–	im	–	s	–	–	–	m	im	–	–	m	–	–	36	F
Fabaceae - M	*Inga*	–	–	–	m	–	–	–	–	–	–	–	–	–	–	7	R
(Mimosoideae)	*Stryphnodendron*	m	m	–	–	m	m	–	–	–	–	im	im	m	m	57	VF
Fabaceae - P	*Cratylia*	–	–	–	–	–	–	–	–	–	–	–	m	–	–	7	R
(Papilionoideae)	*Clathrotropis nitida*	im	im	s	–	–	–	–	–	–	–	–	–	–	–	21	F
	Desmodium	–	–	im	–	–	–	–	–	–	–	–	–	–	–	7	R
Gentianaceae	*Schultesia*	–	–	–	–	–	–	–	–	–	–	–	m	–	–	7	R
Lacistemataceae	*Lacistema*	–	–	–	–	–	–	–	–	–	–	–	m	im	m	21	F
Lamiaceae	*Hyptis*	–	–	–	–	–	m	m	–	–	–	–	–	–	–	14	I
Malpighiaceae	Malpighiaceae type	m	–	–	–	–	–	–	–	–	–	–	–	–	–	7	R
	Byrsonima	–	–	–	im	im	im	–	–	im	–	m	m	s	p	57	VF
Malvaceae	*Ceiba*	–	–	–	–	–	–	–	im	im	–	–	–	–	–	14	I
Melastomataceae	*Clidemia hirta*	m	s	s	s	p	s	p	s	–	–	–	–	p	im	71	VF
Moraceae	*Brosimum*	–	–	–	–	–	–	im	im	–	–	–	–	–	–	14	I
Myrtaceae	*Myrcia*	–	–	–	–	m	m	m	m	–	–	s	s	m	m	57	VF
	Syzygium malaccense	–	–	–	–	–	–	–	–	–	–	–	–	m	im	14	I
Passifloraceae	*Turnera ulmifolia*	–	–	–	–	–	–	–	–	–	–	m	–	–	–	7	R
Phyllanthaceae	*Phyllanthus*	–	–	–	m	–	–	–	–	–	–	–	–	–	–	7	R
Phytolaccaceae	*Microtea*	im	m	–	–	m	im	m	im	s	–	–	m	–	–	57	VF
Poaceae	Poaceae type	–	–	–	–	–	–	–	im	–	–	–	–	m	–	14	I
Rubiaceae	*Borreria verticillata*	–	–	–	–	m	m	m	–	–	–	–	–	–	m	29	F
	Warszewiczia coccinea	im	m	im	s	im	im	im	m	p	m	s	im	im	im	100	VF
Solanaceae	*Solanum paniculatum*	–	–	–	im	–	–	s	im	–	p	–	–	m	m	43	F

Table 2 (Continuation)

Plant Family	Pollen Type	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Mar, 2011	Apr, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Jan, 2012	PO (%)	CO
Urticaceae	*Cecropia*	p	m	m	–	–	m	m	–	–	im	s	s	m	s	71	VF
Verbenaceae	*Lippia*	–	–	–	–	im	m	–	–	–	–	–	–	–	–	14	I
Undetermined		m	–	–	im	im	s	im	–	m	–	–	–	–	–	43	F
H'		1,6	1,8	1,7	1,9	1,6	2,0	1,4	1,7	1,4	0,3	1,8	2,0	1,6	1,6	–	–
J'		0,7	0,7	0,7	0,8	0,6	0,7	0,5	0,7	0,6	0,2	0,8	0,7	0,6	0,6	–	–

Table 3. Pollen concentration estimated in ten grams of *Tetragonisca angustula* (Latreille, 1811) honey in Belterra and Santarém, Lower Amazon, Pará, Brazil.

	Sep, 2010	Oct, 2010	Nov, 2010	Dec, 2010	Jan, 2011	Feb, 2011	Mar, 2011	Apr, 2011	May, 2011	Jun, 2011	Jul, 2011	Aug, 2011	Sep, 2011	Oct, 2011	Nov, 2011	Dec, 2011	Jan, 2012
	TNP-10gr(a)																
Belterra	149,172	89,628	81,326	72,503	48,522	72,241	−	19,388	34,094	950,347	86,864	32,926	73,538	92,038	367,115	99,157	26,892
Santarém	−	224,507	501,623	787,072	35,373	471,186	32,264	500,348	−	14,903	35,663	255,131	12,491	21,634	184,047	−	213,512
	Concentration Groups																
Belterra	III	II	II	II	II	II	−	I	II	IV	II	II	II	II	III	II	II
Santarém	−	III	IV	IV	III	III	II	IV	-	I	II	III	I	II	III	−	III

(a)TNP-10gr: total number of pollen grains in ten grams of honey. Roman numerals indicate concentration groups (Maurizio, 1976; Louveaux et al., 1978): Group I (<20,000), Group II (20,000 - 100,000), Group III (100,001 - 500,000), Group IV (500,001 - 1,000,000), Group V (>1,000,000).

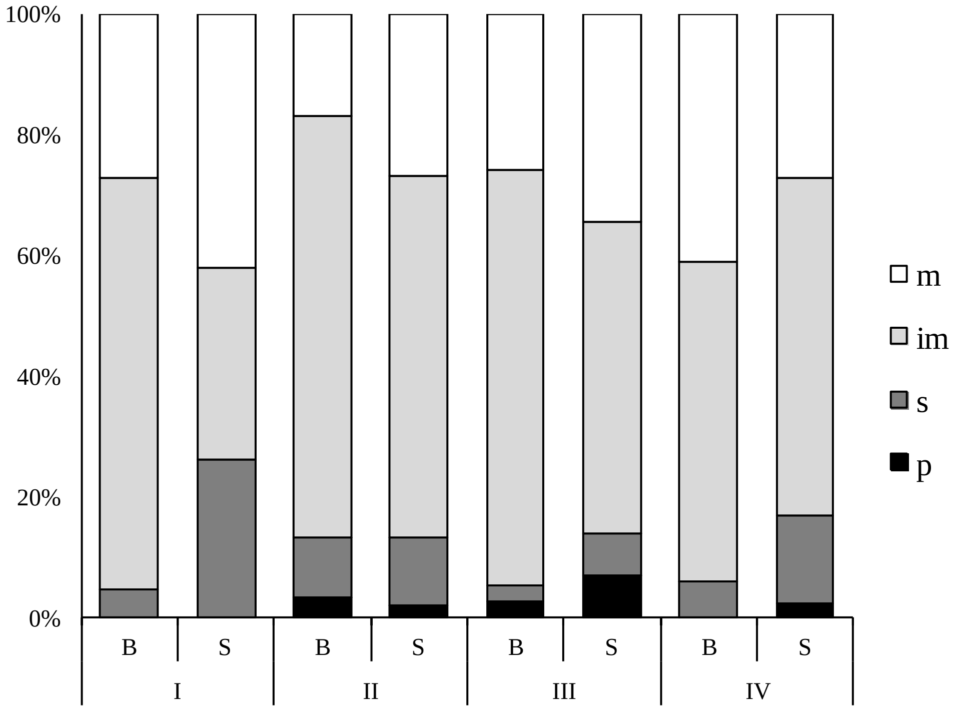


Fig. 5. Mean distribution of pollen type records in honeys from *Tetragonisca angustula* (Latreille, 1811) in Belterra (B) and Santarém (S), Lower Amazon, Pará, Brazil. The Roman numerals represent the concentration groups (Maurizio, 1976; Louveaux *et al.*, 1978) of pollen grains in 10 grams of honey as follows: Group I (<20,000), Group II (20,000-100,000), Group III (100,001-500,000), Group IV (500,001-1,000,000) and Group V (>1,000,000). Frequency classes (Louveaux *et al.* 1978): minor pollen (m; <3%); important minor pollen (im; 3-15%); secondary pollen (s; 16-45%); predominant pollen (p; >45%).

Discussion

Pollen spectra

The number of pollen types recognised in the Belterra and Santarém honey reflects the high number of plant species that maintain the native bee populations in the Amazon region. Previous palynological studies of other species of stingless bees in the Brazilian Amazon also point to a large number of plants used by these insects, which is reflected in the honey pollen spectra (Martins *et al.*, 2011), the corbicular pollen (Kerr *et al.*, 1986/1987; Marques-Souza, 1996; Marques-Souza *et al.*, 2002, 2007; Oliveira *et al.*, 2009) and the stored pollen (Absy *et al.*, 1984; Kerr *et al.*, 1986/1987; Rech and Absy, 2011a,b).

Among these palynological studies, only Rech and Absy (2011a) worked with *T. angustula* in addition to eight other species of stingless bees occurring along the Rio Negro River channel in the Brazilian Amazon. In that study, only two pots of *T. angustula* pollen were analysed; 15 pollen types were identified in one sample and 10 were identified in the other. The pollen types with a frequency greater than 1% were from the following plants: *Cecropia* sp. (Urticaceae), *Piper* sp. (Piperaceae) and *Trymatococcus amazonicus* Poepp. and Endl. (Moraceae). In the Amazon pollen literature, there is a lack of publications regarding *T. angustula* honey, which reinforces the importance of our study.

Iwama and Melhem (1979) performed the main *T. angustula* honey pollen study published in Brazil. The study identified between 11 and 22 plant species represented in the pollen spectra in samples from the State of São Paulo, which is similar to the number determined in this study for the Belterra and Santarém honeys. The main pollen types (predominant and secondary) recorded by Iwama and Melhem (1979) were from species belonging to the families Anacardiaceae (*Schinus terebinthifolius* Raddi), Apiaceae (*Petroselinum hortense* Hoffm.), Asteraceae (*Bidens* sp.), Cannabaceae (*Trema micrantha* (L.) Blume), Euphorbiaceae (*Alchornea triplinervia* (Spreng.) Müll. Arg.), Fabaceae (*Caesalpinia peltophoroides* Benth., *Dalbergia* L. f., *Mimosa daleoides* Benth. e *Piptadenia rigida* Benth.), Malpighiaceae (*Byrsonima intermedia* A. Juss.), Melastomataceae (*Tibouchina chamissoana* Cogn.), Moraceae (*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj.

& Wess. Boer), Myrtaceae (*Eucalyptus* sp.), Paulowniaceae (*Paulownia tomentosa* (Thunb.) Steud.) and Solanaceae (*Solanum* sp.). For the State of Bahia Novais *et al.* (2006) pointed out that *Alternanthera brasiliana*, *Herissantia*, *Mitracarpus*, *Myrcia*, *Sida*, *Zornia* e *Ziziphus joazeiro* were the most expressive pollen types in honeys of *T. angustula*.

In the early 1990s, a review of the important plants for stingless and Africanised bees in the neotropical region, published by Ramalho *et al.* (1990), included a list of 288 species considered relevant for the supply of pollen and/or nectar, especially highlighting the families Anacardiaceae, Arecaceae, Asteraceae, Fabaceae, Euphorbiaceae, Lamiaceae, Melastomataceae, Myrtaceae, Rubiaceae and Solanaceae. Of these, Euphorbiaceae, Fabaceae, Melastomataceae and Rubiaceae belong to the group of the ten most diverse families in the Amazon region, which is the third largest phytogeographic domain in Brazil in terms of angiosperm number (11,349), although the species richness is still undersampled (Hopkins, 2007; Forzza *et al.*, 2010).

For both areas investigated in this study, Fabaceae stood out in terms of the number of pollen types. Cortopassi-Laurino and Gelli (1991) noted the occurrence of the Fabaceae family in *T. angustula* honey from the State of Paraná (with the occurrence of the *Cassia* pollen type) and from the São Paulo State in which the authors identified the pollen types *Myroxylum balsamum* and *Piptadenia*. In addition to being one of the most diverse families in terms of species number in Brazil (2,694 spp., of which 1,458 are endemic) and in the Amazon (1,103 spp.), Fabaceae has three genera that are included among the 30 most diverse in the country, *Mimosa* (323 spp.), *Chamaecrista* (253 spp.) and *Inga* (127 spp.) (Forzza *et al.*, 2010). We identified pollen types from all three genera among the samples analysed in this study. Previous studies have indicated that these genera are also useful to both native and exotic bees in Brazil (Ramalho *et al.*, 1990; Lima *et al.*, 2006; Santos *et al.*, 2006). Although broad scale studies describing plants with potential applications in Amazonian apiculture and meliponiculture are not available, many plant species which occur in the Amazon biome have been reported in bee flora studies from other regions of Brazil. Therefore, we can infer that these species contribute or have the potential to contribute as resources for bees in this region.

In Belterra, the apiary is located near *Byrsonima* spp. crops (known locally as "Muruci"), which are fruit trees common in the region that are cultivated for family consumption or commercial purposes. The proximity of these plants contributed to the pollen types of this genera occurring as the predominant pollen in the honey from that municipality.

The genus *Byrsonima* includes a large number of species in Brazil (approximately 93 spp.) and occurs in all States in the northern region of the country (Mamede, 2011). *Byrsonima* species have been listed on Amazon as suppliers of nectar and pollen for stingless bees of the genera *Cephalotrigona* Schwarz, 1940 (Oliveira *et al.*, 2009; Rech and Absy, 2011a), *Melipona* Illiger, 1806 (Absy *et al.*, 1980; Marques-Souza, 1996; Oliveira *et al.*, 2009), *Scaptotrigona* Moure, 1942 (Marques-Souza *et al.*, 2007) and *Trigona* Jurine, 1807 (Absy *et al.*, 1984; Oliveira *et al.*, 2009), as well as for *A. mellifera* (Marques-Souza *et al.*, 1993; Silva and Absy, 2000).

During several months of collection in Belterra, we observed flowering fields of *Borreria verticillata* (L.) G.Mey (known locally as "relojoeiro"), which are considered by most beekeepers as "weeds" but are a source of pollen and nectar that are highly visited by bees (Freitas and Silva, 2006). Novais and Navarro (2012) observed Rubiaceae species flowering in Belterra year round. Freitas and Silva (2006) argued that the maintenance of honey bee colonies, especially for production purposes, depends on the continuous supply of floral resources. This effect can be achieved through species that bloom all year, such as *Spermacoce capitata* Ruiz & Pav. (Novais and Navarro, 2012), or through species with short flowering periods that are distributed successively and/or with overlapping flowering periods, thereby ensuring a diverse pasture that is constantly available throughout the year.

In the Brazilian Amazon, *Borreria verticillata* occurs in the States of Roraima, Pará, Amazonas and Rondônia (Cabral and Salas, 2011). Studies on abdominal nectar (Absy *et al.*, 1980), stored pollen (Absy *et al.*, 1984), corbicular pollen (Marques-Souza *et al.*, 1993, 2007) and honey (Marques *et al.*, 2011) in this region indicated the presence of this pollen type in the samples. Silva *et al.* (1996) reported that Africanised bees intensively visited *B. verticillata* flowers in Serra de Carajás, Pará State, especially during the periods of transition between the dry and rainy seasons. In Pará, Oliveira *et al.* (1998) identified *B. verticillata* as one of the most significant pollen types for *A. mellifera* in secondary forest areas in the municipality of Igarapé-Açu.

A few plant species characteristic of some Amazonian ecosystems were found into the studied honeys. For example, *Astrocaryum aculeatum* G.Mey, *Attalea speciosa* Mart. ex Spreng., *Mauritia flexuosa* L. f., *Protium* sp. and *Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin correspond to common plant species in Amazon, but pollen types with botanical affinity to these species occurred as minor pollen in a few samples. This may be related to the suppression of native flora, especially in Belterra due to soybean crops, cattle pastures and urbanization. Many of the pollen types recorded in the Belterra and Santarém samples corresponded to ruderal species, typical pioneer species that occupy abandoned areas and open land, belonging to genera such as *Alternanthera*, *Borreria*, *Chamaecrista, Croton, Desmodium*, *Emilia*, *Eriope*, *Microtea*, *Mimosa*, *Scoparia*, *Senna*, *Solanum* and *Zornia*. Studies in Brazil report the contribution of ruderal species, including ornamental and exotic species, as food resources for bees (Carvalho *et al.*, 1999; Silveira, 2012). These plants can play a significant role in the diet of many species of bees in areas where the native vegetation has been suppressed.

Cecropia contributed to the composition of the Santarém honey, especially during the period from September to January. Individuals of the *Cecropia* spp. occupy forest regeneration parcels in the Amazon that arise after tree logging and constitute a characteristic element of secondary forest areas (Zalamea *et al*., 2012). Although *Cecropia* species are considered anemophilous, masking the real nectar sources exploited by bees, when this pollen type is found in honey, it can provide information on the conservation status of the study area and data on the geographical origin of the honey (Oliveira, 2009). A high frequency of *Cecropia* pollen was found in the honey spectra from *A. mellifera* in the States of Bahia (Oliveira, 2009) and Maranhão (Marques *et al.*, 2011). Sosa-Nájera *et al.* (1994) included *Cecropia obtusifolia* Bertol. as a source of nectar for *T. angustula*. Additionally, pollen types related to *Cecropia* commonly predominate in the analysis of bee and stingless bee pollen, as indicated by Imperatriz-Fonseca *et al.* (1984), Ramalho *et al.* (1985, 1990), Cortopassi-Laurino and Ramalho (1988), Marques-Souza *et al.* (1993, 1995), among others, in studies of *A. mellifera*, *Frieseomelitta varia* (Lepeletier, 1836), *Plebeia remota* (Holmberg, 1903), *Melipona (Michmelia) paraensis* Ducke, 1916, *Tetragonisca angustula* and *Trigona spinipes* (Fabricius, 1793).

Clidemia hirta occurred as the predominant or secondary pollen in various honey samples from Santarém, most often between November and June. Among the Melastomataceae, Marques-Souza *et al.* (1995) reported that *Miconia* pollen was one of the most exploited by *Melipona* (*Michmelia*) *paraensis* in Manaus in a secondary forest area containing many species characteristic of primary forest. According to these authors, plants such as these exhibit peaks of pollen production, although they occur in pollen spectra almost continuously throughout the year. Flowering peaks of Melastomataceae species usually occur after periods of rain.

Marques-Souza *et al.* (1995) also recorded pollen from *Myrcia* (Myrtaceae) as one of the most important for stingless bees in the Manaus region. Although flowering was distributed throughout the year, the study demonstrated that *Myrcia* pollen was collected only during part of the flowering period of the species. In the honey samples from Santarém, this pollen type occurred most frequently in the samples collected during September and October and occurred in other months in the minor pollen class. We hypothesize that months with low frequency of this pollen type represent flowering periods of alternative/attractive sources of nectar/pollen for the bees. Other factors may also pressure bees for choosing different feed sources, such as competition caused by honeybees or other stingless bees exploiting the same area.

Warszewiczia coccinea stood out among the honeys from both municipalities. Absy *et al.* (1984) observed this pollen type in pollen samples collected by Trigonini in the Middle Amazon region. Similarly, Absy *et al.* (1980) identified *W. coccinea* (Vahl) Klotzsch as a nectar source for species of stingless bees in the Central Amazon. The authors also observed that this plant flowered in May and August and from October to January.

A number of pollen types occurred as predominant or secondary pollens; however, the percentage occurrence in the samples was below 50%. These pollen types included the following: *Anacardium occidentale*, *Cecropia*, *Chamaecrista*, *Diodia* and *Tapirira guianensis* for Belterra and *Clathrotropis nitida*, *Protium*, *Senna*, *Solanum paniculatum* and *T. guianensis* for Santarém. With the exception of *C. nitida,* the stingless bee literature reports all other pollen types as useful to bees (Absy *et al.*, 1980, 1984; Marques-Souza *et al.*, 1995; Silva and Rebouças, 1998; Santos *et al.*, 2006; Marques-Souza *et al.*, 2007; Marques *et al.*, 2011; Rech and Absy, 2011a). Many sources of pollen and nectar exert a significant contribution over a short period of the year; however, this contribution may constitute alternative recourses for bees, especially during periods of adverse climate when few species flower (Marques-Souza *et al.*, 1995; Freitas and Silva, 2006).

Ecological indices

The mean H' and J' values obtained for the *T. angustula* honey from Santarém and Belterra (H' = 1.6, J' = 0.6, for both municipalities) were similar to the values calculated for the pollen spectrum reported by Novais *et al.* (2006) in a study of honey from the same bee in Bahia in Northeastern Brazil (H' = 1.4, J' = 0.6). The values were also similar to the data reported by Sosa-Nájera *et al.* (1994) in an analysis of honey from *T. angustula* in the regions of Santa Teresita (H' = 1.6, J' = 0.6) and Unión Juárez (H' = 1.5, J' = 0.6), both in the State of Chiapas, southeastern Mexico.

The mean value of Pielou's evenness index obtained in the honey samples from the municipalities of Santarém and Belterra (J' = 0.6) indicated a trend toward homogeneity in the exploitation of the floral resources by *T. angustula* in both areas. A similar phenomenon was observed by Sosa-Nájera *et al.* (1994) in Chiapas, Mexico and by Novais *et al.* (2006) in an area of Caatinga (a type of arid scrubland) in Bahia, Brazil. These values varied according to the resource availability and bee preference. According to Oliveira *et al.* (2009), in areas with low floral richness, such as in gardens and small forests, bees tend to have a reduced pollen niche. This finding may explain the values obtained in Belterra because many ruderal and ornamental species grow near the apiary. In comparison, the Forest School in Santarém, which includes remnants of primary, secondary and tertiary forest, contains fewer ruderal and ornamental species than Belterra.

Compared with Santarém, the samples from Belterra had higher H' values during the period between February and August, which partly coincided with the period of heavy rainfall in the region. *Anacardium occidentale*, *Byrsonima* and *Eriope* occurred as the predominant and secondary pollen types during that period. These pollen types represent the species flowering in the study area (Novais and Navarro, 2012). However, the H' values for the Santarém honey were greater than for the Belterra honey between September and January, which includes the period of low rainfall and high temperature.

Pollen concentration

According to Iwama and Melhem (1979), little or nothing is known about the concentration of pollen grains in Brazilian stingless bees honeys. Studies of the correction factors to estimate the concentration of species under- or over-represented in the pollen spectra are still lacking; studies such as these have been underway in other countries for several decades (Barbier, 1958; Barbier and Pangaud, 1961; Demianowicz, 1964; Lieux, 1981; Moar, 1985; Battesti and Goeury, 1992; Jones and Bryant, 2001).

Comparative data on the amplitude of the estimated concentration of pollen grains in the honey from the *T. angustula* and other bee species (Table 4) demonstrated that the minimum and maximum values recorded for *T. angustula* were close to those obtained by Ramírez-Arriaga and Martinez-Hernandez (2007) in honey from *Scaptotrigona mexicana* (Guérin, 1844), which ranged from 25,472 (Group II) to 938,141 (Group IV) grains/10 g of honey.

Novais *et al.* (2008) investigated honey from *Plebeia* sp. in an area of Caatinga in the State of Bahia and determined that most samples were from Group I (<20,000 grains/10 g of honey). Many of the honey samples from Belterra had values close to the values reported in the Novais study because they were also classified in Group II (20,000-100,000), which is considered normal (Maurizio, 1958; Moar, 1985) in that most honeys fall into this group (Maurizio, 1976).

For the Santarém samples, most belonged to Group III, as did the majority of *Scaptotrigona mexicana* (Guérin, 1844) honeys analysed by Ramírez-Arriaga and Martinez-Hernandez (2007). Species that have small (10-25 μm) or very small (<10 μm) pollen grains (Erdtman, 1952), such as *Byrsonima*, *Cecropia* and *Clidemia*, predominated in the honey from Santarém. According to Demianowicz (1964), the diameter of the pollen grain correlates with its richness in the honey, and the smaller the grain, the greater its prevalence in the samples. In general, honeys with a low pollen grain concentration (Group I) are indicative of underrepresented nectar species (Maurizio, 1976; Moar, 1985; Caccavari and Fagúndez, 2010). Similarly, samples with a high number of pollen grains (>100,000/10 g) may be indicative of overrepresented nectar species (Maurizio, 1976; Moar, 1985).

None of the samples analysed in this study had TNP-10gr values above 1,000,000 (Group V). To date, only studies performed with *A. mellifera* honey in countries such as Australia, Brazil and Mexico have recorded pollen concentrations as elevated as in Group V (Table 4).

Table 4. Comparison of the estimated pollen concentration in ten grams of honey produced by different stingless bee species and *Apis mellifera* L., 1758.

Reference	Bee Species	Country	Min(a)	GMin(b)	Max(c)	GMax(d)
Lieux (1981)	*Apis mellifera* L., 1758	United States	-(e)	I	-(e)	III
Moar (1985)	*A. mellifera*	Australia	9,339	I	1,701,388	V
Ramírez-Arriaga and Martínez-Hernández (2007)	*A. mellifera*	Mexico	2,189(f)	I	2,189(f)	I
	Scaptotrigona mexicana (Guérin, 1844)		25,472	II	938,141	IV
Novais et al. (2008)	*Plebeia* sp.	Brazil	1,349	I	38,026	II
Oliveira (2009)	*A. mellifera*	Brazil	761	I	1,863,875	V
Caccavari and Fagúndez (2010)	*A. mellifera*	Argentine	-(g)	I	-(g)	I
Ramírez-Arriaga et al. (2011)	*A. mellifera*	Mexico	6,757	I	1,049,609	V
Novais and Absy (this study)	*Tetragonisca angustula* (Latreille, 1811)	Brazil	12,491	I	950,347	IV

(a)Min, minimum concentration of pollen grains estimated in 10 grams of honey; (b)GMin, minimum concentration group; (c)Max, maximum concentration of pollen grains estimated in 10 grams of honey; (d)GMax, maximum concentration group; (e)only groups of concentration were informed; (f)the authors only analyzed one sample.

Conclusion

T. angustula demonstrated a polyletic foraging behaviour during the study period in both municipalities, although during a number of months, the collection of floral resources was restricted to a few species. The ecological indices indicated some diversity in the pollen spectra of the honeys, with a tendency toward homogeneity in the use of floral sources. Most of the samples demonstrated concentrations of between 20,000 and 100,000 pollen grains for every 10 g of honey, which is within the normal range established in the palynological literature.

Acknowledgements

We are grateful to Mr. Geancarlo V. Gouveia, president of the Meliponiculturists Association of the Municipality of Belterra, for making available the private meliponary colonies for this research; to the SEMED of Santarém for authorising the collection of samples at the Forest School; to Dr. Favízia Freitas de Oliveira (UFBA), for identifying the stingless bee species; and to Dr. Cláudia Elena Carneiro (UEFS), Dr. Lenise Vargas Flôres da Silva (UFOPA) and M.Sc. Chieno Suemitsu (UFOPA), the research laboratory coordinators who kindly allowed the analyses to be performed at these locations. We thank the Brazilian National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq) for the support (Processes 575747/2008-0 and 143084/2009-7). We are also indebted with two anonymous referees for their helpful comments and criticisms.

References

ABSY, M L; BEZERRA, E B; KERR, W E (1980) Plantas nectaríferas utilizadas por duas espécies de *Melipona* da Amazônia. *Acta Amazonica* 10(2): 271-281.

ABSY, M L; CAMARGO, J M F; KERR, W E; MIRANDA, I P A (1984) Espécies de plantas visitadas por Meliponinae (Hymenoptera; Apoidea), para coleta de pólen na região do médio Amazonas. *Revista Brasileira de Biologia* 44(2): 227-237.

ALBUQUERQUE, M F; SOUZA, E B; OLIVEIRA, M C F; SOUZA JÚNIOR, J A (2010) Precipitação nas mesorregiões do estado do Pará: climatologia, variabilidade e tendências nas últimas décadas (1978-2008). *Revista Brasileira de Climatologia* 6(6): 151-168.

ANDRADA, A; VALLE, A; ARAMAYO, E; LAMBERTO, S; CANTAMUTTO, M (1998) Analisis polinico de las mieles de las sierras australes de la provincia de Buenos Aires, Argentina. *Investigación Agraria. Producción y Protección Vegetales* 13(3): 265-275.

BARBIER, E (1958) Examen pollinique de quelques miels unifloraux. *Annales de l'Abeille* 1(2): 73-76. http://dx.doi.org/10.1051/apido:19580201

BARBIER, E; PANGAUD, C-Y (1961) Origine botanique et caractéristiques physicochimiques des miels. *Annales de l'Abeille* 4(1): 51-65. http://dx.doi.org/10.1051/apido:19610103

BATTESTI, M-J; GOEURY, C (1992) Efficacité de l'analyse mélitopalynologique quantitative pour la certification des origines géographique et botanique des miels: le modèle des miels corses. *Review of Palaeobotany and Palynology* 75: 77-102. http://dx.doi.org/10.1016/0034-6667(92)90151-6

BENNINGHOF, W S (1962) Calculation of pollen and spore density in sediments by addition of exotic pollen in known quantities. *Pollen et Spores* 4: 332-333.

BRYANT, JR., V M (2001) Pollen contents of honey. *CAP Newsletter* 24(1): 10-24.

CABRAL, E; SALAS, R (2011) *Borreria*. In *Lista de Espécies da Flora do Brasil*. Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/2011/FB020712>. Accessed on 25 September 2012.

CACCAVARI, M; FAGÚNDEZ, G (2010) Pollen spectra of honeys from the Middle Delta of the Paraná River (Argentina) and their environmental relationship. *Spanish Journal of Agricultural Research* 8(1): 42-52. http://doi:10.5424/1142

CAMARGO, J M F; PEDRO, S R M (2012) Meliponini Lepeletier, 1836. In *Moure, J S; Urban, D; Melo, G A R (Orgs). Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region - online version*. Available at <http://www.moure.cria.org.br/catalogue>. Accessed on 24 Sep 2012.

CARREIRA, L M M; LOPES, J R C; SILVA, M F; NASCIMENTO, L A S (1996) *Catálogo de pólen das leguminosas da Amazônia brasileira*. Museu Paraense Emílio Goeldi, Belém, PA. 137 p.

CARVALHO, C A L; MARCHINI, L C; ROS, P B (1999) Fontes de pólen utilizadas por *Apis mellifera* L. e algumas espécies de Trigonini (Apidae) em Piracicaba (SP). *Bragantia* 58(1): 49-56. http://dx.doi.org/10.1590/S0006-87051999000100007

CORTOPASSI-LAURINO, M; RAMALHO, M (1988) Pollen harvest by *Apis mellifera* and *Trigona spinipes* in São Paulo: Botanical and ecological views. *Apidologie* 19(1): 1-24. http://dx.doi.org/10.1051/apido:19880101

CORTOPASSI-LAURINO, M; GELLI, G S (1991) Analyse pollinique, propriétés physico-chimiques et action antibactérienne des miels d'abeilles africanisées *Apis mellifera* et de Méliponinées du Brésil. *Apidologie* 22: 61-73. http://dx.doi.org/10.1051/apido:19910108

DE KLERK, P; JOOSTEN, H (2007) The difference between pollen types and plant taxa: a plea for clarity and scientific freedom. *Eiszeitalter und Gegenwart* 56(3): 162-171.

DEMIANOWICZ, Z (1964) Charakteristik der einartenhonige. *Annales de l'Abeille* 7(4): 273-288. http://dx.doi.org/10.1051/apido:19640401

EMBRAPA-EMPRESA BRASILEIRA DE PESQUISA AGROPECUÁRIA (2012) *Banco de dados climáticos do Brasil*. Available on: <http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=pa&COD=121>. Accessed on 5 October 2012.

ERDTMAN, G (1952) *Pollen morphology and plant taxonomy. Angiosperms*. Almqvist & Wiksell, Stockholm. 539 pp.

ERDTMAN, G (1960) The acetolysis method - a revised description. *Svensk Botanisk Tidskrift* 54(4): 561-564.

FAO-FOOD AND AGRICULTURE ORGANISATION (2010) *Global forest resources assessment 2010 – main report*. Food and Agriculture Organization of the United Nations, Rome. 340 pp.

FEARNSIDE, P M (2001) Soybean cultivation as a threat to the environment in Brazil. *Environmental Conservation* 28(1): 23-38. doi:10.1017/S0376892901000030.

FORZZA, R C; BAUMGRATZ, J F A; COSTA, A; HOPKINS, M; LEITMAN, P M; LOHMANN, L G; MARTINELLI, G; MORIM, M P; COELHO, M A N; PEIXOTO, A L; PIRANI, J R; QUEIROZ, L P; STEHMANN, J R; WALTER, B M T; ZAPPI, D (2010) As angiospermas do Brasil. In *Forzza, R.C. et al. (Orgs). Catálogo de plantas e fungos do Brasil. v.1*. Andrea Jakobsson Estúdio/Instituto de Pesquisas Jardim Botânico do Rio de Janeiro; Rio de Janeiro, RJ. pp. 78–89.

FREITAS, B M; IMPERATRIZ-FONSECA, V L; MEDINA, L M; KLEINERT, A M P; GALETTO, L; NATES-PARRA, G; QUEZADA-EUÁN, J J G (2009) Diversity, threats and conservation of native bees in the Neotropics. *Apidologie* 40(3): 332–346. http://dx.doi.org/10.1051/apido/2009012

FREITAS, B M; SILVA, E M S (2006) Potencial apícola da vegetação do Semi-Árido brasileiro. In *Santos, F A R (Ed). Apium plantae*. IMSEAR; Recife, PE. pp. 19–32.

HAMMER, Ø; HARPER, D A T; RYAN, P D (2001) PAST: Palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9 pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

HOPKINS, M J G (2007) Modelling the known and unknown plant biodiversity of the Amazon Basin. *Journal of Biogeography* 34: 1400-1411. http://dx.doi.org/10.1111/j.1365-2699.2007.01737.x

IMPERATRIZ-FONSECA, V L; KLEINERT-GIOVANNINI, A; CORTOPASSI-LAURINO, M; RAMALHO, M (1984) Hábitos de coleta de *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Boletim de Zoologia da Universidade de São Paulo* 8: 115-131.

INPE-INSTITUTO NACIONAL DE PESQUISAS ESPACIAIS (2012) *Taxas anuais do desmatamento - 1998 até 2011*. Available at <http://www.obt.inpe.br/prodes/prodes_1988_2011.htm>. Accessed on 5 October 2012.

IWAMA, S; MELHEM, T S (1979) The pollen spectrum of the honey of *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Apidologie* 10(3): 275-295. http://dx.doi.org/10.1051/apido:19790305

JONES, G D; BRYANT, JR., V M (1996) Melissopalynology. In *Jansonius, J; McGregor, D C (Eds). Palynology: principles and applications, v. 3.* AASP Foundation; Dallas, TX. pp. 933–938.

JONES, G D; BRYANT, JR., V M (2001) Is one drop enough? In *Goodman, D K; Clarke, R T (Eds). Proceedings of the 9th International Palynological Congress, 1996*. AASP Foundation; Houston, TX. pp. 483–487.

JONES, G D; BRYANT, JR., V M (2004) The use of ETOH for dilution of honey. *Grana* 43(3): 174-182. http://dx.doi.org/10.1080/00173130410019497

JOOSTEN, H; DE KLERK, P (2002) What's in a name? Some thoughts on pollen classification, identification, and nomenclature in Quaternary palynology. *Review of Palaeobotany and Palynology* 122: 29-45. http://dx.doi.org/10.1016/S0034-6667(02)00090-8

KERR, W E; ABSY, M L; MARQUES-SOUZA, A C (1986/1987) Espécies nectaríferas e poliníferas utilizadas pela abelha *Melipona compressipes fasciculata* (Meliponinae, Apidae) no Maranhão. *Acta Amazonica* 16/17: 145-156.

LAURANCE, W F; ALBERNAZ, A K M; FEARNSIDE, P M; VASCONCELOS, L V; FERREIRA, L V (2004) Deforestation in Amazonia. *Science* 304: 1109-1111. http://dx.doi.org/10.1126/science.304.5674.1109b

LIEUX, M H (1981) An analysis of Mississipi (U.S.A.) honey: pollen, color and moisture. *Apidologie* 12(2): 137-158. http://dx.doi.org/10.1051/apido:19810205

LIMA, L C L; SANTOS, F A R; SILVA, F H M (2006) Morfologia polínica de espécies de *Mimosa* L. (Leguminosae) apícolas do semi-árido. In *Santos, F A R (Ed). Apium plantae*. IMSEAR; Recife, PE. pp. 87–102.

LIMA, L C L (2007) *Espécies de* Mimosa *L. (Leguminosae) do semi-árido nordestino: palinologia, fenologia, biologia floral e potencial apícola*. Ph.D. Thesis (Botany), Univ. Estadual de Feira de Santana; Feira de Santana, BA, Brazil.

LINDAUER, M; KERR, W E (1960) Communication between the workers of stingless bees. *Bee World* 41: 29-41.

LOUVEAUX, J; MAURIZIO, A; VORWOHL, G (1970) Methods of mellissopalynology. *Bee World* 51: 125-138.

LOUVEAUX, J; MAURIZIO, A; VORWOHL, G (1978) Methods of melissopalynology. *Bee World* 59: 139-153.

LUDWIG, J A; REYNOLDS, J F (1988) *Statistical ecology: a primer on methods and computing*. John Wiley & Sons; New York, NY. 337 pp.

LUTIER, P M; VAISSIÈRE, B E (1993) An improved method for pollen analysis of honey. *Review of Palaeobotany and Palynology* 78: 129-144. http://dx.doi.org/10.1016/0034-6667(93)90019-Q

MAMEDE, M C H (2011) *Byrsonima*. *In: Lista de Espécies da Flora do Brasil*. Jardim Botânico do Rio de Janeiro. Available in <http://floradobrasil.jbrj.gov.br/2011/FB 008827>. Accessed on 25 September 2012.

MARQUES, L J P; MUNIZ, F H; LOPES, G S; SILVA, J M (2011) Levantamento da flora apícola em Santa Luzia do Paruá, Sudoeste da Amazônia, Maranhão. *Acta Botanica Brasilica* 25(1): 141-149.

MARQUES-SOUZA, A C (1996) Fontes de pólen exploradas por *Melipona compressipes manaosensis* (Apidae: Meliponinae), abelha da Amazônia Central. *Acta Amazonica* 26(1/2): 77-86.

MARQUES-SOUZA, A C; ABSY, M L; CONDÉ, P A A; COELHO, H A (1993) Dados da obtenção do pólen por operárias de *Apis mellifera* no município de Ji-Paraná (RO), Brasil. *Acta Amazonica* 23(1): 59-76.

MARQUES-SOUZA, A C; ABSY, M L; KERR, W E; AGUILERA PERALTA, F J (1995) Pólen coletado por duas espécies de meliponíneos (Hymenoptera: Apidae) da Amazônia. *Revista Brasileira de Biologia* 55(4): 855-864.

MARQUES-SOUZA, A C; MIRANDA, I P A; MOURA, C O; RABELO, A; BARBOSA, E M (2002) Características morfológicas e bioquímicas do pólen coletado por cinco espécies de meliponíneos da Amazônia Central. *Acta Amazonica* 32(2): 217-229.

MARQUES-SOUZA, A C; ABSY, M L; KERR, W E (2007) Pollen harvest features of the Central Amazonian bee *Scaptotrigona fulvicutis* Moure 1964 (Apidae: Meliponinae), in Brazil. *Acta Botanica Brasilica* 21(1): 11-20. http://dx.doi.org/10.1590/S0102-33062007000100002

MARTINS, A C L; RÊGO, M M C; CARREIRA, L M M; ALBUQUERQUE, P M C (2011) Espectro polínico de mel de tiúba (*Melipona fasciculata* Smith, 1854, Hymenoptera, Apidae). *Acta Amazonica* 41(2): 183-190.

MAURIZIO, A (1958) Beitraege zur quantitativen pollenanalyse des honigs. 3. - Absoluter gehalt pflanzlicher bestandteile in esparsette-, luzerne-, orangen- und rapshonigen. *Annales de l'Abeille* 1(2): 93-106. http://dx.doi.org/10.1051/apido:19580204

MAURIZIO, A (1976) Microscopy of honey. In *Crane, E (Ed). Honey: a comprehensive survey*. Heinemann; London. pp. 240–257.

MOAR, N T (1985) Pollen analysis of New Zealand honey. *New Zealand Journal of Agricultural Research* 28: 39-70. http://dx.doi.org/10.1080/00288233.1985.10426997

MOLAN, P (1998) The limitations of the methods of identifying the floral source of honeys. *Bee World* 79: 59-68.

NEPSTAD, D; SOARES-FILHO, B S; MERRY, F; LIMA, A; MOUTINHO, P; CARTER, J; BOWMAN, M; CATTANEO, A; RODRIGUES, H; SCHWARTZMAN, S; MCGRATH, D G; STICKLER, C M; LUBOWSKI, R; PIRIS-CABEZAS, P; RIVERO, S; ALENCAR, A; ALMEIDA, O; STELLA, O (2009) The end of deforestation in the Brazilian Amazon. *Science* 326: 1350-1451. http://dx.doi.org/10.1126/science.1182108

NOVAIS, J S; NAVARRO, E D M (2012) A flowering calendar of plants growing near hives of native bees in the Lower Amazon region, Pará State, Brazil. *Uludağ Bee Journal* 12(3): 83-88.

NOVAIS, J S; LIMA, L C L; SANTOS, F A R (2006) Espectro polínico de méis de *Tetragonisca angustula* Latreille, 1811 coletados na caatinga de Canudos, Bahia, Brasil. *Magistra* 18(4): 257-264.

NOVAIS, J S; LIMA, L C L; SANTOS, F A R (2008) Uso de marcador exótico em investigações palinológicas de amostras de mel e pólen coletadas na caatinga de Canudos, Nordeste do Brasil. In *Anais eletrônicos da 60ª. Reunião Anual da SBPC, Campinas, Brazil, 13-18 July 2008*. Available at <http://www.sbpcnet.org.br/livro/60ra>. Accessed on 5 November 2012.

OLIVEIRA, F P M; CARREIRA, L M M; JARDIM, M A G (1998) Carcaterização polínica do mel de *Apis mellifera* L. em área de floresta secundária no muncípio de Igarapé-Açu - Pará. *Boletim do Museu Paraense Emílio Goeldi, série Botânica* 14(2): 157-176.

OLIVEIRA, F P M; ABSY, M L; MIRANDA, I S (2009) Recurso polínico coletado por abelhas sem ferrão (Apidae, Meliponinae) em um fragmento de floresta na região de Manaus - Amazonas. *Acta Amazonica* 39(2): 505-518. http://dx.doi.org/10.1590/S0044-59672009000300004

OLIVEIRA, P P (2009) *Análise palinológica de amostras de mel de* Apis mellifera *L. produzidas no estado da Bahia*. Ph.D. Thesis (Botany), Univ. Estadual de Feira de Santana; Feira de Santana, BA, Brazil.

PIELOU, E C (1977) *Mathematical ecology*. John Wiley & Sons; New York, NY. 385 pp.

RAMALHO, M; IMPERATRIZ-FONSECA, V L; KLEINERT-GIOVANNINI, A; CORTOPASSI-LAURINO, M (1985) Exploitation of floral resources by *Plebeia remota* Holmberg (*Apidae, Meliponinae*). *Apidologie* 16(3): 307-330. http://dx.doi.org/10.1051/apido:19850306

RAMALHO, M; KLEINERT-GIOVANNINI, A; IMPERATRIZ-FONSECA, V L (1990) Important bee plants for stingless bees (*Melipona* and Trigonini) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. *Apidologie* 21: 469-488. http://dx.doi.org/10.1051/apido:19900508

RAMÍREZ-ARRIAGA, E; MARTÍNEZ-HERNÁNDEZ, E (2007) Melitopalynological characterization of *Scaptotrigona mexicana* Guérin (Apidae: Meliponini) and *Apis mellifera* L. (Apidae: Apini) honey samples in Northern Puebla State, Mexico. *Journal of The Kansas Entomological Society* 80(4): 377-391.

RAMÍREZ-ARRIAGA, E; NAVARRO-CALVO, L A; DÍAZ-CARBAJAL, E (2011) Botanical characterisation of Mexican honeys from a subtropical region (Oaxaca) based on pollen analysis. *Grana* 50(1): 40-54. http://dx.doi.org/10.1080/00173134.2010.537767

RECH, A R; ABSY, M L (2011a) Pollen sources used by species of Meliponini (Hymenoptera: Apidae) along the Rio Negro channel in Amazonas, Brazil. *Grana* 50(2): 150-161. http://dx.doi.org/10.1080/00173134.2011.579621

RECH, A R; ABSY, M L (2011b) Pollen storages in nests of bees of the genera *Partamona*, *Scaura* and *Trigona* (Hymenoptera, Apidae). *Revista Brasileira de Entomologia* 55(3): 361-372. http://dx.doi.org/10.1590/S0085-56262011005000026

ROUBIK, D W; MORENO P., J E (1991) *Pollen and spores of Barro Colorado Island*. Missouri Botanical Garden; St. Louis, MO. (Monographs in Systematic Botany, v. 36)

ROUBIK, D; MORENO P., E (2009) *Trigona corvina*: an ecological study based on unusual nest structure and pollen analysis. *Psyche* Vol. 2009, Article ID 268756, 7 pages, doi:10.1155/2009/268756.

SANTOS, F A R; OLIVEIRA, J M; OLIVEIRA, P P; LEITE, K R B; CARNEIRO, C E (2006) Plantas do semi-árido importantes para as abelhas. In *Santos, F A R (Ed). Apium plantae*. IMSEAR; Recife, PE. pp. 61–86.

SILVA, S J R; ABSY, M L (2000) Análise do pólen encontrado em amostras de mel de *Apis mellifera* L. (Hymenoptera, Apidae) em uma área de savana de Roraima, Brasil. *Acta Amazonica* 30(4): 579-588.

SILVA, S J R; REBOUÇAS, M A P (1998) Plantas melíferas de Roraima - Parte II. *Boletim do Museu Integrado de Roraima* 4: 31-38.

SILVA, M F F; SECCO, R S; LOBO, M G A (1996) Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. *Acta Amazonica* 26(1/2): 17-44.

SILVEIRA, F A; MELO, G A R; ALMEIDA, E A B (2002) *Abelhas brasileiras: sistemática e identificação*. Fernando A. Silveira; Belo Horizonte. 253 pp.

SILVEIRA, T A (2012) *Caracterização sazonal do pólen apícola quanto à origem botânica, aspectos físico-químicos e elementos traços como bioindicadora de poluição ambiental*. M.Sc. Diss. (Entomology), Univ. de São Paulo Escola Superior de Agricultura "Luiz de Queiroz"; Piracicaba, SP, Brazil.

SORKUN, K; DOĞAN, C (2002) The importance of the total number of pollen types in 10 gr of honey in distinguishing between natural honey and artificial honey produced in Turkey. *Mellifera* 2-3: 34-38.

SOSA-NÁJERA, M S; MARTÍNEZ-HENÁNDEZ, E; LOZANO-GARCÍA, M S; CUADRIELLO-AGUIAR, J I (1994) Nectaropolliniferous sources used by *Trigona* (*Tetragonisca*) *angustula* in Chiapas, southern México. *Grana* 33(4): 225-230. http://dx.doi.org/10.1080/00173139409429003

STOCKMARR, J (1971) Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13(4): 615-621.

VELOSO, H P; RANGEL FILHO, A L R; LIMA, J C A (1991) *Classificação da vegetação brasileira, adaptada a um sistema universal*. IBGE, Departamento de Recursos Naturais e Estudos Ambientais; Rio de Janeiro, RJ. 123 pp.

VERGERON, P (1964) Interprétation statistique des résultats en matière d’analyse pollinique des miels. *Annales de l’Abeille* 7(4): 349-364. http://dx.doi.org/10.1051/apido:19640407

YOUNG, W J (1908) *A microscopical study of honey pollen*. United States Bureau of Chemistry, Bulletin 110; Washington, DC. 93 pp.

ZALAMEA, P-C; HEURET, P; SARMIENTO, C; RODRÍGUEZ, M; BERTHOULY, A; GUITET, S; NICOLINI, E; DELNATTE, C; BARTHÉLÉMY, D; STEVENSON, P R (2012) The genus *Cecropia*: a biological clock to estimate the age of recently disturbed areas in the Neotropics. *PLoS ONE* 7: e42643. doi:10.1371/journal.pone.0042643

Capítulo II

Novais, J.S. & Absy, M.L. 2013. Palynological examination of the pollen pots of native stingless bees from the Lower Amazon region in Pará, Brazil. *Palynology* DOI: 10.1080/01916122.2013.787127 (no prelo)

Palynological examination of the pollen pots of native stingless bees from the Lower Amazon region in Pará, Brazil

We performed the first palynological study using pollen stored by *Tetragonisca angustula* (Apidae: Meliponini) in the Lower Amazon region in Pará, Brazil. The samples were directly collected from the pollen pots of *T. angustula* in apiaries located in Belterra and Santarém. The samples were dried, weighed, diluted in warm water and ethanol, centrifuged and then processed following the acetolysis method. After mounting the samples on slides, we identified and counted at least 500 pollen grains per sample. The results indicate that the main pollen combinations in the pollen pots of *T. angustula* in Belterra include pollen from *Byrsonima*, *Cecropia* and *Eriope*, and the combinations from Santarém include pollen from *Byrsonima*, *Cecropia*, *Clidemia hirta*, *Davilla kunthii*, *Myrcia* and *Vismia guianensis*. The most pollen types came from the families Fabaceae and Asteraceae. The pollen diversity (H') ranged from 0.03 to 1.95, and the evenness (J') ranged from 0.04 to 0.79, with the average trend indicating heterogeneity in the collection pattern. Temporary specialisation events typified five of the samples that we studied, directly detecting pollen from *Byrsonima*, *Cecropia* and *Clidemia hirta*. Such events appear to be unrelated to the direct processes of effective pollination. The pollen spectra obtained corroborate pollen types that have previously been described in palynological analyses involving *Tetragonisca angustula* in other areas of Brazil.

Keywords: melissopalynology; entomopalynology; meliponiculture; “jataí” stingless bee; *Tetragonisca angustula*; Meliponini

1. Introduction

Palynology provides data that help to understand the trophic, ecological and evolutionary links between bees and plant groups. Over the past few decades, studies of this type have been infrequent in the Amazon region, a vast area encompassing the planet's largest tropical biodiversity. Palynological analyses of honey (Oliveira et al. 1998; Silva and Rebouças 1998; Silva and Absy 2000; Marques et al. 2011; Martins et al. 2011), nectar from the honey stomach (Absy et al. 1980), corbicular pollen (Marques-Souza 1996, 2010; Marques-Souza et al. 1993, 1995, 1996, 2002, 2007; Oliveira et al. 2009) and food pots (Absy et al. 1984; Kerr et al. 1986–1987; Rech and Absy 2011a, 2011b) have identified the main floral rewards collected by bees in the Amazon region.

Silveira et al. (2002) estimate that the species richness of native bees found in the Amazon rainforest exceeds 100 and that it plays a key role in the maintenance of regional ecosystems through pollination mechanisms. Among native bees, *Tetragonisca angustula* (Latreille, 1811) (Hymenoptera: Apidae: Meliponini) is one of the most popularly known, and is distributed virtually throughout Brazil (Silveira et al. 2002; Camargo and Pedro 2012). Since the 1970s, studies have been published on the pollen and nectar sources sought by this species in Brazil (Iwama and Melhem 1979; Imperatriz-Fonseca et al. 1984; Novais et al. 2006; Morgado et al. 2011; Braga et al. 2012). However, systematic data on the floral preferences of *T. angustula* in the Amazon are not available, except for two studies. Rech and Absy (2011a) palynologically analysed only two food pots of *T. angustula* at the Rio Negro channel region and Novais and Absy (in press) analysed the honey of *T. angustula* from the same localities where the present study was conducted.

The lack of knowledge on the relationship between *T. angustula* and the regional Amazonian flora makes it difficult to propose actions to maintain the native vegetation that is significant for beekeeping. Therefore, we conducted a palynological study of pollen samples that were periodically collected directly from the food pots of *T. angustula* in two areas of the Lower Amazon region. The goal of this study was to evaluate the main pollen sources by analysing the pollen spectrum and to assess the pollen combinations that typify the analysed pollen. The impact of this study is the additional knowledge regarding *T. angustula*’s foraging activities and to provide the beekeeping industry in the interior of the Lower Amazon with information to develop a strategy that alleviates the constant pressure typically endured by regional ecosystems. This pressure is primarily in the form of the advance of deforestation resulting from the rapid expansion of the agricultural frontier toward the interior of the Brazilian Amazon.

2. Materials and methods

2.1 Study area

The study was conducted in two areas of the Lower Brazilian Amazon, in the districts of Santarém and Belterra, Lower Amazon mesoregion of Pará, Brazil (Figure 1). In Belterra (02°38'07"S, 54°55'53.2"W, 126 m.a.s.l.), samples were collected monthly from the food pots of colonies of *T. angustula* (locally known as "jataí" or "mosquito-amarela") in the apiary owned by the chairman of the Beekeepers Association of the District of Belterra (Associação de Meliponicultores do Município de Belterra, AMEMBEL) (Plate 1, figure 1). Samples from Santarém were also collected from the food pots of *T. angustula* in the apiary of the Forest School (Escola da Floresta) (02°30'49.3"S, 54°56'07.7"W, 72 m.a.s.l.), an institution supported by the Borough Education Council (Secretaria Municipal de Educação, SEMED) (Plate 1, figures 2 and 3).

The Lower Amazon encompasses one of six geographic mesoregions in Pará, with an average annual rainfall of approximately 1,900 mm and an average temperature of 25ºC. The regional climate is hot and humid (Am) (Albuquerque et al. 2010; EMBRAPA 2012). The stingless bees apiary (meliponary) in Belterra is located in an urban area, mainly surrounded by ruderal and ornamental vegetation, including native fruit trees, namely "muruci" (craboo) (*Byrsonima* spp., Malpighiaceae). The meliponary of the Forest School (Escola da Floresta) is intended for environmental education activities and occupies an area of mostly secondary forest, with remnants of primary forest, in addition to some ornamental plants.

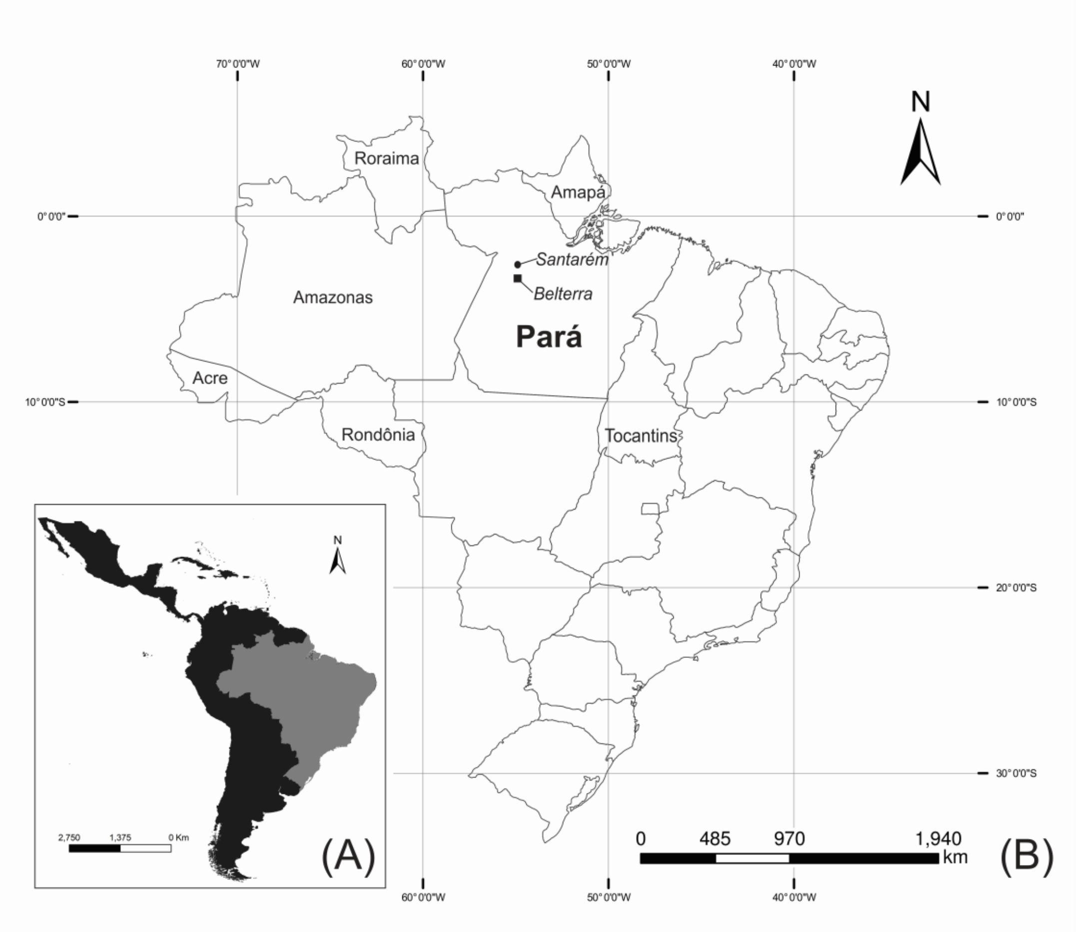


Figure 1. A map showing were Brazil (shaded in light gray) is located within South America (A) and a map (B) showing all the States of Brazil, and the location of the two study sites (Belterra and Santarém). The States of Brazil that are considered the northern region are labeled.

Plate 1. Study areas inside the Lower Amazon region, Pará State (PA), Brazil. Figure 1. Meliponary (stingless bee apiary) sited in the urban zone of Belterra. Figure 2. Hive of *Tetragonisca angustula* located at the Forest School, Santarém, PA. Figure 3. View from the Forest School in Santarém.

2.2 Sample collection and laboratory processing

In Belterra 15 pollen samples were collected between September 2010 and January 2012 (except February and March 2011) and in Santarém 08 samples were obtained from October 2010 to May 2011. From each site one sample was harvested monthly from the same hive of *Tetragonisca angustula*.

A total of 23 pollen samples were collected using sections (approximately 4 cm) of disposable plastic straws that were pressed against what appeared to be the most recent pollen pots of *T. angustula*, and a profile was obtained for subsequent processing. After collection, the pollen was placed into plastic vials, properly identified and refrigerated until laboratory preparation.

The following steps were used to process the pollen samples collected from *T. angustula* pollen pots. These steps are based on a previous protocol (Novais et al. 2009) for processing pollen collected by Africanised honeybees (*Apis mellifera* L., 1758) with some modifications and the usual protocols for the pollen analysis of honey (Louveaux et al. 1978; Iwama and Melhem 1979):

(1) Dry the samples in an oven at approximately 40 ºC for 48 h or until weight stabilisation occurs (Alvarado and Delgado 1985);

(2) Dissolve 2 to 5 g of stingless bee pollen in a beaker with of 5 mL of warm water and mix with a glass rod;

(3) Add 5 mL of research grade ethanol (ETOH) 95% into the beaker and stir the solution. ETOH minimises the loss of pollen grains when removing the supernatant after centrifugation, given the low specific gravity of alcohol compared to water (Jones and Bryant 2004). If necessary, let the solution stand for approximately 3 h to ensure complete dissolution of the pollen loads;

(4) After homogenising the solution using a glass rod, centrifuge (1048 × g for 10 min) and discard the supernatant liquid;

(5) Add 3 to 5 mL of anhydrous acetic acid to each sample. Let the mixture stand for at least 3 h to promote the dehydration of the pollen residue. Centrifuge and discard the supernatant;

(6) Add 3 to 5 mL of acetolysis mixture (Erdtman 1960) to each sample. Place the tubes in a 100ºC water bath for 3 min. Centrifuge and discard the supernatant;

(7) Add 3 to 5 mL of distilled water to the test tube containing the pollen residue and stir sufficiently to remove the excess acetolysis mixture. Add a few drops of ETOH to the tube and then centrifuge it and discard the supernatant;

(8) Add 3 mL of 50% glycerine to each tube and let stand between 1 and 24 h. Centrifuge the tube and discard the supernatant and leave the test tube upside down until no more water is left;

(9) Mount the pollen residue in glycerinated gelatine between a glass slide and a cover slip;

(10) Analyse the slides under a microscope, identify the pollen types and count at least 500 pollen grains per sample. In the pollen spectrum, the percentages represent the frequency of each pollen type, based on the total amount of pollen grains counted (at least 500) in one sample. These values show the contribution of each pollen type to the analysed sample.

2.3 Identification, categorisation and analysis

The botanical identification of pollen types found in the samples was based on pollen catalogues (Roubik and Moreno 1991; Carreira et al. 1996) and comparison with palinotheca reference samples from the Palynology Laboratory of the National Institute of Amazon Research (Instituto Nacional de Pesquisas da Amazônia, INPA). We adopted the definitions of pollen type according to Joosten and de Klerk (2002) and de Klerk and Joosten (2007), understanding that the concept of pollen type, as a morphological entity, may include more than one species or taxonomic entity. Thus, the author of a species is indicated only when referring to a distinct plant species. However, this is not necessary when only the pollen type is mentioned, as in the tables.

We adopted the classes proposed by Jones and Bryant (1996), rare (< 10%), infrequent (10 to 20%), frequent (21 to 50%) or very frequent (> 50%), based on the percentage of occurrence of each pollen type in the sample set (regarding only its presence or absence in the samples instead of its frequency). This value may represent "long-term" pollen and nectar resource through the year, for example. The range of pollen types based on the Shannon-Weaver diversity index (H') was calculated and a pollen diversity index was developed for each sample (Ludwig and Reynolds 1988). Complementing H', Pielou's evenness index (J'), ranging from 0 to 1 was calculated and indicated a trend towards heterogeneity (0) or homogeneity (1) in the bees' use of resources in each study area (Pielou 1977). The analyses were performed using the PAST (*PAlaeontological STatistics*, version 2.16) software (Hammer et al. 2001).

3. Results

Thirty-two morphologically distinct pollen types were found in the pollen spectrum of samples taken from *Tetragonisca angustula* in Belterra. These types have botanical affinity with 22 plant families found in the study area. The families with the highest number of pollen types were Fabaceae (four types), Asteraceae (three), Euphorbiaceae (three), Myrtaceae (three) and Amaranthaceae (two). The remaining families (17) were represented by only one pollen type each (Table 1).

Analysis of the pollen samples collected from the colonies of *T. angustula* in Santarém distinguished 24 pollen types from 19 families. The Fabaceae and the Asteraceae families had the highest number of pollen types (five and two, respectively). The remaining plant families (17) were represented by only one pollen type each (Table 2).

We recorded the presence of six pollen types that are considered very frequent in the pollen samples from Belterra, occurring in over 50% of the samples: *Alternanthera* (Amaranthaceae), *Borreria verticillata* (Rubiaceae, plate 2, figure 1), *Cecropia* (Urticaceae, plate 2, figure 2), *Eupatorium* (Asteraceae), *Schefflera morototoni* (Araliaceae, plate 2, figure 3) and *Tabebuia* (Bignoniaceae, plate 2, figure 4). The remaining types were frequent (seven), infrequent (11) or rare (eight) in the samples (Table 1). Conversely, there were neither very frequent nor rare pollen types from Santarém. However, 15 frequent (between 21% and 50% of the samples) and nine infrequent types were found (Table 2).

Pollen types such as *Alternanthera* (Amaranthaceae), *Borreria verticillata* (Rubiaceae), *Byrsonima* (Malpighiaceae), *Emilia fosbergii* (Asteraceae), *Schefflera morototoni* (Araliaceae), *Tabebuia* (Bignoniaceae) and *Tapirira guianensis* (Anacardiaceae) occurred for at least four consecutive months in the samples from Belterra (Table 1). *Borreria verticillata* stood out among these types with consecutive occurrence from June 2011 through January 2012 (Table 1). In Santarém only *Serjania* (Sapindaceae) occurred for three consecutive months, from October through December

2010 (Table 2). Meanwhile, the remaining pollen types occurred for one or two consecutive months (Table 2).

In Belterra, three pollen types had a high frequency (>45%) in one or more of the samples: *Byrsonima* (Malpighiaceae, 49.06% – Oct 2011; 82.68% – Nov 2011; 55.56% – Dec 2011; 73.96% – Jan 2012, plate 2, figures 1, 2, 5 and 6), *Cecropia* (Urticaceae, 82.02% – Nov 2010; 99.6% – Jan 2011; 58% – Apr 2011; 97.03% – May 2011; 49.08% – Aug 2011; 76.78% – Set 2011) and *Eriope* (Lamiaceae, 74.07% – Jul 2011, plate 2, figure 6) (Table 1, Figure 2). Thus, the data suggest that these 3 types are the most relevant pollen combinations in the pollen pots of *Tetragonisca angustula* from this region.

In Santarém, the highest frequencies were associated with six pollen types: *Byrsonima* (Malpighiaceae, 92.1% – Feb 2011), *Cecropia* (Urticaceae, 60.71% – Oct 2010), *Clidemia hirta* (Melastomataceae, 98.31% – Nov 2010; 90.65% – Mar 2011; 74.41% – May 2011, plate 2, figure 7), *Davilla kunthii* (Dilleniaceae, 83.11% – Apr2011, plate 2, figure 8), *Myrcia* (Myrtaceae, 88.27% – Jan 2011, plate 2, figure 9) and *Vismia guianensis* (Hypericaceae, 72.44% – Dec 2010) (Table 2, Figure 2). These, therefore, represent the pollen combinations that were most exploited by *Tetragonisca angustula* in Santarém.

The data indicate that in Belterra, the pollen types with the highest frequency have a botanical affinity to species that typically have herbaceous or arboreal habits (Table 1). Conversely, the pollen pots from Santarém consisted of pollen types that are predominantly linked to tree and shrub species (Table 2).

In Belterra, the lowest richness of pollen types per sample (6 types on average) was found between December and May, which corresponds to the rainy season in most parts of the Lower Amazon (Albuquerque et al., 2010). On average, 11 different pollen types comprised each sample from this area between June and November, which is the driest period in the region (Table 1). The small number of samples studied from Santarém compared to Belterra prevents making conclusive statements for this region.

The Shannon-Weaver diversity index (H') ranged from 0.03 to 1.95 (1.04 ± s.d. 0.62 (n=15)) in the pollen samples collected in Belterra and from 0.10 to 1.00 (0.59 ± s.d. 0.34 (n=8)) in the samples from Santarém. Complementing H', the evenness (J') ranged from 0.04 to 0.79 (0.46 ± s.d. 0.21 (n=15)) in Belterra and from 0.07 to 0.46 (0.32 ± s.d. 0.15 (n=8)) in Santarém (Tables 1 and 2, Figures 2 and 3). At the beginning of the study in Belterra, H' was decreasing each month from September through

November 2010 (Figure 2). January 2011 had the lowest H' of any month and December 2010 had the highest one (Figure 2). In Santarém, November 2010 showed the lowest H', whereas the highest one was found in December 2010 (Figure 3). J' matched H' for the samples in Belterra but not in Santarém. There was a slight difference in them from January through March 2011, showing opposite trend in H' and J' values (Figure 3).

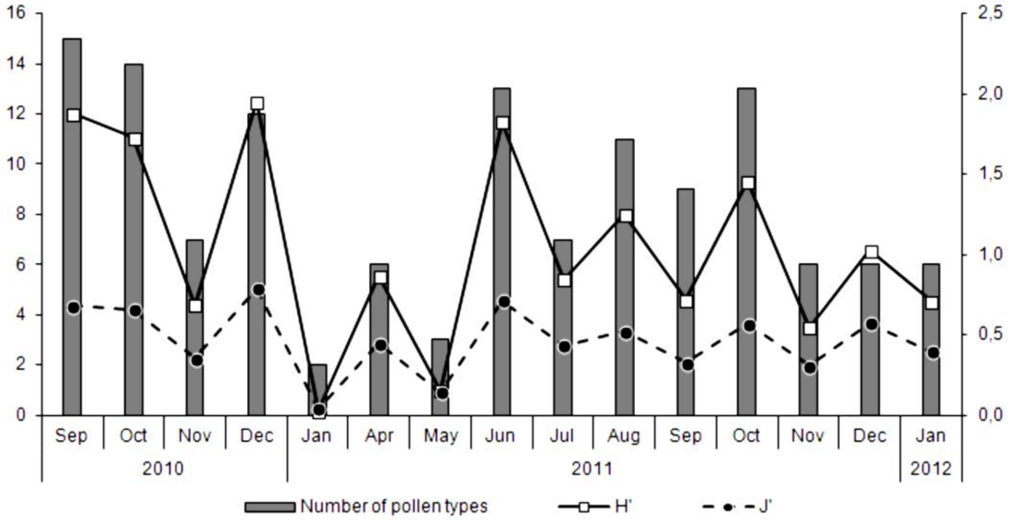


Figure 2. Seasonal distribution in the number of pollen types, Shannon-Weaver diversity (H') and Pielou's evenness (J') indexes among pollen samples obtained from pollen pots of *Tetragonisca angustula* in Belterra, Lower Amazon region, Pará State, Brazil.

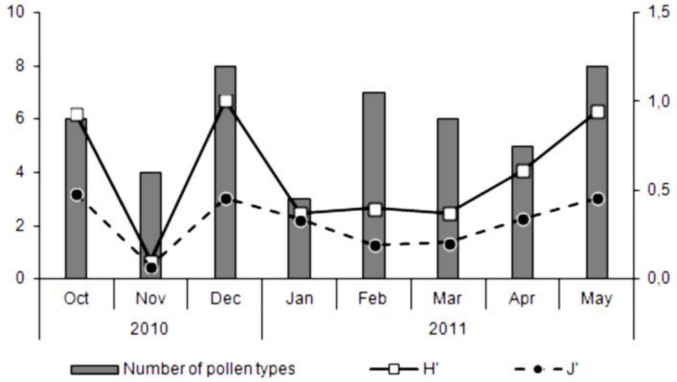


Figure 3. Seasonal distribution in the number of pollen types, Shannon-Weaver diversity (H') and Pielou's evenness (J') indexes among pollen samples harvested from pollen pots of *Tetragonisca angustula* in Santarém, Lower Amazon region, Pará State, Brazil.

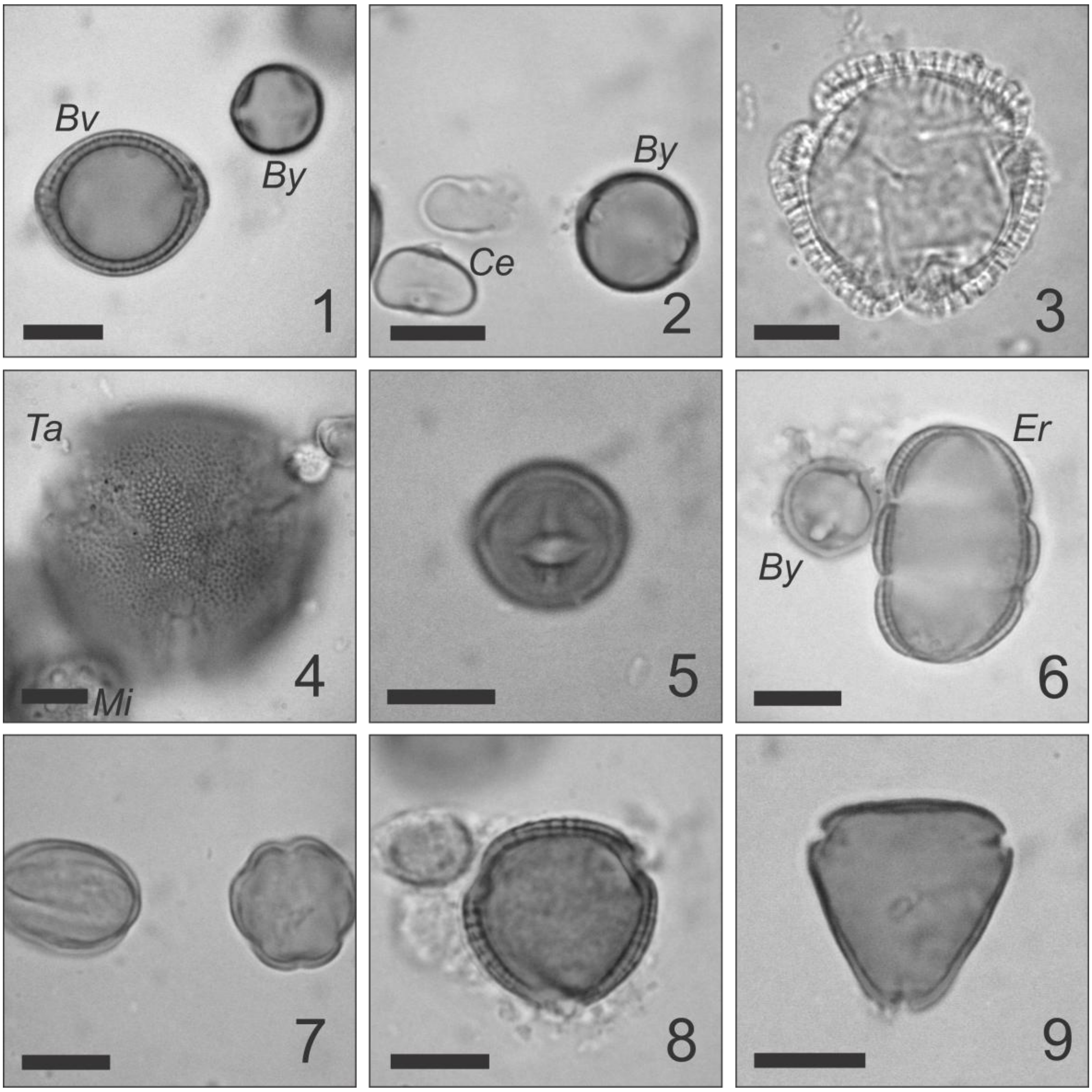


Plate 2. Photomicrographs of some pollen types found in stingless bee pollen samples from Belterra and Santarém, Lower Amazon region, Pará State, Brazil. Bars = 10 μm. Figure 1. *Bv*, *Borreria verticillata* (Rubiaceae); *By*, *Byrsonima* (Malpighiaceae). Figure 2. *By*, *Byrsonima* (Malpighiaceae); *Ce*, *Cecropia* (Urticaceae). Figure 3. *Schefflera morototoni* (Araliaceae). Figure 4. *Mi*, *Microtea* (Phytolaccaceae); *Ta*, *Tabebuia* (Bignoniaceae). Figure 5. *Byrsonima* (Malpighiaceae). Figure 6. *By*, *Byrsonima* (Malpighiaceae); *Er*: *Eriope* (Lamiaceae). Figure 7. *Clidemia hirta* (Melastomataceae). Figure 8. *Davilla kunthii* (Dilleniaceae). Figure 9. *Myrcia* (Myrtaceae).

Table 1. Pollen spectrum, frequency (%) of pollen types in each pollen sample monthly collected, Shannon-Weaver Diversity Index (H'), Pielou's Evenness Index (J'), the overall totals, and the taxon's habit of the pollen stored by *Tetragonisca angustula* (Latreille) from Belterra, Lower Amazon region, Pará State, Brazil. P.O.: percentage of occurrence (%) of each pollen type considering all the analysed samples (presence/absence). C.O.: classes of occurrence (R: rare. I: infrequent. F: frequent. VF: very frequent.).

Plant Family, Pollen Type	**2010**				**2011**										**2012**	**P.O. (%)**	**C.O.**	**Habit**
	Sep	**Oct**	**Nov**	**Dec**	**Jan**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**			
Achariaceae, *Lindackeria paludosa*	0,00	0,00	0,00	16,25	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7	R	tree
Amaranthaceae, *Alternanthera*	2,74	22,66	0,00	0,00	0,00	0,53	1,58	3,58	0,18	1,11	0,17	0,00	0,00	0,00	0,00	53	VF	herb/sub-shrub
Amaranthaceae, *Amaranthus viridis*	3,94	6,23	0,00	0,36	0,00	0,00	0,00	0,16	0,00	0,18	0,00	0,00	0,00	0,00	0,19	40	F	herb
Anacardiaceae, *Tapirira guianensis*	0,51	0,35	2,81	6,14	0,00	0,00	0,00	1,30	0,00	0,00	1,82	16,74	0,00	0,00	0,00	47	F	tree
Araliaceae, *Schefflera morototoni*	37,16	41,87	0,00	2,53	0,00	0,00	0,00	0,49	0,00	0,00	0,00	6,20	0,98	18,95	2,26	53	VF	tree
Arecaceae, *Astrocaryum aculeatum*	0,00	0,17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,17	0,00	0,00	0,00	0,00	13	I	tree
Asteraceae, *Emilia fosbergii*	2,05	1,38	0,00	0,00	0,00	0,00	0,00	1,46	1,59	0,18	0,17	0,14	0,00	0,00	0,00	47	F	herb
Asteraceae, *Eupatorium*	2,57	2,25	0,00	2,53	0,00	0,35	0,00	1,79	0,88	1,48	0,00	0,29	0,49	0,33	0,00	67	VF	herb/sub-shrub
Asteraceae, *Vernonia*	0,34	0,17	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	13	I	herb/sub-shrub
Bignoniaceae, *Tabebuia*	13,18	4,50	0,19	5,05	0,00	0,88	0,00	23,90	0,00	20,85	0,66	0,14	0,00	0,00	0,00	60	VF	tree
Burseraceae, *Protium*	0,00	0,00	5,99	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7	R	shrub/tree
Dilleniaceae, *Davilla kunthii*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7	R	shrub/liana
Euphorbiaceae, *Acalypha*	0,00	0,00	0,00	0,00	0,40	37,79	1,39	0,00	0,18	0,00	0,00	0,00	0,00	0,00	0,00	27	F	herb/sub-shrub
Euphorbiaceae, *Aparisthmium cordatum*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,02	0,00	0,00	0,00	7	R	tree

Table 1 (Continuation)

Plant Family, Pollen Type	**2010**				**2011**										**2012**	**P.O. (%)**	**C.O.**	**Habit**
	Sep	**Oct**	**Nov**	**Dec**	**Jan**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**			
Euphorbiaceae, *Croton*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,16	0,38	20	I	shrub/tree
Fabaceae, *Senna/Cassia*	0,00	1,56	0,19	1,44	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	20	I	tree
Fabaceae, *Mimosa pudica*	3,42	1,04	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	13	I	herb
Fabaceae, *Stryphnodendron pulcherrimum*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,66	1,01	0,00	0,00	0,00	13	I	shrub/tree
Fabaceae, *Phaseolus*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,29	0,00	0,00	0,57	13	I	herb
Goupiaceae, *Goupia glabra*	2,23	3,29	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	13	I	tree
Lamiaceae, *Eriope*	3,42	0,52	0,00	0,00	0,00	0,00	0,00	6,67	74,07	0,55	0,00	0,00	0,00	0,00	0,00	33	F	herb
Loranthaceae, *Psittacanthus*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,14	0,00	0,00	0,00	7	R	hemiparasite
Malpighiaceae, *Byrsonima*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	33,50	0,00	25,46	19,07	49,06	82,68	55,56	73,96	47	F	shrub/tree
Melastomataceae, *Clidemia hirta*	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7	R	shrub
Moraceae, *Brosimum paraense*	0,00	0,00	0,00	31,23	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	7	R	tree
Myrtaceae,*Eugenia stipitata*	0,00	0,00	8,43	5,05	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	13	I	tree
Myrtaceae,*Myrcia*	0,34	0,00	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	13	I	shrub
Myrtaceae,*Psidium*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,44	0,00	0,00	0,00	7	R	shrub
Phytolaccaceae, *Microtea*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,79	8,82	0,37	0,00	0,00	0,16	0,16	0,00	33	F	herb
Rubiaceae, *Borreria verticillata*	25,68	14,01	0,00	9,03	0,00	2,28	0,00	17,56	14,29	0,37	0,50	1,44	15,36	24,84	22,64	80	VF	herb/sub-shrub
Sapotaceae, *Pouteria*	0,68	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,37	0,00	0,00	0,00	0,00	0,00	13	I	tree
Urticaceae, *Cecropia*	1,20	0,00	82,02	20,22	99,60	58,00	97,03	7,48	0,00	49,08	76,78	21,07	0,00	0,00	0,00	67	VF	tree
Undetermined	0,51	0,00	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	–	–	–
TOTAL	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	–	–	–
Total number of pollen types identified	15	14	7	12	2	6	3	13	7	11	9	13	6	6	6	–	–	–
Shannon-Weaver diversity index (H')	1,88	1,73	0,68	1,95	0,03	0,87	0,15	1,83	0,84	1,25	0,72	1,46	0,55	1,03	0,71	–	–	–
Pielou's evenness index (J')	0,68	0,65	0,35	0,79	0,04	0,45	0,14	0,71	0,43	0,52	0,33	0,57	0,30	0,57	0,39	–	–	–

Table 2. Pollen spectrum, frequency (%) of pollen types in each pollen sample monthly collected, Shannon-Weaver Diversity Index (H'), Pielou's Evenness Index (J'), the overall totals, and the taxon's habit of the pollen stored by *Tetragonisca angustula* (Latreille) from Santarém, Lower Amazon region, Pará State, Brazil. P.O.: percentage of occurrence (%) of each pollen type considering all the analysed samples (presence/absence). C.O.: classes of occurrence (R: rare. I: infrequent. F: frequent. VF: very frequent.).

Plant Family, Pollen Type	**2010**			**2011**					**P.O. (%)**	**C.O.**	**Habit**
	Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**			
Acanthaceae, *Justicia*	0,00	0,00	0,00	0,00	0,00	0,00	0,57	0,00	13	I	shrub
Amaranthaceae, *Amaranthus viridis*	0,00	0,00	0,00	0,00	0,00	0,00	1,14	0,00	13	I	herb
Anacardiaceae, *Tapirira guianensis*	0,00	0,94	0,00	0,00	0,00	0,00	0,00	0,00	13	I	tree
Asteraceae, *Emilia fosbergii*	0,00	0,37	0,39	0,00	0,00	0,00	0,00	11,87	38	F	herb
Asteraceae, *Eupatorium*	1,79	0,00	0,00	0,00	0,15	0,19	0,00	0,00	38	F	herb/sub-shrub
Burseraceae, *Protium*	0,00	0,00	1,57	0,00	0,00	0,00	0,00	0,00	13	I	shrub/tree
Dilleniaceae, *Davilla kunthii*	0,00	0,00	0,00	0,00	0,00	0,00	83,11	1,17	25	F	shrub/liana
Euphorbiaceae, *Acalypha*	0,00	0,00	0,00	11,55	0,00	0,00	0,00	0,00	13	I	herb/sub-shrub
Fabaceae, *Machaerium*	0,00	0,00	10,04	0,00	0,00	0,00	0,00	0,00	13	I	shrub/tree
Fabaceae, *Macrolobium*	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,68	13	I	tree
Fabaceae, *Senna*	0,00	0,00	10,63	0,00	0,00	0,00	0,00	0,00	13	I	tree
Fabaceae, *Piptadenia*	0,00	0,00	0,98	0,00	0,00	0,00	0,00	0,00	13	I	shrub/tree/liana
Fabaceae, *Stryphnodendron pulcherrimum*	1,07	0,00	0,00	0,18	0,00	0,00	0,00	0,00	25	F	shrub/tree
Hypericaceae, *Vismia guianensis*	33,21	0,00	72,44	0,00	0,00	0,00	0,00	0,00	25	F	tree
Malpighiaceae, *Byrsonima*	0,00	0,00	0,00	0,00	92,10	0,19	0,00	0,00	25	F	shrub/tree
Malvaceae, Bombacoideae	0,00	0,00	0,00	0,00	0,00	0,19	0,00	2,01	25	F	tree
Melastomataceae, *Clidema hirta*	0,00	98,31	0,00	0,00	0,00	90,65	0,00	74,41	38	F	shrub
Myrtaceae, *Myrcia*	0,00	0,00	0,00	88,27	1,98	0,00	0,00	0,00	25	F	shrub

Table 2 (Continuation)

Plant Family, Pollen Type	**2010**			**2011**					**P.O. (%)**	**C.O.**	**Habit**
	Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**			
Poaceae, Type 1	0,00	0,00	0,00	0,00	1,82	0,95	0,00	0,17	38	F	herb
Rubiaceae, *Warszewiczia coccinea*	0,00	0,00	0,00	0,00	2,89	0,00	0,38	0,00	25	F	shrub/tree
Sapindaceae, *Serjania*	0,71	0,37	0,79	0,00	0,00	0,00	0,00	0,00	38	F	liana
Sapotaceae, *Pouteria*	0,00	0,00	0,00	0,00	0,15	0,00	0,00	1,51	25	F	Tree
Urticaceae, *Cecropia*	60,71	0,00	1,38	0,00	0,46	7,82	0,00	0,00	50	F	Tree
Undetermined	1,96	0,00	1,77	0,00	0,46	0,00	11,76	0,00	–	–	–
TOTAL	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	–	–	–
Total number of pollen types identified	6	4	8	3	7	6	5	8	–	–	–
Shannon-Weaver diversity index (H')	0,93	0,10	1,00	0,37	0,40	0,37	0,61	0,95	–	–	–
Pielou's evenness index (J')	0,48	0,07	0,46	0,34	0,19	0,21	0,34	0,46	–	–	–

4. Discussion

The number of pollen types recorded in our study exceeds that found by Rech and Absy (2011a) in the pollen pots of *Tetragonisca angustula* from the Upper Rio Negro region of the Amazon basin. The richness of plant species shown by the pollen spectrum of a given bee species varies according to several factors, including the phenological aspects of the local flora, the seasonal changes in nectar flow, the presence of several species of bees foraging in the same area and the protein needs of the colony (Imperatris-Fonseca et al. 1984; Marques-Souza 2010). In both Belterra and in Santarém, colonies of *T. angustula* share the apiary area with other stingless bees, possibly sharing some species of the surrounding vegetation. However, we ignored the degree of overlap in floral resource use by the species that cohabit with *T. angustula* in the study areas because this is one of the first palynological studies conducted in the region.

The Fabaceae and the Asteraceae families had the highest number of pollen types identified in both Belterra and Santarém. Imperatriz-Fonseca et al. (1984) also reported these families to be the most significant in samples of pollen stored by *T. angustula* in beehives at the Institute of Biosciences at the University of São Paulo (Universidade de São Paulo, USP). Other studies have found a strong contribution from these families in the diet of *T. angustula*, in addition to the Euphorbiaceae, Moraceae, Myrtaceae and Rubiaceae families (Carvalho et al. 1999; Novais et al. 2006; Morgado et al. 2011; Rech and Absy 2011a).

Most pollen types in the samples occurred in frequencies below 10%, which reflects, according to Sosa-Nájera et al. (1994), the dispersion rate of individuals from the colony and the degree of polylectism. These authors also reported a few species with a frequency above 10% (termed primary sources) in honey, stored pollen and larval food extracted from colonies of *T. angustula* in Chiapas, Mexico.

However, Imperatriz-Fonseca et al. (1984), citing Heinrich (1976), stress that although some plant species are prominent in the pollen spectrum in terms of their high frequencies, bees tend to continue collecting from species that provide small amounts of food. Such plants would become alternative sources of trophic resources for the colony and are especially useful when other providers of pollen and nectar are saturated by other pollinators or are diminished. Moreover, a priori, those secondary sources could, over time, occupy a central position in the food supply. Marques-Souza (2010) also argues that although stingless bees tend to use a potential food source to the fullest upon its discovery, these insects continue collecting from less-rewarding sources. However, the bees can develop the skills required to best use new food sources, including the manipulation of floral parts.

Byrsonima, *Cecropia*, *Clidemia hirta*, *Davilla kunthii*, *Eriope*, *Myrcia* and *Vismia guianensis* were the most significant pollen types, as their frequency was above 70% in some samples. Rech and Absy (2011a) recorded the occurrence of “temporary specialisation” events in 19 of 51 pollen pots of Amazonian stingless bees. They identified such an event as when a given pollen type had an occurrence above 90% of the total pollen grains counted. Based on this, we can infer from our data that temporary specialisation occurred in five samples, which included the following pollen types: *Byrsonima* (Feb 2011, in Santarém), *Cecropia* (Jan and May 2011, in Belterra) and *Clidemia hirta* (Oct 2010 and Mar 2011, in Santarém).

However, it is worth noting three aspects regarding our recording of temporary specialisation in the pollen collections of *Tetragonisca angustula*: *i)* Species of *Byrsonima*, as found in most genera of the Malpighiaceae, are usually pollinated by oil-collecting bees, such as those from the Centridini group (Teixeira and Machado 2000; Rêgo et al. 2006). However, pollen types linked to *Byrsonima* are part of the pollen spectra generated from studies of stingless bees in the Amazon, including the genera *Cephalotrigona*, *Melipona*, *Partamona*, *Scaptotrigona*, *Scaura* and *Trigona* (Absy et al. 1980, 1984; Marques-Souza et al. 2007; Oliveira et al. 2009; Rech and Absy 2011a, 2011b); *ii) Cecropia* mainly comprises anemophilous species despite being a genus frequently cited in studies of stingless bees (Ribeiro et al. 2002; Rech and Absy 2011a). However, while we can infer that *Tetragonisca angustula* contributes negligibly to the pollination of *Cecropia*, we emphasise the relevance of this genus in the composition of pollen samples in addition to its significance in providing clues about the vegetation surrounding the colonies because its presence is indicative of degraded areas and is crucial for their recovery (Ribeiro et al. 2002); *iii) Clidemia hirta* (L.) D. Don has poricidal anthers, a characteristic shared by almost all species of Melastomataceae (Ribeiro et al. 2002). Thus, *C. hirta* depends on bees that are able to vibrate these anthers to extrude the pollen mass, thereby enabling the transport of the microgametophyte enclosed within the microspore wall to another flower and completing the pollination process. Therefore, small bees, including *Tetragonisca* *angustula*, gain advantages by collecting residual pollen from the previous work performed by larger bees that can promote pollen extrusion from the anthers of Malpighiaceae (Imperatriz-Fonseca et al. 1984). Therefore, we conclude that the events of temporary specialisation noted in the foraging pattern of *T. angustula* in Belterra and Santarém appear to have no direct link with the effective pollination of the plant species involved, which preferably rely on other agents to ensure such processes.

Another finding is that the pollen grains of *Byrsonima*, *Cecropia* and *Clidemia* are small or very small (< 25 μm), which favours their detection in the palynological analyses of honey and pollen (Demianowicz 1964). This factor should be considered when estimating the actual contribution of different species with pollen grains of markedly different sizes (Silveira 1991; Marques-Souza et al. 2002).

In general, the greater the trophic niche amplitude is, represented here by the Shannon-Weaver diversity index (H'), the higher the uniformity or trend of homogeneity (J' = 1) in the bees' pattern of floral resource collection, which is inferred by Pielou's evenness index (J'). In both Belterra and in Santarém, *Tetragonisca angustula* showed low uniformity in their collection. In their study in Piracicaba, São Paulo, Brazil, Carvalho et al. (1999) found that a colony of *T. angustula* showed the lowest uniformity when compared to colonies of three other species of stingless bees (*Nannotrigona testaceicornis* (Lepeletier, 1836), *Partamona helleri* (Friese, 1900) and *Plebeia droryana* (Friese, 1900)) and *Apis mellifera* from the same area. These authors also noted that *Tetragonisca angustula* showed the smallest niche amplitude, similar to *Nannotrigona testaceicornis*, and the lowest percentage of pollen sources (25%) found above 1% in the pollen spectrum. Morgado et al. (2011) also recorded low diversity of pollen types ($0.23 \leq H' \leq 0.85$) while analysing the pollen loads of *Tetragonisca angustula* classified by colouration, which were collected in an area of the Atlantic Forest (Mata Atlântica) in Rio de Janeiro, Brazil. According to Oliveira *et al*. (2009), pollen spectra present higher diversity in sites covered by secondary and primary forests than in areas with gardens and reduced primary forests. Conversely, the opposite was observed here. Belterra presented the highest averages for H' and J', although beehives were placed near gardens. However, pollen types related to native species, such as *Astrocaryum aculeatum* G. Mey. and *Goupia glabra* Aubl., were also registered in the samples and contributed to increasing the local trophic niche of *Tetragonisca angustula*.

Imperatriz-Fonseca et al. (1984) argue that the small size of *T. angustula* implies a relatively low energy requirement. This may be responsible for attracting *T. angustula* to a higher number of plants, and these species would also be relevant as a food source if there are competitors in their foraging area.

We emphasise the need for future studies investigating the co-existence of *T. angustula* with other native species of stingless bees in the study areas because several species occur together in this region. In Belterra, for example, the meliponary houses approximately fifteen different species of stingless bees, in some cases with more than one colony per species. Therefore, we can hypothesise possible intra- and interspecific pressure on the bees for food resources in this area, given the increasing suppression of native vegetation resulting from the expansion of urban areas.

5. Conclusion

Tetragonisca angustula used plant species common to the study areas as pollen sources and even displayed a pattern that can be characterised, among other factors, by temporary specialisation events, which appear to be unrelated to effective pollination processes. Ecological indices indicate a small range of pollen niche, which corroborates some previously published data in the literature. In addition, such indices also indicate a heterogeneous pattern of resource collection by *Tetragonisca angustula*.

Acknowledgments

We express our sincere thanks to Mr. Geancarlo V. Gouveia, chairman of AMEMBEL (Stingless Beekeepers Association of the District of Belterra), for authorising the collection of pollen samples at his private apiary; to the board of the Forest School (Escola da Floresta) and to SEMED (Borough Education Council) for allowing the collection of samples at the institution’s apiary; to Dr. Cláudia Elena Carneiro of UEFS (Bahia State University at Feira de Santana), M.Sc. Chieno Suemitsu and Dr. Lenise Vargas Flores, both of UFOPA (Western Pará Federal University), who are supervisors of the laboratories used for processing and analysing the palynological samples; to Dr. Favízia Freitas de Oliveira of UFBA (Bahia Federal University) for identifying the stingless bee species; to the research fellows Alcides Froes Dias Jr., Ângelo Márcio Barbosa Bastos Jr. and Bruno Henrique Andrade-Silva for helping with laboratory activities; to M.Sc. Leilton Santos Damascena, for helping with the maps; to the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq) for funding the project (Processes 575747/2008-0, 143084/2009-7 and 477127/2011-8); and to the anonymous referees for helping us with valuable comments on this manuscript.

References

Absy ML, Bezerra EB, Kerr WE. 1980. Plantas nectaríferas utilizadas por duas espécies de *Melipona* da Amazônia. *Acta Amazonica* 10, 271–281.

Absy ML, Camargo JMF, Kerr WE, Miranda IPA. 1984. Espécies de plantas visitadas por Meliponinae (Hymenoptera; Apoidea), para coleta de pólen na região do médio Amazonas. *Revista Brasileira de Biologia* 44, 227–237.

Albuquerque MF, Souza EB, Oliveira MCF, Souza JA Jr. 2010. Precipitação nas mesorregiões do estado do Pará: climatologia, variabilidade e tendências nas últimas décadas (1978–2008). *Revista Brasileira de Climatologia* 6, 151–168.

Alvarado JL, Delgado M. 1985. Flora apicola en Uxpanapa, Veracruz, Mexico. *Biotica* 10, 257–275.

Braga JA, Sales EO, Soares Neto J, Conde MM, Barth OM, Lorenzon MC. 2012. Floral sources to *Tetragonisca angustula* (Hymenoptera: Apidae) and their pollen morphology in a Southeastern Brazilian Atlantic Forest. *Revista de Biología Tropical (International Journal of Tropical Biology)* 60, 1491–1501.

Camargo JMF, Pedro SRM. 2012. Meliponini Lepeletier, 1836 [Internet]. In: Moure JS, Urban D, Melo GAR, organizers. Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region. [cited 2012 Sep 24]. Available from: http://www.moure.cria.org.br/catalogue

Carreira LMM, Lopes JRC, Silva MF, Nascimento LAS. 1996. Catálogo de pólen das leguminosas da Amazônia brasileira. Belém (PA, Brazil): Museu Paraense Emílio Goeldi.

Carvalho CAF, Marchini LC, Ros PB. 1999. Fontes de pólen utilizadas por *Apis mellifera* L. e algumas espécies de Trigonini (Apidae) em Piracicaba (SP). *Bragantia* 58, 49–56.

de Klerk P, Joosten H. 2007. The difference between pollen types and plant taxa: a plea for clarity and scientific freedom. *Eiszeitalter und Gegenwart* 56, 162–171.

Demianowicz Z. 1964. Charakteristik der einartenhonige. *Annales de l'Abeille* 7, 273–288.

[EMBRAPA] Empresa Brasileira de Pesquisa Agropecuária (BR). 2012. Banco de dados climáticos do Brasil [Internet]. [cited 2012 Oct 5]. Available from: http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=pa&COD=121

Erdtman G. 1960. The acetolysis method – a revised description. *Svensk Botanisk Tidskrift* 54, 561–564.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Palaeontological Statistics software package for education and data analysis [Internet]. *Palaeontologia Electronica*, 4. [cited 2012 Oct 5]. Available from: http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Heinrich B. 1976. The foraging specializations of individual bumblebees. *Ecological Monographs* 46, 105–128.

Imperatriz-Fonseca VL, Kleinert-Giovannini A, Cortopassi-Laurino M, Ramalho M. 1984. Hábitos de coleta de *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Boletim de Zoologia da Universidade de São Paulo* 8, 115–131.

Iwama S, Melhem TS. 1979. The pollen spectrum of the honey of *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Apidologie* 10, 275–295.

Jones GD, Bryant VM Jr. 1996. Melissopalynology. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications. Dallas: American Association of Stratigraphic Palynologists Foundation, 3, 933–938.

Jones GD, Bryant VM Jr. 2004. The use of ETOH for dilution of honey. *Grana* 43, 174–182.

Joosten H, de Klerk P. 2002. What's in a name? Some thoughts on pollen classification, identification, and nomenclature in Quaternary palynology. *Review of Palaeobotany and Palynology* 122, 29–45.

Kerr WE, Absy ML, Marques-Souza AC. 1986–1987. Espécies nectaríferas e poliníferas utilizadas pela abelha *Melipona compressipes fasciculata* (Meliponinae, Apidae) no Maranhão. *Acta Amazonica* 16/17, 145–156.

Louveaux J, Maurizio A, Vorwohl G. 1978. Methods of melissopalynology. *Bee World* 59, 139–157.

Ludwig JA, Reynolds JF. 1988. Statistical ecology: a primer on methods and computing. New York: John Wiley & Sons.

Marques LJP, Muniz FH, Lopes GS, Silva JM. 2011. Levantamento da flora apícola em Santa Luzia do Paruá, Sudoeste da Amazônia, Maranhão. *Acta Botanica Brasilica* 25, 141–149.

Marques-Souza AC. 1996. Fontes de pólen exploradas por *Melipona compressipes manaosensis* (Apidae: Meliponinae), abelha da Amazônia Central. *Acta Amazonica* 26, 77–86.

Marques-Souza AC. 2010. Ocorrência do pólen de *Podocarpus* sp. (Podocarpaceae) nas coletas de *Frieseomelitta varia* Lepeletier 1836 (Apidae: Meliponinae) em uma área de Manaus, AM, Brasil. *Acta Botanica Brasilica* 24, 558–566.

Marques-Souza AC, Absy ML, Condé PAA, Coelho HA. 1993. Dados da obtenção do pólen por operárias de *Apis mellifera* no município de Ji–Paraná (RO), Brasil. *Acta Amazonica* 23, 59–76.

Marques-Souza AC, Absy ML, Kerr WE, Aguilera-Peralta FJ. 1995. Pólen coletado por duas espécies de meliponíneos (Hymenoptera: Apidae) da Amazônia. *Revista Brasileira de Biologia* 55, 855–864.

Marques-Souza AC, Moura CO, Nelson BW. 1996. Pollen collected by *Trigona williana* (Hymenoptera: Apidae) in Central Amazonia. *Revista de Biología Tropical* 44, 567–573.

Marques-Souza AC, Miranda IPA, Moura CO, Rabelo A, Barbosa EM. 2002. Características morfológicas e bioquímicas do pólen coletado por cinco espécies de meliponíneos da Amazônia Central. *Acta Amazonica* 32, 217–229.

Marques-Souza AC, Absy ML, Kerr WE. 2007. Pollen harvest features of the Central Amazonian bee *Scaptotrigona fulvicutis* Moure 1964 (Apidae: Meliponinae), in Brazil. *Acta Botanica Brasilica* 21, 11–20.

Martins ACL, Rêgo MMC, Carreira LMM, Albuquerque PMC. 2011. Espectro polínico de mel de tiúba (*Melipona fasciculata* Smith, 1854, Hymenoptera, Apidae). *Acta Amazonica* 41, 183–190.

Morgado LN, Andrade RC, Lorenzon MCA, Gonçalves-Esteves V. 2011. Padrão polínico utilizado por *Tetragonisca angustula* Latreille (Apidae: Meliponina). *Acta Botanica Brasilica* 25, 932–934.

Novais JS, Absy ML. Forthcoming 2013. First melissopalynological records in honeys from *Tetragonisca angustula* (Latreille, 1811) in Lower Amazon, Brazil: pollen spectrum and concentration. *Journal of Apicultural Research*.

Novais JS, Lima LCL, Santos FAR. 2006. Espectro polínico de méis de *Tetragonisca angustula* Latreille, 1811 coletados na caatinga de Canudos, Bahia, Brasil. *Magistra* 18, 257–264.

Novais JS, Lima LCL, Santos FAR. 2009. Botanical affinity of pollen harvested by *Apis mellifera* L. in a semi-arid area from Bahia, Brazil. *Grana* 48, 224–234.

Oliveira FPM, Carreira LMM, Jardim MAG. 1998. Caracterização polínica do mel de *Apis mellifera* L. em área de floresta secundária no município de Igarapé-Açu – Pará. *Boletim do Museu Paraense Emílio Goeldi, Série Botânica* 14, 157–176.

Oliveira FPM, Absy ML, Miranda IS. 2009. Recurso polínico coletado por abelhas sem ferrão (Apidae, Meliponinae) em um fragmento de floresta na região de Manaus – Amazonas. *Acta Amazonica* 39, 505–518.

Pielou EC. 1977. Mathematical ecology. New York: John Wiley & Sons.

Rech AR, Absy ML. 2011a. Pollen sources used by species of Meliponini (Hymenoptera: Apidae) along the Rio Negro channel in Amazonas, Brazil. *Grana* 50, 150–161.

Rech AR, Absy ML. 2011b. Pollen storages in nests of bees of the genera *Partamona*, *Scaura* and *Trigona* (Hymenoptera, Apidae). *Revista Brasileira de Entomologia* 55, 361–372.

Rêgo MMC, Albuquerque PMC, Ramos MC, Carreira LM. 2006. Aspectos da biologia de nidificação de *Centris flavifrons* (Friese) (Hymenoptera: Apidae, Centridini), um dos principais polinizadores do murici (*Byrsonima crassifolia* L. Kunth, Malpighiaceae), no Maranhão. *Neotropical Entomology* 35, 579–587.

Ribeiro JELS, Hopkins MJG, Vicentini A, Sothers CA, Costa MAS, Brito JM, Souza MAD, Martins LHP, Lohmann LG, Assunção PACL, Pereira EC, Silva CF, Mesquita MR, Procópio LC. 2002. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central. Manaus (AM, Brazil): Instituto Nacional de Pesquisas da Amazônia.

Roubik DW, Moreno JE. 1991. Pollen and spores of Barro Colorado island. St. Louis (MO): Missouri Botanical Garden Press.

Silva SJR, Absy ML. 2000. Análise do pólen encontrado em amostras de mel de *Apis mellifera* L. (Hymenoptera, Apidae) em uma área de savana de Roraima, Brasil. *Acta Amazonica* 30, 579–588.

Silva SJR, Rebouças MAP. 1998. Plantas melíferas de Roraima – Parte II. *Boletim do Museu Integrado de Roraima* 4, 31–38.

Silveira FA. (1991) Influence of pollen grain volume on the estimation of the relative importance of its source to bees. *Apidologie* 22, 495–502.

Silveira FA, Melo GAR, Almeida EAB. 2002. Abelhas brasileiras: sistemática e identificação. Belo Horizonte (MG, Brazil): Fernando A. Silveira.

Sosa-Nájera MS, Martínez-Henández E, Lozano-García MS, Cuadriello-Aguiar JI. 1994. Nectaropolliniferous sources used by *Trigona* (*Tetragonisca*) *angustula* in Chiapas, southern México. *Grana* 33, 225–230.

Teixeira LAG, Machado IC. 2000. Sistema de polinização e reprodução de *Byrsonima sericea* DC. (Malpighiaceae). *Acta Botanica Brasilica* 14, 347–357.

Capítulo III

Novais, J.S.; Absy, M.L. & Santos, F.A.R.
Flora exploited by *Tetragonisca angustula*
(Latreille, 1811) (Hymenoptera: Apidae) in
tropical semiarid areas of Northeastern Brazil.
Submetido ao *Arthropod-Plant Interactions*

Flora exploited by *Tetragonisca angustula* (Latreille, 1811) (Hymenoptera: Apidae) in tropical semiarid areas of Northeastern Brazil

Abstract

The flora of the northeastern Brazil holds a nectariferous-polliniferous potential that supports many native pollinators. However, few studies have examined the plant – Meliponini interaction, especially from the melissopalynological aspect. We assessed the flora exploited by *Tetragonisca angustula* in two *caatinga* (dry vegetation) areas in the Brazilian semiarid region through pollen analysis of honeys with the goal of answering the following questions: a) what are the most representative pollens found in the honeys? b) do certain pollen types function as regional geographic markers? and c) what are the characteristics of the trophic niche of *T. angustula* in these areas? The honeys (*n* = 27) were collected every month from October 2010 to December 2011 in Itaberaba and Ruy Barbosa, diluted in tepid water and 95% ethanol and subsequently acetolysed. The results revealed 67 pollen types in the honeys, with 25 common to both study areas and most belonging to the family Fabaceae (>10 types). The most commonly encountered types of pollen were *Heteropterys*, *Mikania*, *Myrcia*, *Prosopis juliflora* and *Solanum* for Itaberaba and *Heteropterys*, *Mimosa tenuiflora*, *Prosopis juliflora*, *Schinus*, *Senna macranthera*, *Solanum* and *Syagrus coronata* for Ruy Barbosa. *Anadenanthera colubrina*, *Poincianella pyramidalis* and *Ziziphus joazeiro* were considered markers of *caatinga* flora. The amplitude of the trophic niche varied between 0.36 and 2.55, while the evenness ranged from 0.15 to 0.77, thus characterising the foraging habit of *T. angustula* as polylectic with a more homogeneous use of the flora in Ruy Barbosa than in Itaberaba.

Keywords *Caatinga* vegetation. Entomopalynology. Melissopalynology. Pot-honey. Seasonally dry tropical forest. Tropical stingless bees

Introduction

The Brazilian semiarid region comprises a geographic area of 980,133.079 km², equivalent to 11.53% of the national territory, and is known as the "Drought Polygon" (locally known as “Polígono das Secas”) (Medeiros et al. 2012). The semiarid region encompasses ~800,000 km^2 of the Caatinga Phytogeographic Domain and composed mostly of *caatinga* vegetation (seasonally dry tropical forest) (Giulietti et al. 2002; Albuquerque et al. 2012). As the only genuinely Brazilian biome, the *caatinga* contains a flora with high adaptability to the demands imposed by the singularities of the regional climate; indeed, the region experiences rainfall with an irregular spatial and temporal distribution, a short period of rainfall lasting between three and five months per year and an average annual rainfall generally lower than 750 mm (Nimer 1972). The lack of rain has led to the occurrence of xeric features such as shedding, microphyll leaves, succulence, twisted trunks, and spines in many species that make up the vegetation of the region (Giulietti et al., 2002, 2004a; Prado 2003; Queiroz 2006).

The rational exploitation and adequate management of the floristic richness of the *caatinga* contributes to the timber, energy, agriculture, forage, and apiculture sectors, among others (Sampaio 2002; Giulietti et al. 2004a). In the latter sector, it is crucial to know which plant species have the potential to support apiculture and meliponiculture in the *caatinga* for the production of honey and pollen (Freitas 1991, Lima 2007). In this context, palynological studies are critical, as they can elucidate ecological issues involving pollinators and native plant species and assess the floral resources available to the more than 180 species of bees that populate the Brazilian *caatinga* (Zanella and Martins 2003). Of these 180 species, native social stingless bees are the most abundant species in semiarid regions (Maia-Silva et al. 2012). Most melissopalynological studies conducted in areas with *caatinga* vegetation in northeastern Brazil have examined honeys from *Apis mellifera* L., 1758 (Aires and Freitas 2001; Santos Jr and Santos 2003; Almeida et al. 2005; Sodré et al. 2007; Oliveira et al. 2010). Pollen spectra focusing on honeys produced by Meliponini in this type of vegetation were mainly analysed in the state of Bahia where native species such as *Melipona mandacaia* Smith, 1863 (Alves et al. 2006), *Melipona quadrifasciata* Lepeletier, 1836 (Carvalho et al. 2006), *Plebeia* sp. (Lima 2007) and *Tetragonisca angustula* (Latreille, 1811) (Novais et al. 2006) were examined. Of these species, *T. angustula*, regionally known as *jataí* or *jati* bee, is one of the most popular native bees in tropical America because it is easy to manage, nests in accessible locations, shows no aggressive behaviour, and produces (albeit in small amounts) a honey much appreciated for human consumption and the treatment of diseases (Iwama and Melhem 1979; Imperatriz-Fonseca et al. 1984).

Constant pressures have been exerted on the populations of native pollinators in the Neotropics, usually due to deforestation, intensification of agricultural activities and the introduction of exotic species, resulting in habitat loss and population declines (Freitas et al. 2009; Giannini et al. 2012). As a result, studies that can guide the sustainable management of Meliponini by identifying the floral preferences and seasonal fluctuations in the foraging activities of these insects are essential for maintaining the native flora. The lack of knowledge of the flora of the *caatinga* (Giulietti et al., 2002, 2004a) and the lack of systematic data on the use of this flora by native pollinators may be contributing to the accelerating loss in biodiversity in the area, a situation that has already been documented in other areas of the world.

Our objective in this study was to characterise the pollen niche of *T. angustula* through the palynological analysis of honeys produced by this native species in two tropical semiarid regions of northeastern Brazil. In particular, we sought to: i) determine the pollen spectra of the samples; ii) identify the most representative commonly encountered pollen types in both study areas; iii) determine whether certain types of pollen function as geographic markers of *caatinga* vegetation; and iv) assess the amplitude of the trophic niche and the patterns of use of pollen resources by *T. angustula* through the calculation of ecological indices.

Methods

Study areas

The study areas were located in the municipalities of Itaberaba (12º26'18.8" S × 40º13'12.7" W, 270 m.a.s.l.) and Ruy Barbosa (12º17'27.6" S × 40º30'03.0" W, 383 m.a.s.l.), which belong to the Paraguaçu economic microregion, Bahia State, NE Brazil (Fig. 1). Both municipalities are situated in the region of Bahia and have a semiarid climate and a vegetation mosaic composed of areas of seasonal deciduous and semi-deciduous forest, *caatinga*-seasonal forest contact areas and *caatinga* vegetation (SEI 2013). Sierra Orobó is also located in the Itaberaba and Ruy Barbosa municipalities near the study areas and is composed of shrubby *caatinga* habitats on sandy and rocky soils and outcrops of sedimentary rocks associated with areas of transition to semi-deciduous forests in the higher altitudes (Giulietti et al. 2004b). Sierra Orobó contains close to 615 plant species with a large number of endemic species and is considered one of the priority areas for the conservation of the *caatinga* biome, mainly because of its important hydrologic link to the Paraguaçu River valley (Giulietti et al. 2004b; Cardoso and Queiroz 2008).

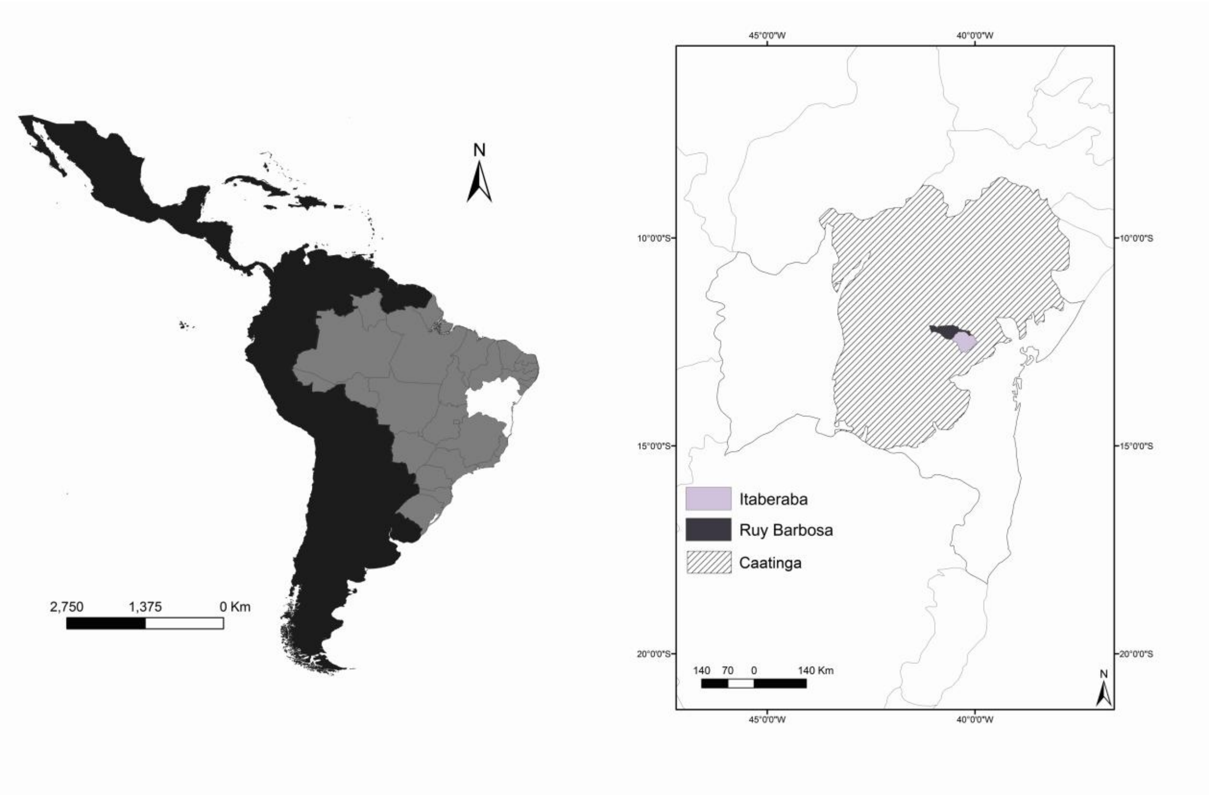


Fig. 1 On the map on the left, the grey area indicates the location of Brazil in South America, with emphasis on the State of Bahia (white) on the northeastern coast. The map on the right highlights the Itaberaba and Ruy Barbosa municipalities within the area of *caatinga* vegetation (patterned area) in Bahia State, Northeast Brazil.

Collection, processing and analyses

Sampling was conducted monthly from October 2010 to December 2011 in the two study areas. Because of the scarcity of available food in the colonies, it was not possible to obtain samples in Itaberaba in June 2011 and December 2011 or in Ruy Barbosa in November 2011. In total, 27 honey samples were obtained from monthly collections from storage pots produced in *T. angustula* colonies. Whenever possible, the collections were performed from the same colony or from pots that appeared to have been recently operculated given their colour and location inside the colony. At each monthly visit to the bee yards, approximately 5 mL of honey were collected using disposable plastic syringes. The material was then stored in labelled acrylic jars and refrigerated until processing in the laboratory. Although the usual technique for pollen analysis is based on the use of 10 mL of honey, studies conducted with *T. angustula* and other Meliponini generally use a smaller volume of material (Iwama and Melhem 1979; Novais et al. 2006) because the honey production of these insects is lower than that of *Apis mellifera*.

In the laboratory, we adopted the protocol proposed by Iwama and Melhem (1979) that included the use of acetolysis (Erdtman 1960), a procedure widely adopted in melissopalynological analyses with very satisfactory results (Lieux, 1980; Moar, 1985). We followed the recommendation of Jones and Bryant (2004) and used 95% ethanol (ETOH) for the initial dilution of honey in an effort to reduce the loss of pollen grains during the disposal of the supernatant liquid after centrifugation.

Three slides per sample were prepared for microscopic analysis. The pollen types present in the slides were quantified (at least 500 per sample whenever possible) and identified by consulting specialised catalogues (Roubik and Moreno 1991; Silva 2007) and the slide collection from the Pollen Collection at the Bahia State University at Feira de Santana (Palinoteca da Universidade Estadual de Feira de Santana — PUEFS). Throughout this paper, starting with the identification of the pollen types, the authorship of the botanical species is mentioned only when we specifically refer to a taxonomic entity; therefore, the authorship is not mentioned when only the pollen type is referred to, as pollen type represents a morphological entity that may include many species.

Frequency classes were established based on the percentage of each pollen type in a given sample: predominant pollen (>45%), secondary pollen (16-45%), important minor pollen (3-15%), minor pollen (<3%) (Louveaux et al. 1978). Classes of occurrence were established based on the presence or absence of pollen types in the set of samples: very frequent (occurrence in more than 50% of the samples), frequent (21-50%), infrequent (10-20%) and rare (<10%) (Jones and Bryant 1996).

The Shannon-Weaver (H') diversity index and Pielou's evenness index (J'), indicating the size of the trophic (pollen) niche and the homogeneous or heterogeneous use of pollen resources by *T. angustula,* respectively, were calculated (Pielou 1977; Ludwig and Reynolds 1988).

Results

The pollen spectrum of the honey samples of *Tetragonisca angutula* consisted of a total of 67 pollen types; 18 of these (26.87%) were common to the pollen spectra of honey from both Itaberaba and Ruy Barbosa. The samples from Itaberaba (*n* = 13) contained a total of 43 pollen types (Table 1) and the honeys produced in Ruy Barbosa (*n* = 14) contained 49 pollen types (Table 2), representing, respectively, 23 and 28 plant families (Tables 1 and 2). Of these families, Fabaceae (12 types), Malvaceae (4), Euphorbiaceae (3) and Anacardiaceae, Arecaceae, Asteraceae and Myrtaceae (two types each) were predominant in Itaberaba; Fabaceae (13), Amaranthaceae (4) and Euphorbiaceae, Malvaceae and Myrtaceae (three types each) predominated in Ruy Barbosa. Pollen identification is based on morphological diversity (Fig. 2). However, some pollen types from our study remain with undetermined botanical affinities. These types were found in five samples from Itaberaba and four samples from Ruy Barbosa.

We considered the most representative pollen types in pollen spectra obtained from both locations as those that occurred in over 50% of the samples (included thus in the occurrence class "very frequent") and with a frequency higher than 10% in at least one of those samples. In Itaberaba, pollen types *Heteropterys*, *Mikania*, *Myrcia*, *Prosopis juliflora* and *Solanum* met the abovementioned criteria (Figs. 2 and 3). In Ruy Barbosa, *Heteropterys*, *Mimosa tenuiflora*, *Prosopis juliflora*, *Schinus*, *Senna macranthera*, *Solanum* and *Syagrus coronata* met the criteria (Fig. 2 and 4). Although not having a high occurrence in the set of samples analysed, the pollen types *Alchornea*, *Cecropia*, *Schinus* and *Syagrus coronata* in Itaberaba, and *Acalypha*, *Brosimum,* Caesalpinioideae type, *Euphorbia* and *Gomphrena demissa* in Ruy Barbosa exhibited a frequency greater than 10% in at least one of the samples, indicating their periodic significance in the composition of the pollen spectra (Tables 1 and 2).

In Itaberaba, we encountered the following sequence of occurrence classes of pollen types: rare types (32.56%), frequent (27.91%), infrequent (20.93%) and very frequent (18.60%) (Table 1). In Ruy Barbosa, the sequence was as follows: frequent types (32.65%), rare (30.61%), infrequent and very frequent (18.37% each) (Table 2).

Frequency classes evaluate the periodic contribution of each pollen type to the composition of the pollen spectrum of a sample. Thus, predominant pollen types have a botanical affinity for plant species with a more significant monthly contribution to the composition of a given spectrum. In Itaberaba, *Cecropia* (Oct 2010 and May 2011), *Prosopis juliflora* (Nov 2010), *Schinus* (Oct and Nov 2011) and *Solanum* (Sep 2011) pollen types occurred in the predominant pollen class (Table 1). In Ruy Barbosa, *Gomphrena demissa* (Dec 2010), *Prosopis juliflora* (Apr 2011), *Schinus* (Oct 2010, Jun and Jul 2011) and *Solanum* (Oct 2011) pollen types occurred in the predominant class (Table 2). Predominant types were sparser in samples than the other frequency classes (Figs. 5 and 6).

In addition to the predominant pollen types, secondary pollen types also stood out, as they constituted more than 15% of the spectra. In Itaberaba, nine samples exhibited secondary pollen types, including *Heteropterys*, *Hyptis*, *Myrcia*, *Prosopis juliflora*, *Schinus*, *Solanum* and *Syagrus coronata*. Among these, we highlight *Prosopis juliflora*, which was found in six samples throughout the entire period from December 2010 to April 2011, and *Solanum*, which occurred in seven samples in all months from November 2010 to April 2011 (Table 1). The samples from Ruy Barbosa contained eight secondary pollen types in over 11 samples: *Brosimum*, Caesalpinioideae type, *Euphorbia*, *Heteropterys*, *Prosopis juliflora*, *Schinus*, *Senna macranthera* and *Solanum*. *Prosopis juliflora* occurred in five samples in the period from January to March of 2011, and *Solanum* occurred in seven honey samples during two trimesters (March–May and July–September of 2011) (Table 2).

Pollen types related to predominantly polliniferous plant species were found at frequencies exceeding 10%. *Solanum* was found in Itaberaba in 10 consecutive samples from November 2010 to September 2011, and in nine consecutive samples in Ruy Barbosa from March 2011 to December 2011. *Brosimum* and *Cecropia* are also related to genera with polliniferous species and occurred at a high frequency in some of the samples. Of the honeys analysed, we considered those produced in Itaberaba in the months of October 2011 and November 2011 to be monofloral; of these, the predominant type was *Schinus* (93.21% and 69.49%, respectively), and no other types occurred at frequencies of more than 10% (Table 1). In Ruy Barbosa, the sample collected in June 2011 suggested a unifloral honey characterised mostly by type *Schinus* (74.39%); the sample collected in October 2010 contained pollen types *Schinus* (55.30%) and *Prosopis juliflora* (24.06%), suggesting a bifloral honey (Table 2). Because of the high frequency of types representative of polliniferous species in the remaining samples and because of the lack of precise data on the actual production of nectar by the nectar-producing species found, we chose to characterise the remaining samples as multifloral honeys.

Species characteristic of areas with *caatinga* vegetation in the semiarid region of Bahia were represented in the pollen spectra by types such as *Anadenanthera colubrina*, *Poincianella pyramidalis* and *Ziziphus joazeiro*. While these species function as good geographic markers, they were encountered with low frequencies in the samples.

In Itaberaba, the amplitude of the trophic niche of *Tetragonisca angustula* calculated using the Shannon-Weaver (H') diversity index ranged from 0.36 (October 2010 to October 2011) to 1.82 (February 2011) and averaged 1.28 ± 0.51 s.d. (*n* = 13). Pielou’s evenness index (J') ranged from 0.15 (October 2011) to 0.67 (February 2011) and averaged 0.49 ± 0.17 s.d. (*n* = 13), indicating a heterogeneous use of floral sources by *T. angustula* in Itaberaba. H' and J' similarly increased or decreased over the months except on two occasions. Between December 2010 and January 2011, the H' index declined and the value of J' increased; the opposite trend was observed between the months of March 2011 and April 2011 (Fig. 7). In Ruy Barbosa, the value of H' ranged from 0.92 (May 2011) to 2.55 (December 2011) and averaged 1.66 ± 0.41 s.d. (*n* = 14). J' ranged from 0.38 (June 2011) to 0.77 (December 2011) and averaged 0.63 ± 0.15 s.d. (*n* = 14), indicating a more homogeneous use of floral resources in this municipality than in Itaberaba. In Ruy Barbosa, H' and J' values were similar in all months of the experiment except between February and March 2011, when the value of H' increased and J' decreased (Fig. 7).

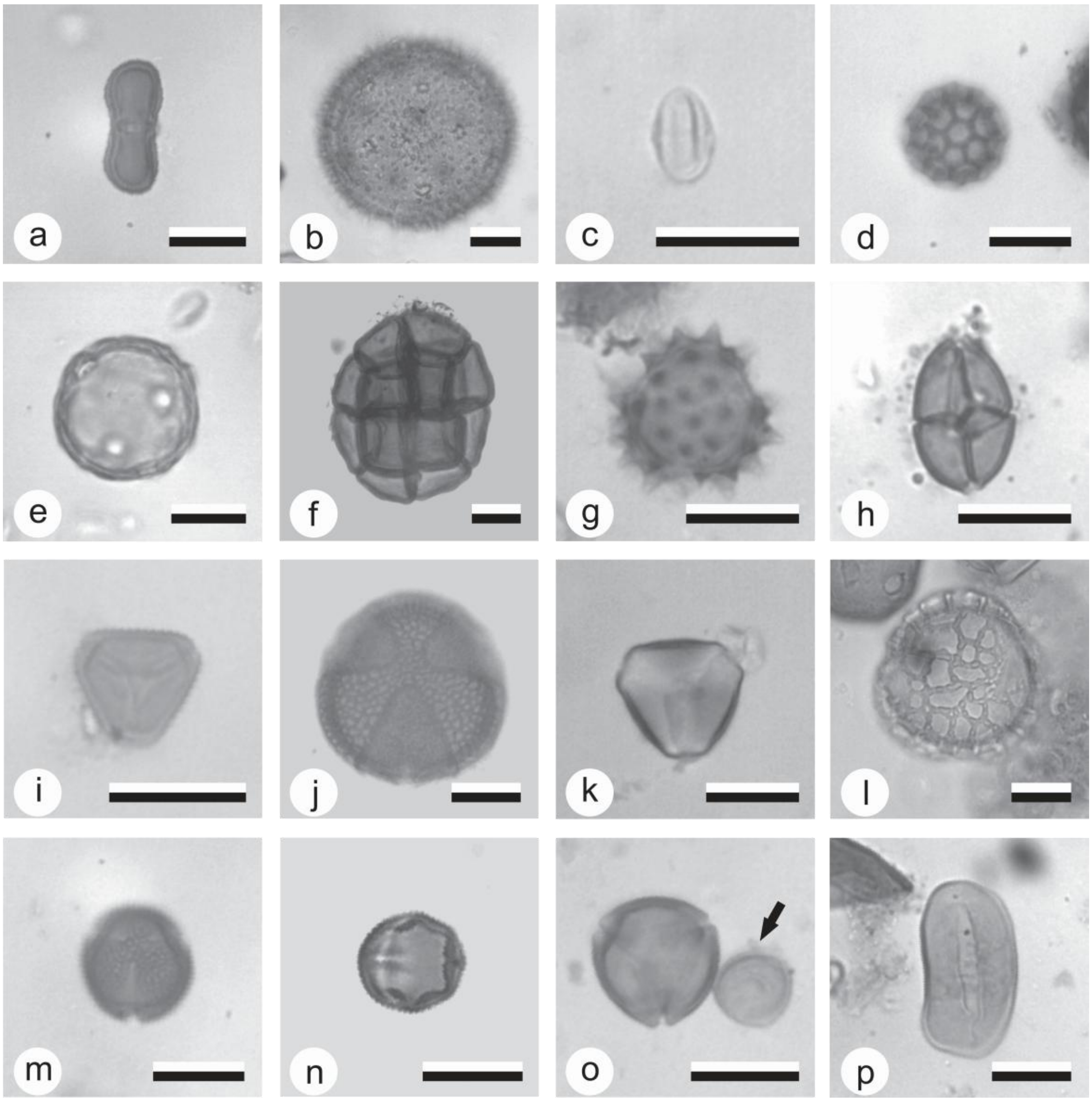


Fig. 2 Photomicrographs of pollen types recorded in honeys of *T. angustula* from tropical semiarid areas in northeastern Brazil, South America. **a** Apiaceae type - equatorial view (ev), **b** *Boerhaavia* (Nyctaginaceae) - general view (gv), **c** *Cecropia* (Urticaceae) - ev, **d** *Gomphrena demissa* (Amaranthaceae) - gv, **e** *Heteropterys* (Malpighiaceae) - gv, **f** *Inga* (Fabaceae) - polyad, **g** *Mikania* (Asteraceae) - polar view (pv), **h** *Mimosa tenuiflora* (Fabaceae) - tetrad, **i** *Myrcia* (Myrtaceae) - pv, **j** *Poincianella pyramidalis* (Fabaceae) - pv, **k** *Prosopis juliflora* (Fabaceae) - pv, **l** *Quararibea* (Malvaceae) - pv, **m** *Schinus* (Anacardiaceae) - pv, **n** *Schinus* - ev, **o** *Solanum* (Solanaceae) - pv and *Brosimum* (Moraceae - arrow), **p** *Syagrus coronata* (Arecaceae) - ev. Bars = 20 µm.

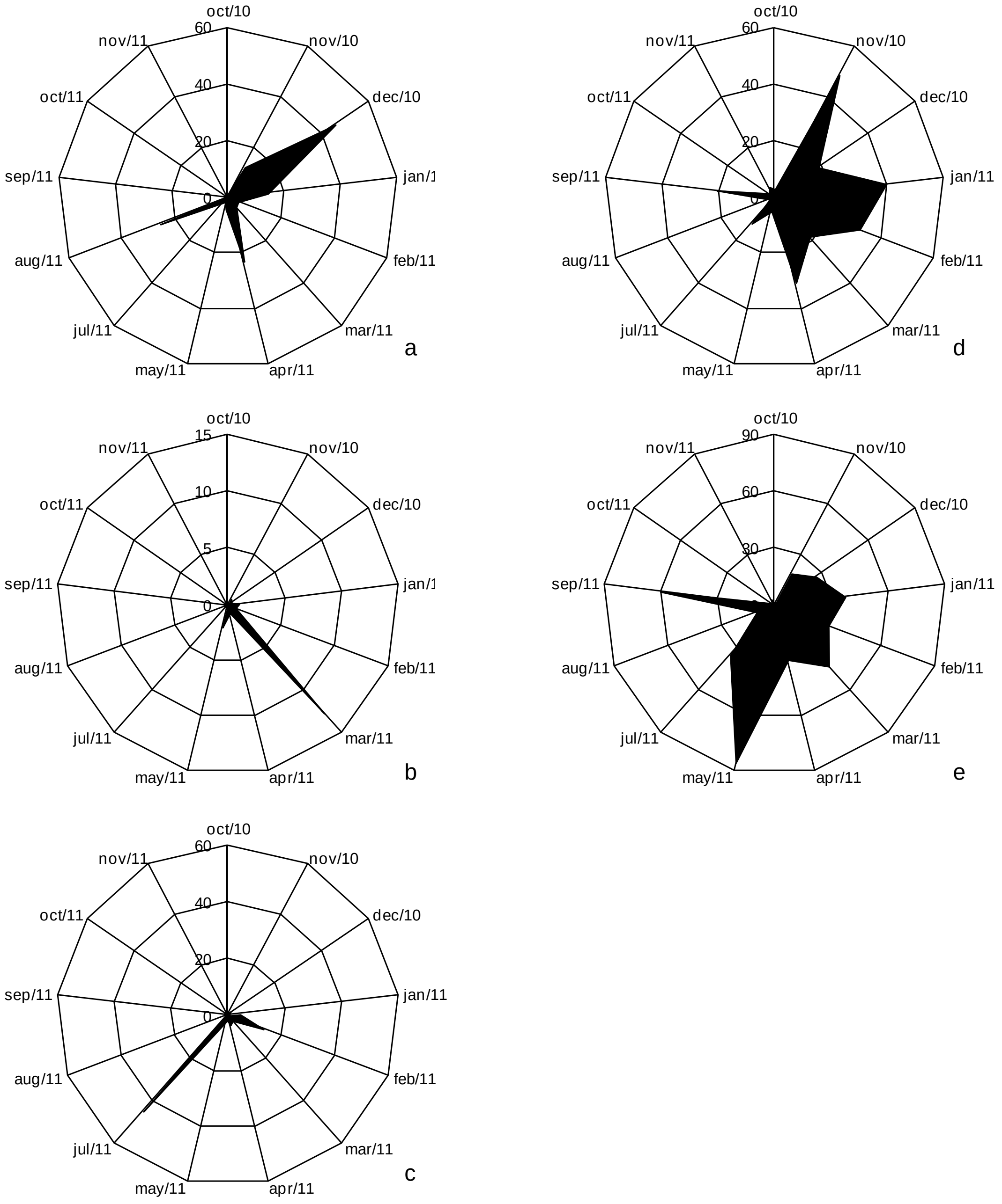


Fig. 3 Monthly frequency (%) of pollen types most represented in honeys of *T. angustula* from Itaberaba (Bahia, NE Brazil) encountered at a relative frequency above 10% in at least one sample and percentages of occurrence exceeding 50% in all samples: **a** *Heteropterys*, **b** *Mikania*, **c** *Myrcia*, **d** *Prosopis juliflora*, **e** *Solanum*

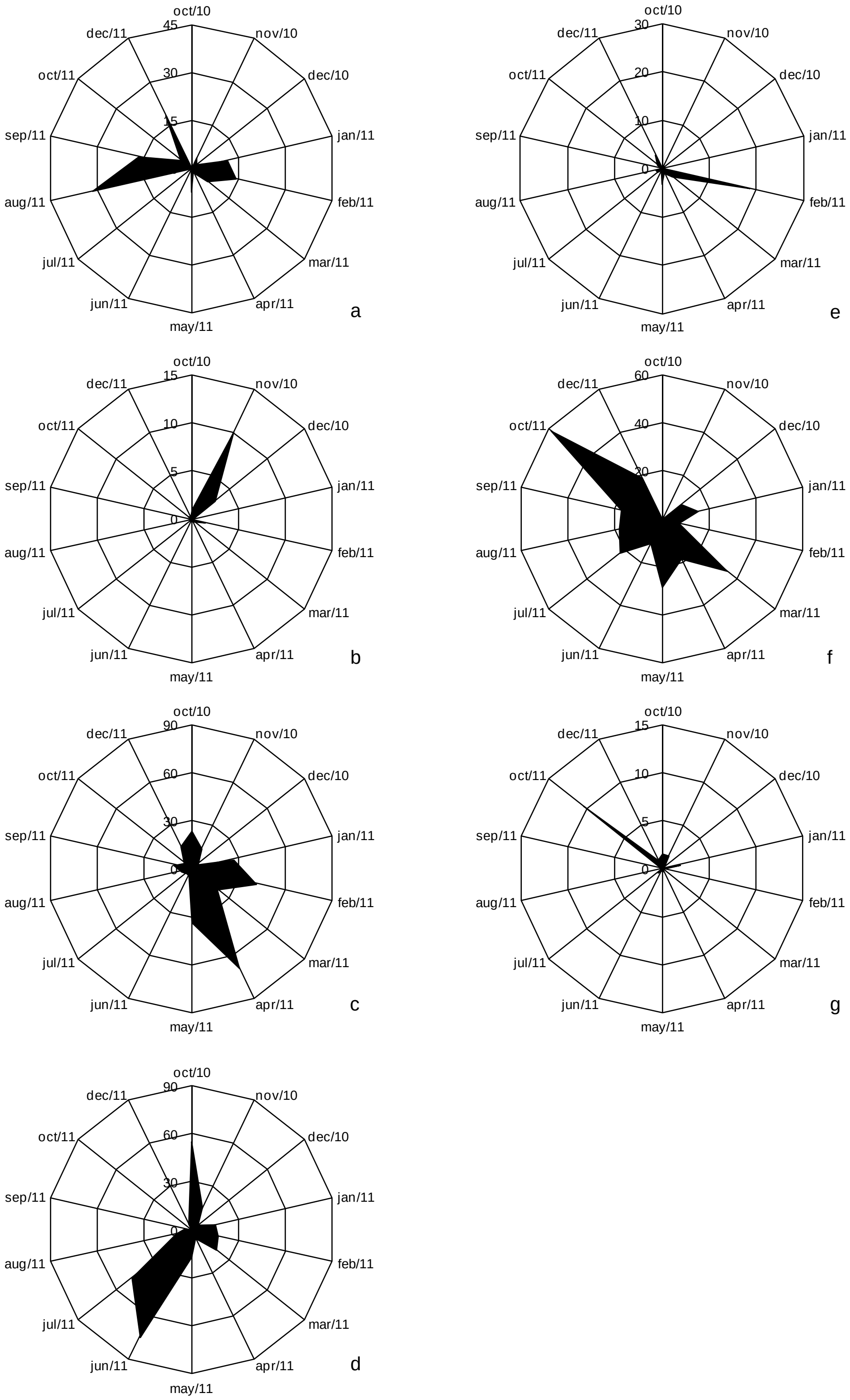


Fig. 4 Monthly frequency (%) of pollen types most represented in honeys of *T. angustula* from Ruy Barbosa (Bahia, NE Brazil) encountered at a relative frequency above 10% in at least one sample and percentages of occurrence exceeding 50% in all samples: **a** *Heteropterys*, **b** *Mimosa tenuiflora*, **c** *Prosopis juliflora*, **d** *Schinus*, **e** *Senna macranthera*, **f** *Solanum*, **g** *Syagrus coronata*

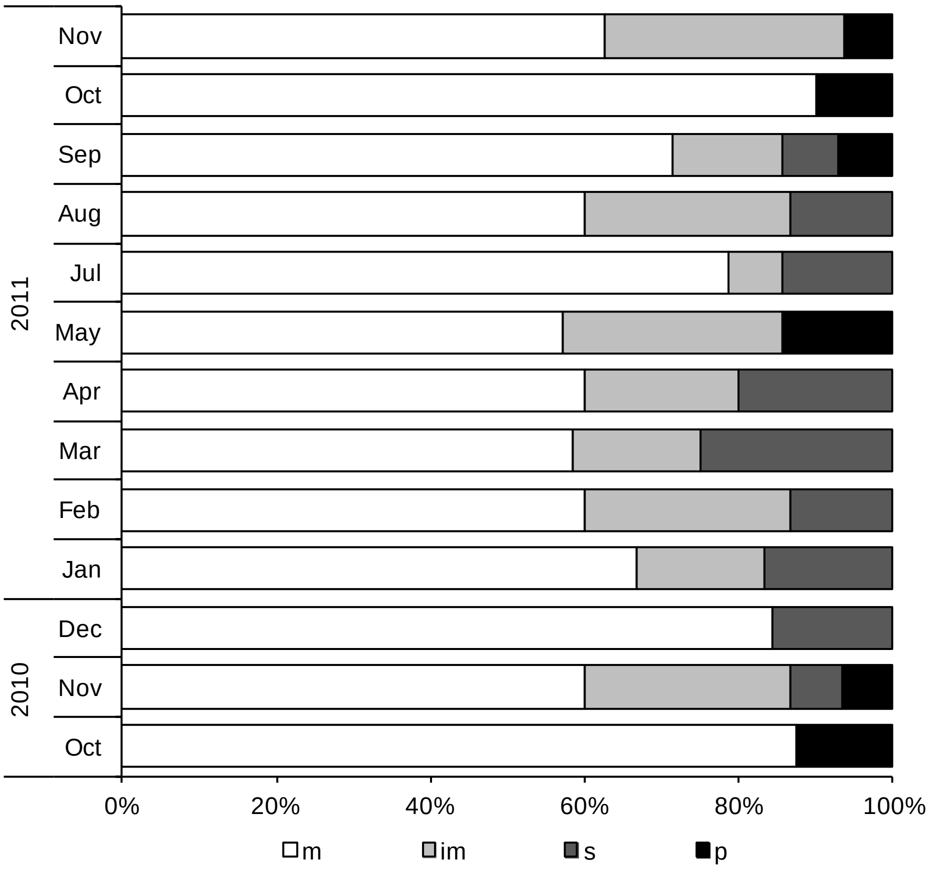


Fig. 5 Seasonal distribution of frequency classes of pollen types in honeys of *T. angustula* collected in Itaberaba (Bahia, NE Brazil); **p** predominant pollen, **s** secondary pollen, **im** important minor pollen, **m** minor pollen

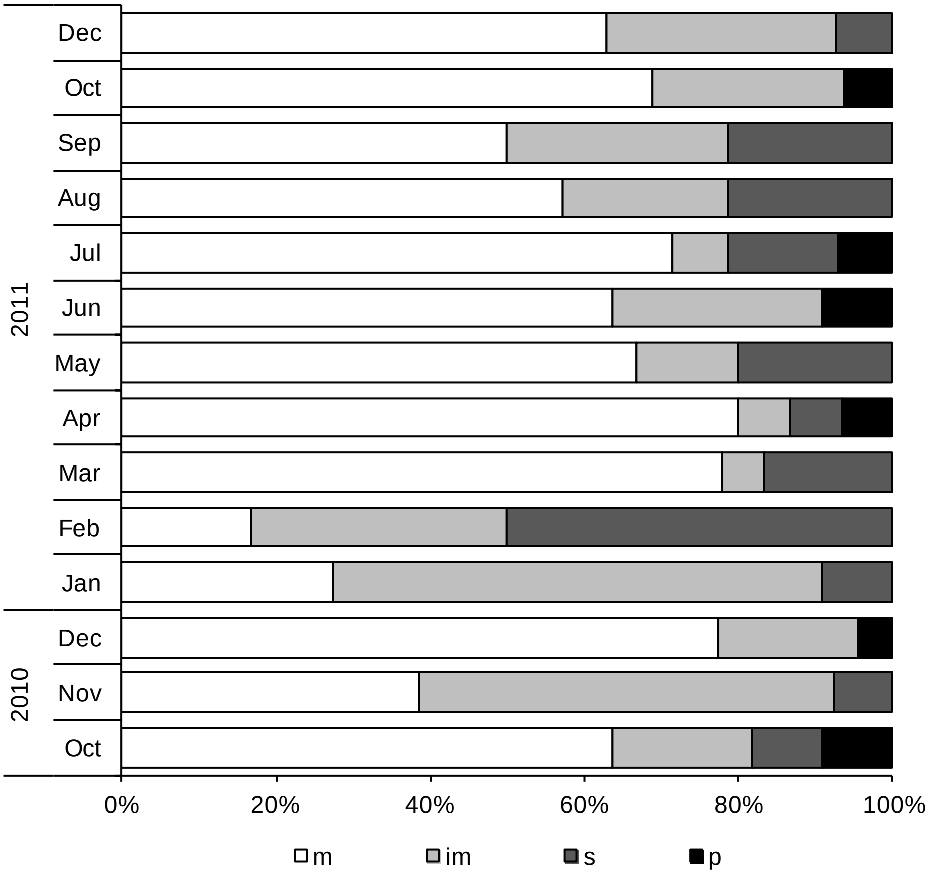


Fig. 6 Seasonal distribution of frequency classes of pollen types in honeys of *T. angustula* collected in Ruy Barbosa (Bahia, NE Brazil); **p** predominant pollen, **s** secondary pollen, **im** important minor pollen, **m** minor pollen

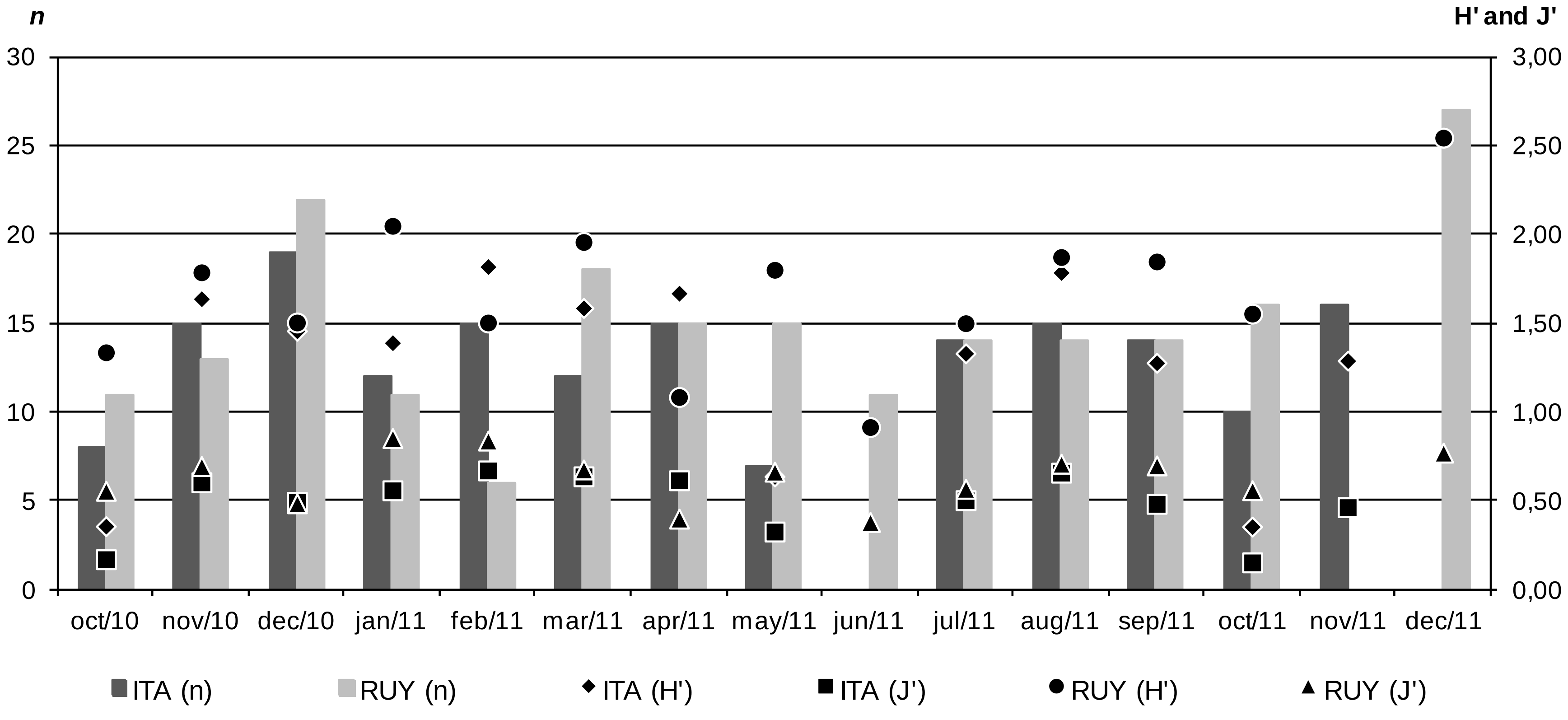


Fig. 7 Number of pollen types (*n*), Shannon-Weaver Diversity Index (H') and Pielou’s Evenness Index (J') for samples of honeys produced by *T. angustula* in Itaberaba (ITA) and Ruy Barbosa (RUY), Bahia State, NE Brazil

Table 1 Seasonal pollen spectrum of honeys of *T. angustula* from Itaberaba (Bahia, NE Brazil), indicating the frequency classes of pollen types per sample and the occurrence classes based on the presence or absence of the pollen types in the set of samples analysed. Frequency classes: **p** predominant pollen, **s** secondary pollen, **im** important minor pollen, **m** minor pollen. Classes of occurrence (C.O.): **VF** very frequent, **F** frequent, **I** infrequent, **R** rare

Plant Family	**Pollen type**	**2010**			**2011**										**C.O.**
		Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	
Amaranthaceae	*Alternanthera brasiliana*	–	–	–	–	m	m	m	–	m	m	m	–	–	F
Anacardiaceae	*Schinus*	–	–	–	–	–	–	–	–	–	s	im	p	p	F
Anacardiaceae	*Tapirira guianensis*	–	–	–	–	–	–	–	–	–	–	–	m	–	R
Apiaceae	Apiaceae type	–	–	–	–	–	–	–	–	–	im	m	–	im	F
Arecaceae	*Cocos nucifera*	–	–	m	m	–	–	–	–	–	–	–	–	–	I
Arecaceae	*Syagrus coronata*	–	m	–	–	–	s	m	–	–	–	–	–	m	F
Asteraceae	*Gomphrena demissa*	–	–	m	–	m	–	im	–	m	–	–	–	–	F
Asteraceae	*Mikania*	–	m	m	m	m	im	m	m	–	–	m	–	m	VF
Cucurbitaceae	*Cayaponia*	–	–	m	–	–	–	m	–	–	–	–	–	–	I
Euphorbiaceae	*Alchornea triplinervia*	–	–	–	–	–	–	–	–	–	im	im	–	m	F
Euphorbiaceae	*Croton*	–	–	m	–	–	–	–	–	–	–	–	–	–	R
Euphorbiaceae	*Euphorbia*	–	–	m	–	m	m	–	–	m	–	–	–	–	F
Fabaceae	*Aeschynomene*	–	–	–	–	–	–	–	–	m	im	–	–	–	I
Fabaceae	Caesalpinioideae type	–	–	–	–	m	m	–	–	–	–	–	–	–	I
Fabaceae	*Chamaecrista nictitans*	m	–	–	–	–	–	–	–	–	–	–	–	–	R
Fabaceae	*Copaifera langsdorffii*	–	–	m	m	–	–	–	–	–	–	–	–	–	I
Fabaceae	*Inga*	–	–	–	–	–	–	–	–	–	–	m	–	–	R
Fabaceae	*Machaerium*	–	–	m	–	–	–	–	–	–	–	–	–	–	R
Fabaceae	*Mimosa invisa*	–	–	–	–	–	–	–	–	m	–	–	–	–	R
Fabaceae	*Mimosa pudica*	–	–	–	–	–	–	–	–	m	m	–	–	–	I
Fabaceae	*Mimosa tenuiflora*	–	m	m	–	m	–	m	–	m	m	m	m	m	VF
Fabaceae	*Poincianella pyramidalis*	–	–	m	m	–	–	m	–	–	–	–	–	m	F
Fabaceae	*Prosopis juliflora*	m	p	s	s	s	s	s	im	im	m	s	m	im	VF
Fabaceae	*Senna macranthera*	m	m	–	m	im	m	im	m	–	m	–	m	im	VF
Lamiaceae	*Hyptis suaveolens*	–	–	m	–	–	–	–	–	–	–	–	–	–	R

Table 1 (Continuation)

Plant Family	**Pollen type**	**2010**			**2011**										**C.O.**
		Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	
Malpighiaceae	*Heteropterys*	m	im	s	im	im	im	s	im	m	s	m	m	m	VF
Malvaceae	Bombacoideae type	m	im	–	–	–	–	–	–	–	–	–	–	–	I
Malvaceae	*Quararibea*	–	im	m	m	m	–	m	m	–	–	m	–	–	VF
Malvaceae	*Sidastrum micranthum*	–	–	–	–	–	–	m	–	–	–	–	–	–	R
Malvaceae	*Waltheria indica*	–	–	–	–	–	–	–	–	m	–	–	–	–	R
Melastomataceae	*Clidemia hirta*	–	m	–	m	–	m	–	–	–	–	–	–	–	F
Moraceae	*Brosimum*	–	–	–	–	–	–	–	–	–	m	m	m	m	F
Myrtaceae	*Eucalyptus*	–	m	–	–	–	–	–	–	–	–	m	–	–	I
Myrtaceae	*Myrcia*	m	m	m	im	im	m	im	m	s	m	m	m	m	VF
Nyctaginaceae	*Boerhaavia*	–	–	–	–	–	–	–	–	–	–	–	–	m	R
Phytolaccaceae	*Microtea paniculata*	–	m	–	–	im	–	m	–	–	–	–	m	–	F
Poaceae	Poaceae type	–	–	m	m	–	–	–	–	m	m	–	–	m	F
Polygonaceae	*Coccoloba*	–	–	m	–	–	–	–	–	–	–	–	–	–	R
Rhamnaceae	*Ziziphus joazeiro*	–	–	–	–	–	–	–	–	–	–	–	–	im	R
Rutaceae	*Citrus*	–	–	–	–	m	–	–	–	–	–	–	–	–	R
Solanaceae	*Solanum*	m	s	s	s	s	s	s	p	s	im	p	m	im	VF
Urticaceae	*Cecropia*	p	im	–	–	–	–	–	–	–	–	–	–	–	I
Verbenaceae	*Lantana camara*	–	–	–	–	–	–	–	–	–	m	–	–	–	R
Undetermined		–	m	m	–	m	m	–	–	m	–	–	–	–	F
Number of pollen types		8	15	19	12	15	12	15	7	14	15	14	10	16	–
Shannon-Weaver's Index (H')		0.36	1.64	1.46	1.39	1.82	1.59	1.67	0.64	1.33	1.79	1.28	0.36	1.29	–
Pielou's Index (J')		0.17	0.61	0.50	0.56	0.67	0.64	0.62	0.33	0.51	0.66	0.48	0.15	0.47	–

Table 2 Seasonal pollen spectrum of honeys of *T. angustula* from Ruy Barbosa (Bahia, NE Brazil), indicating the frequency classes of pollen types per sample and the occurrence classes based on the presence or absence of the pollen types in the set of samples analysed. Frequency classes: **p** predominant pollen, **s** secondary pollen, **im** important minor pollen, **m** minor pollen. Classes of occurrence (C.O.): **VF** very frequent, **F** frequent, **I** infrequent, **R** rare

Plant Family	**Pollen Type**	**2010**			**2011**											**C.O.**
		Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Dec**	
Acanthaceae	*Justicia*	–	–	m	im	–	–	–	–	–	–	–	–	–	–	I
Amaranthaceae	*Alternanthera brasiliana*	m	m	–	–	–	m	m	m	–	–	m	m	–	m	VF
Amaranthaceae	*Amaranthus*	–	–	–	–	–	–	–	–	–	–	–	–	–	m	R
Amaranthaceae	*Chenopodium*	–	–	–	–	–	–	m	–	m	–	–	–	–	–	I
Amaranthaceae	*Gomphrena demissa*	–	–	p	–	–	–	–	m	m	–	–	–	m	–	F
Anacardiaceae	*Schinus*	p	im	im	im	s	s	im	s	p	p	im	im	–	im	VF
Apiaceae	Apiaceae type	m	im	m	–	–	m	m	m	m	–	m	m	m	–	VF
Apocynaceae	Apocynaceae type	–	–	–	–	–	–	–	–	–	–	–	–	–	m	R
Arecaceae	*Syagrus coronata*	m	m	m	m	–	–	m	–	m	m	–	–	im	m	VF
Asteraceae	*Mikania*	–	–	–	–	–	m	–	m	–	–	m	m	–	m	F
Boraginaceae	Boraginaceae type	–	–	–	–	–	–	–	–	–	–	m	–	–	–	R
Bromeliaceae	Bromeliaceae type	–	–	–	–	–	–	–	–	–	–	–	–	–	m	R
Euphorbiaceae	*Acalypha*	–	–	m	im	–	–	–	–	m	–	–	–	–	m	F
Euphorbiaceae	*Croton*	–	–	m	–	–	–	–	–	–	–	–	–	–	–	R
Euphorbiaceae	*Euphorbia*	–	–	–	–	–	–	–	–	–	–	s	im	m	im	F
Fabaceae	*Anadenanthera colubrina*	–	–	–	–	–	–	–	–	–	–	–	m	m	m	F
Fabaceae	Caesalpinioideae type	–	s	m	–	–	m	m	–	–	m	–	–	–	–	F
Fabaceae	*Chamaecrista nictitans*	–	–	–	–	–	–	–	m	–	–	–	–	–	im	I
Fabaceae	*Copaifera langsdorffii*	–	–	m	–	–	–	–	–	–	–	–	–	–	m	I
Fabaceae	Fabaceae type 1	im	–	m	im	–	–	–	–	–	–	–	–	–	–	F
Fabaceae	Fabaceae type 2	–	–	–	–	–	–	–	–	im	–	–	–	–	–	R
Fabaceae	*Mimosa invisa*	–	–	m	–	–	–	–	–	–	–	–	–	–	–	R
Fabaceae	*Mimosa tenuiflora*	m	im	im	–	m	m	m	–	–	m	–	–	m	m	VF

Table 2 (Continuation)

Plant Family	Pollen Type	2010			2011											C.O.
		Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Dec**	
Fabaceae	*Peltogyne*	m	–	–	–	–	–	–	–	–	–	–	–	–	–	R
Fabaceae	*Poincianella pyramidalis*	–	im	m	–	–	m	–	–	–	m	–	–	–	–	F
Fabaceae	*Prosopis juliflora*	s	im	im	s	s	s	p	s	im	im	im	im	im	im	VF
Fabaceae	*Senna macranthera*	–	–	m	–	s	m	m	im	m	m	m	m	m	im	VF
Fabaceae	*Senna/Cassia*	–	–	–	–	–	–	m	m	–	–	–	–	m	m	F
Gentianaceae	Gentianaceae type	–	–	–	–	–	–	–	m	–	–	–	–	–	–	R
Malpighiaceae	*Heteropterys*	–	im	m	im	im	im	m	im	m	–	s	s	im	s	VF
Malvaceae	*Helicteres macropetala*	–	–	–	–	–	m	–	–	–	m	–	–	–	–	I
Malvaceae	*Herissantia*	–	–	m	–	–	m	–	–	–	–	–	–	–	–	I
Malvaceae	*Quararibea*	–	–	–	–	–	–	–	m	–	–	–	–	–	m	I
Melastomataceae	*Clidemia hirta*	–	–	m	m	–	–	–	m	–	m	m	m	–	im	F
Moraceae	*Brosimum*	–	–	–	–	–	–	m	–	–	s	im	s	im	m	F
Myristicaceae	*Virola*	–	–	–	–	–	–	–	–	–	–	–	im	m	–	I
Myrtaceae	*Eucalyptus*	m	–	–	–	–	–	–	–	–	–	–	–	–	–	R
Myrtaceae	*Myrcia* sp. 1	m	–	–	–	–	m	m	–	–	–	m	–	–	im	F
Myrtaceae	*Myrcia* sp. 2	–	–	–	–	–	–	–	–	–	m	m	–	–	–	I
Nyctaginaceae	*Boerhaavia*	–	–	m	–	–	m	–	–	–	–	–	–	m	m	F
Phytolaccaceae	*Microtea paniculata*	–	–	–	–	–	m	–	m	–	–	–	m	m	m	F
Poaceae	Poaceae type	im	im	–	–	–	m	–	–	–	m	–	–	–	im	F
Rhamnaceae	*Ziziphus joazeiro*	–	m	–	–	–	–	–	–	–	–	–	–	–	–	R
Rubiaceae	*Psychotria*	–	–	–	–	–	–	m	–	–	–	–	–	–	–	R
Sapindaceae	*Serjania*	–	–	–	m	–	–	–	–	–	–	–	–	–	–	R
Sapotaceae	*Pouteria*	–	–	m	–	–	–	–	–	–	–	–	–	–	–	R
Solanaceae	*Solanum*	–	m	im	im	im	s	s	s	im	s	s	s	p	s	VF
Urticaceae	*Cecropia*	–	–	m	–	–	–	–	–	–	m	–	–	–	m	F
Verbenaceae	*Verbesina*	–	m	–	–	–	–	–	–	–	–	–	–	–	–	R
Undetermined		–	–	–	im	–	m	–	–	–	–	–	–	m	m	F
Number of pollen types		11	13	22	11	6	18	15	15	11	14	14	14	16	27	–
Shannon-Weaver's Index (H')		1.34	1.79	1.51	2.05	1.51	1.96	1.09	1.80	0.92	1.50	1.88	1.85	1.56	2.55	–
Pielou's Index (J')		0.56	0.70	0.49	0.86	0.84	0.68	0.40	0.67	0.38	0.57	0.71	0.70	0.56	0.77	–

Discussion

The flora of the *caatinga* region has shown great potential for enabling the rational breeding of exotic bees (apiculture) and native bees (meliponiculture) (Freitas 1991; Sampaio 2002; Freitas and Silva 2006; Santos et al., 2005; Santos FAR et al. 2006). Several melissopalynologic studies undertaken in this biome have confirmed this potential by identifying the range of plant species that supply pollen and nectar, outlining an intrinsic relationship between bees and plants, especially on issues related to pollination services (Aires and Freitas 2001; Alves et al. 2006; Borges et al. 2006; Novais et al. 2006; Oliveira et al. 2010).

The number of pollen types recognised in the spectra was higher than that recorded by Novais et al. (2006) who analysed *Tetragonisca angustula* honeys collected in *caatinga* vegetation in the Canudos Biological Station of Bahia State; this study, the only other palynological study ever conducted in Bahia with *T. angustula* honeys, identified 35 pollen types belonging mostly to the families Fabaceae, Asteraceae and Malvaceae; these families were also well represented in number of pollen types identified in our study. The large proportion of pollen types belonging to the families Euphorbiaceae, Myrtaceae and Solanaceae encountered in our study reflects the centres of diversity of these families in Neotropical South America (Ramalho et al. 1990). Studying the floristic composition of the Sierra Orobó, which borders Itaberaba and Ruy Barbosa, Cardoso and Queiroz (2008) found that Fabaceae, Euphorbiaceae, Asteraceae, Malvaceae and Myrtaceae were among the 10 most diverse families and accounted for 187 of the 597 species of Angiosperms recognised by the authors.

In Itaberaba and Ruy Barbosa, the pollen type *Solanum* (Solanaceae) occurred as the predominant and secondary pollen in many samples and was the most significant of all other types identified. The data suggest that the high content of this pollen in honey samples may be related to the use by *Tetragonisca angustula* of species of this genus for protein, as the species related to this pollen type represent primarily polliniferous plants (Machado and Lopes 2003). The genus *Solanum*, for example, is represented in the flora of Bahia by 79 species, 27 of which were found in *caatinga* areas (Stehmann et al. 2013). The genus is easily found in open and disturbed areas, and the plants are highly visited by larger bees able to perform buzz pollination (Symon 1979; Machado and Lopes 2003). Smaller bees such as *Tetragonisca angustula* are not effective pollinators of this genus and only benefit from residual pollen due to the vibration of anthers caused by other bees.

After *Solanum*, *Prosopis juliflora* was the pollen type most frequently encountered in the spectra. Even though it is not considered an endemic species of the *caatinga*, *P. juliflora* (Sw.) DC. (Fabaceae), locally known as "algaroba", is considered subspontaneous in some areas of the biome (Queiroz 2009) and occurs frequently in the study sites, as it is sown as a forage plant and resistant to dry periods typical of the semiarid region.

Giulietti et al. (2002) listed 318 plant species spanning 148 genera distributed among 42 families as endemic to the *caatinga* biome. Of these families, Arecaceae (*Syagrus*), Euphorbiaceae (*Croton*), Fabaceae (*Chamaecrista*, *Mimosa*, *Poincianella* and *Senna*), Lamiaceae (*Hyptis*), Malvaceae (*Herissantia*, *Waltheria*), Rhamnaceae (*Ziziphus*), Solanaceae (*Solanum*) and Verbenaceae (*Lantana*) were represented in the pollen spectra from Itaberaba and Ruy Barbosa.

Fabaceae is the third largest plant family worldwide and the most diverse in the *caatinga* region, with 320 species in the biome, 80 of which are endemic (Giulietti et al. 2002, 2004a; Queiroz 2009). Pollen types from this family, such as *Anadenanthera colubrina* and *Poincianella pyramidalis*, thus function as markers of *caatinga* vegetation in apicultural products and have been found in pollen spectra and on lists of regional apicultural flora (Borges et al. 2006; Santos FAR et al. 2006, Lima 2007, Oliveira 2009, Oliveira et al. 2010). According to Queiroz (2009), *Anadenanthera colubrina* (Vell.) Brenan and *Poincianella pyramidalis* (Tul.) L.P.Queiroz are keystone species of the *caatinga sensu stricto*, which consists of the most characteristic vegetation of the *caatinga* biome and is characterised by a low-stature arboreal stratum (3 to 7 m tall) often without a continuous canopy, trees and shrubs with thin stems and small or compound leaves that are deciduous in the dry season, and an ephemeral herbaceous stratum. In addition to being represented by the largest number of pollen types in samples from both study areas, Fabaceae also stood out due to the high frequency (>10%) of the Caesalpinioideae type, *Mimosa tenuiflora*, *Senna macranthera*, and *Prosopis juliflora* (mentioned previously). According to Machado and Lopes (2003), *Anadenanthera colubrina* (Vell.) Brenan and *Mimosa tenuiflora* (Willd.) Poir. are species with small flowers arranged in dense inflorescences that are quite attractive to many bee species in the *caatinga* region.

Ziziphus joazeiro Mart. (Rhamnaceae) is another species characteristic of *caatinga* vegetation (Giulietti et al., 2002, 2004a), and its pollen was found in the honeys we analysed. Santos RF et al. (2006) include *Z. joazeiro* among relevant nectar-producing plants for bees in *caatinga* areas; other such species include species of the genera *Alternanthera*, *Aeschynomene, Cocos, Croton, Hyptis* and *Waltheria*, and all of these pollen types were found in honeys of *Tetragonisca angustula*. *Chamaecrista, Mimosa, Senna* and *Solanum* may be cited as genera represented by predominantly polliniferous species (Machado and Lopes 2003; Santos et al. 2006; Dutra et al. 2009).

Few samples of the honeys were classified as unifloral, i.e., with pollen from a single floral source with nectariferous potential. *Schinus* was the unifloral pollen type most frequently encountered in our study. Cesário and Gaglianone (2008) studied the floral biology and reproductive phenology of *Schinus terebinthifolius* Raddi (Anacardiaceae) and considered this species very important for the collection of pollen and nectar in the *restinga* (sandy coastal plains). However, we believe that further studies on the actual production of nectar by *Schinus* species occurring in the *caatinga* are needed to clarify whether these species are suppliers of raw materials for the production of honey.

The number of polliniferous species in the honey spectra makes it difficult to characterise exactly which samples represent unifloral honeys, especially in regions with a flora as diverse as that of tropical regions. According to Molan (1998), the pollen spectrum is insufficient to pinpoint the botanical origin of honey. One must assume that no honey is completely unifloral and that the amount of pollen and nectar produced by plants varies according to different factors linked to seasonality, climate and soil conditions, among others (Moar 1985; Molan 1998; Oliveira 2009). Thus, studies focused on floral morphology and biology, nectar secretion, pollen production and pollination mechanisms can confirm the polliniferous or nectariferous potential of a species in relation to honey production (Moar 1985). We believe that taking these factors into account is crucial, especially when studying honeys produced in tropical areas where knowledge of the native flora is still limited in light of the plant diversity found therein. However, when we determine the pollen types that comprise a given honey spectrum, we not only assess the nectariferous sources but also the sources of pollen and, therefore, of protein for bees. Because some honeys in Itaberaba and Ruy Barbosa had many pollen types related to polliniferous taxa such as *Brosimum*, *Cecropia* and *Solanum*, these honeys can have particular sensorial and organoleptic characteristics; however, the pollen types do not necessarily reflect the crucial sources of nectar for *Tetragonisca angustula* in these areas.

The amplitude of the temporal trophic niche recorded in Itaberaba and Ruy Barbosa, ranging from 0.36 to 2.55, was similar to the value found by Sosa-Nájera et al. (1994) who studied *T. angustula* honey at two sites in southeastern Mexico. Niche diversity depends on the seasonally availability of floral resources, and flowering can occur in periods of mass flowering (Freitas and Silva 2006), constant flowerings throughout the year, flowerings without a defined boom or flowerings restricted to a given period. The mass flowerings of some species may be the cause of their periodic dominances in pollen spectra. *Prosopis juliflora*, *Schinus* and *Solanum*, the main predominant pollen types in the spectra of Itaberaba and Ruy Barbosa, occurred in the honeys of most months sampled, indicating that species related to these pollen types flower throughout much of the year but with different intensity at different months. However, less than 20% of the species detected in pollen spectra occurred in more than 50% of the samples, indicating that their flowering is reduced to a few months. According to Machado et al. (1997), plant phenological patterns in very dry areas are highly seasonal and most species are extended-deciduous. The reduced temporal record of certain species in the honey therefore coincides with periodic flowering, which usually accompanies the period of leaf formation (Machado et al. 1997).

Evenness values (J') usually follow the same trend as the diversity index. In Ruy Barbosa, the mean J' was higher than the J’ recorded in Itaberaba, indicating a more heterogeneous use of pollen sources in the latter municipality. The trend toward the homogeneous use of floral resources in Ruy Barbosa followed the greater size of the pollen niche for *Tetragonisca angustula* detected in this location. The high number of pollen types with low representativity in the spectra contributes to increasing the value of the indices; according to Sosa-Nájera et al. (1994), the high variety of pollen types reflects the dispersion rate of *T. angustula* workers and therefore demonstrates that the foraging habits of this species are polylectic. In general, the few published studies on the pollen spectra of honeys of this bee do not calculate ecological indices such as diversity and evenness, which can help characterise the foraging pattern of the species. Thus, we suggest that authors include these basic ecological analyses in their studies.

Acknowledgments

Many thanks to Prof. Carleandro de Souza Dias, M.Sc. for helping us establish contact with beekeepers and with the Bahia Agricultural Development Company S.A. (Empresa Baiana de Desenvolvimento Agrícola S.A. - EBDA) in Itaberaba, and for providing honey samples from his private bee yard; to the directors of the Mãe Jovina Agricultural Family School (Escola Família Agrícola Mãe Jovina) for granting access to the institution's bee yard in Ruy Barbosa; to the beekeepers Alex and Manoel for providing samples; to the intern Bruno Henrique Andrade-Silva for his assistance in monthly collections in the field and in the laboratory; to the regional management and staff of EBDA in Itaberaba for logistical support during field trips; to colleagues from the Laboratory of Plant Micromorphology at the Bahia State University at Feira de Santana (Universidade Estadual de Feira de Santana - UEFS) for help in the laboratory identifying pollen types and for discussions throughout this work; to Leilton Santos Damascena, M.Sc. for help with the map; to the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq) for partially funding this project and for the grants awarded (processes 575747/2008-0, 143084/2009-7, 303557/2010-9 and 477127/2011-8).

References

Aires ERB, Freitas BM (2001) Caracterização palinológica de algumas amostras de mel do Estado do Ceará. Ciên Agron 32(1/2):22–29

Albuquerque UP, Araújo EL, El-Deir ACA, Lima ALA, Souto A, Bezerra BM, Ferraz EMN, Freire EMX, Sampaio EVSB, Las-Casas FMG, Moura GJB, Pereira GA, Melo JG, Ramos MA, Rodal MJN, Schiel N, Lyra-Neves RM, Alves RRN, Azevedo-Júnior SM, Telino Júnior WR, Severi W (2012) Caatinga revisited: ecology and conservation of an important seasonal dry forest. The Scientific World Journal 2012, Article ID 205182. doi: 10.1100/2012/205182

Almeida AMM, Carvalho CAL, Abreu RD, Santos FAR, Araújo RCMS, Oliveira PP (2005) Espectro polínico de amostras de mel de *Apis mellifera* L. provenientes de Nova Soure, Bahia. Rev Agric 80(2):131–147

Alves RMO, Souza BA, Carvalho CAL (2006) Espectro polínico de amostras de mel de *Melipona mandacaia* Smith. 1863 (Hymenoptera - Apidae). Acta Sci Biol Sci 28(1):33–38

Borges RLB, Lima LCL, Oliveira PP, Silva FHM, Novais JS, Dórea MC, Santos FAR (2006) O pólen no mel do semi-árido brasileiro. In: Santos FAR (ed) Apium plantae. IMSEAR, Recife, PE, pp 103–118

Cardoso DBOS, Queiroz LP (2008) Floristic composition of seasonally dry tropical forest fragments in Central Bahia, Northeastern Brazil. J Bot Res Inst Texas 2(1):551–573

Carvalho CAL, Nascimento AS, Pereira LL, Machado CS, Clarton L (2006) Fontes nectaríferas e poliníferas utilizadas por *Melipona quadrifasciata* (Hymenoptera: Apidae) no Recôncavo Baiano. Magistra 18:249–256

Cesário LF, Gaglianone MC (2008) Biologia floral e biologia reprodutiva de *Schinus terebinthifolius* Raddi (Anacardiaceae) em restinga do Norte Fluminense. Acta bot bras 22(3):828–833

Dutra VF, Vieira MF, Garcia FCP, Lima HC (2009) Fenologia reprodutiva, síndromes de polinização e dispersão em espécies de Leguminosae dos campos rupestres do Parque Estadual do Itacolomi, Minas Gerais, Brasil. Rodriguésia 60(2):371–387

Erdtman G (1960) The acetolysis method – a revised description. Sv Bot Tidskr 54(4):561–564

Freitas BM (1991) Potencial da caatinga para produção de pólen e néctar para a exploração apícola. Dissertation, Federal University of Ceará

Freitas BM, Silva EMS (2006) Potencial apícola da vegetação do Semi-Árido brasileiro. In: Santos FAR (ed) Apium plantae. IMSEAR, Recife, PE, pp 19–32

Freitas BM, Imperatriz-Fonseca VL, Medina LM, Kleinert AMP, Galetto L, Nates-Parra G, Quezada-Euán JJG (2009) Diversity, threats and conservation of native bees in the Neotropics. Apidologie 40:332–346. doi: 10.1051/apido/2009012

Giannini TC, Acosta AL, Garófalo CA, Saraiva AM, Alves-dos-Santos I, Imperatriz-Fonseca VL (2012) Pollination services at risk: bee habitats will decrease owing to climate change in Brazil. Ecological Modelling 244:127–131. doi: 10.1016/j.ecolmodel.2012.06.035

Giulietti AM, Harley RM, Queiroz LP, Barbosa MRV, Du Bocage Neta AL, Figueiredo MA (2002) Espécies endêmicas da caatinga. In: Sampaio EVSB, Giulietti AM, Virgínio J, Gamarra-Rojas CFL (eds) (2002) Vegetação e flora da caatinga. APNE/CNIEB, Recife, PE, pp 103–108

Giulietti AM, Du Bocage Neta AL, Castro AAJF, Gamarra-Rojas CFL, Sampaio EVSB, Virgínio JF, Queiroz LP, Figueiredo MA, Rodal MJN, Barbosa MRV, Harley RM (2004a) Diagnóstico da vegetação nativa do bioma caatinga. In: Silva JMC, Tabarelli M, Fonseca MT, Lins LV (orgs) (2004) Biodiversidade da caatinga: áreas e ações prioritárias para a conservação. MMA, Brasília, DF, pp 47–90

Giulietti AM, Du Bocage Neta AL, Paula DC, Barbosa DC, Nogueira E, Sampaio EVSB, Silva GC, Machado IC, Virgínio JF, Maia LC, Griz LMS, Queiroz LP, Lima JLS, Silva MA, Figueiredo MA, Rodal MJN, Barradas MM, Barbosa MRV, Harley RM, Chaves SM (2004b) Vegetação: áreas e ações prioritárias para a conservação da caatinga. In: Silva JMC, Tabarelli M, Fonseca MT, Lins LV (orgs) (2004) Biodiversidade da caatinga: áreas e ações prioritárias para a conservação. MMA, Brasília, DF, pp 113–131

Imperatriz-Fonseca VL, Kleinert-Giovannini A, Cortopassi-Laurino M, Ramalho M (1984) Hábitos de coleta de *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). Bolm Zool Univ S Paulo 8:115–131

Iwama S, Melhem TS (1979) The pollen spectrum of the honey of *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). Apidologie 10(3):275–295. doi: 10.1051/apido:19790305

Jones GD, Bryant VM Jr (1996) Melissopalynology. In: Jansonius J, McGregor DC (eds) Palynology: principles and applications, v. 3. AASP Foundation, Dallas, pp 933–938

Jones GD, Bryant VM Jr (2004) The use of ETOH for dilution of honey. Grana 43(3):174–182. doi: 10.1080/00173130410019497

Lieux MH (1980) Acetolysis applied to microscopical honey analysis. Grana 19:57–61

Lima LCL (2007) Espécies de *Mimosa* L. (Leguminosae) do semi-árido nordestino: palinologia, fenologia, biologia floral e potencial apícola. Thesis, Bahia State University at Feira de Santana

Louveaux J, Maurizio A, Vorwohl G (1978) Methods of melissopalynology. Bee World 59(4), 139–157

Ludwig JA, Reynolds JF (1988) Statistical ecology: a primer on methods and computing. John Wiley & Sons, New York

Machado IC, Lopes AV (2003) Recursos florais e sistemas de polinização e sexuais em caatinga. In: Leal IR, Tabarelli M, Silva JMC (eds) Ecologia e conservação da caatinga. Ed. Universitária da UFPE, Recife, PE, pp 515–563

Machado ICS, Barros LM, Sampaio EVSB (1997) Phenology of caatinga species at Serra Talhada, PE, Northeastern Brazil. BIOTROPICA 29(1):57–68

Maia-Silva C, Silva CI, Hrncir M, Queiroz RT, Imperatriz-Fonseca VL (2012) Guia de plantas visitadas por abelhas na caatinga. Fundação Brasil Cidadão, Fortaleza, CE

Medeiros SS, Cavalcante AMB, Marin AMP, Tinôco LBM, Salcedo IH, Pinto TF (2012) Sinopse do censo demográfico para o semiárido brasileiro. INSA, Campina Grande, PB

Moar NT (1985) Pollen analysis of New Zealand honey. New Zeal J Agr Res 28:39–70. doi: 10.1080/00288233.1985.10426997

Molan P (1998) The limitations of the methods of identifying the floral source of honeys. Bee World 79(2):59–68

Nimer E (1972) Climatologia da região Nordeste do Brasil: introdução à climatologia dinâmica – subsídios à geografia regional do Brasil. R Bras Geogr 34(2):3–51

Novais JS, Lima LCL, Santos FAR (2006) Espectro polínico de méis de *Tetragonisca angustula* Latreille, 1811 coletados na caatinga de Canudos, Bahia, Brasil, Magistra 18(4):257–264

Oliveira PP (2009) Análise palinológica de amostras de mel de *Apis mellifera* L. produzidas no estado da Bahia. Thesis, Bahia State University at Feira de Santana

Oliveira PP, van den Berg C, Santos FAR (2010) Pollen analysis of honeys from Caatinga vegetation of the state of Bahia, Brazil, Grana 49(1):66–75. doi: 10.1080/00173130903485122

Pielou EC (1977) Mathematical ecology. John Wiley & Sons, New York

Prado D (2003) As caatingas da América do Sul. In: Leal IR, Tabarelli M, Silva JMC (eds) Ecologia e conservação da caatinga. Ed. Universitária da UFPE, Recife, PE, pp 3–73

Queiroz LP (2006) The Brazilian Caatinga: phytogeographical patterns inferred from distribution data of the Leguminosae. In: Pennington RT, Lewis GP, Ratter JA (orgs) Neotropical savannas and dry forests: diversity, biogeography, and conservation. Taylor & Francis, CRC Press, Boca Raton, FL, pp 113–149

Queiroz LP (2009) Leguminosas da caatinga. UEFS, Feira de Santana, BA

Ramalho M, Kleinert-Giovannini A, Imperatriz-Fonseca VL (1990) Important bee plants for stingless bees (*Melipona* and Trigonini) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. Apidologie 21:469–488. doi: 10.1051/apido:19900508

Roubik DW, Moreno P JE (1991) Pollen and spores of Barro Colorado Island. MBG Press, St. Louis, MO

Sampaio EVSB (2002) Uso das plantas da caatinga. In: Sampaio EVSB, Giulietti AM, Virgínio J, Gamarra-Rojas CFL (eds) Vegetação e flora da caatinga. APNE, Recife, PE, pp 49–90

Santos FAR, Oliveira AV, Lima LCL, Barros RFM, Schlindwein CP, Martins CF, Camargo RCR, Freitas BM, Kiill LHP (2005) Apícolas. In: Sampaio EVSB, Pareyn FGC, Figueroa JM, Santos Jr AG (eds) Espécies da flora nordestina com importância econômica potencial. APNE, Recife, PE, pp 15–26

Santos FAR, Oliveira JM, Oliveira PP, Leite KRB, Carneiro CE (2006) Plantas do semi-árido importantes para as abelhas. In: Santos FAR (ed) Apium plantae. IMSEAR, Recife, PE, pp 61–86

Santos RF, Kiill LHP, Araújo JLP (2006) Levantamento da flora melífera de interesse apícola no município de Petrolina - PE. Caatinga 19(3):221–227

Santos Júnior MC, Santos FAR (2003) Espectro polínico de amostras de méis coletadas na microrregião do Paraguassu, Bahia. Magistra 15(1):79–85

SEI (2013) Informações geográficas. Sistema de Dados Estatísticos. http://www.sei.ba.gov.br/side/consulta_frame.wsp?tmp.codpai=gr1&tmp.pesquisa=false. Accessed 19 March 2013

Silva FHM (2007) Contribuição à palinologia das caatingas. Thesis, Bahia State University at Feira de Santana

Sodré GS, Marchini LC, Carvalho CAL, Moreti ACCC (2007) Pollen analysis in honey samples from the two main producing regions in the Brazilian northeast. An Acad Bras Ciênc 79(3):381–388

Sosa-Nájera MS, Martínez-Henández E, Lozano-García MS, Cuadriello-Aguiar JI (1994) Nectaropolliniferous sources used by *Trigona* (*Tetragonisca*) *angustula* in Chiapas, southern México. Grana 33(4):225–230. doi: 10.1080/00173139409429003

Stehmann JR, Mentz LA, Agra MF, Vignoli-Silva M, Giacomin L (2013) Solanaceae. In: Lista de espécies da flora do Brasil. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB14716 Acccessed 29 March 2013

Symon DE (1979) Sex forms in *Solanum* (Solanaceae) and the role of pollen collecting insects. In: Hawkes JG, Lester RNL, Skelding AD (eds) The biology and taxonomy of the Solanaceae. Academic Press, London, pp 385–397

Zanella FCV, Martins CF (2003) Abelhas da caatinga: biogeografia, ecologia e conservação. In: Leal IR, Tabarelli M, Silva JMC (eds) Ecologia e conservação da caatinga. Ed. Universitária da UFPE, Recife, PE, pp 75–134

Capítulo IV

Novais, J.S.; Absy, M.L. & Santos, F.A.R.
Pollen preferences of *Tetragonisca angustula* (Hymenoptera: Apidae) in dry vegetation in Northeastern Brazil. Manuscrito em preparação para *European Journal of Entomology*

Pollen preferences of *Tetragonisca angustula* (Hymenoptera: Apidae) in dry vegetation in Northeastern Brazil

Key words. Stingless bee foraging, *caatinga* dry vegetation, entomopalynology, melissopalynology, pot-pollen, *Tetragonisca angustula*

Abstract. Knowing the floral preferences of native bees in Neotropical ecosystems allows for an understanding of the dynamics of the interdependent relationships established between the insects and the native flora. The objectives of this study were as follows: (i) investigate the spectrum of plant species that comprise the pollen pasture used by *Tetragonisca angustula* in *caatinga* (dry vegetation) areas in the semiarid region of Northeastern Brazil; (ii) identify pollen types that function as regional geographical markers; and (iii) access the pollen niche breadth and the pattern of use of floral resources by this stingless bee. In total, 23 samples of pollen stored by *T. angustula* were collected monthly, and were subjected to acetolysis. Of the 45 pollen types of pollen recognized, the *Prosopis juliflora* (Fabaceae) and *Solanum* (Solanaceae) pollens were the most representative pollen types in the samples, and 19 pollen types were shared by the spectra generated for both study areas. Species characteristic of the *caatinga*, such as *Poincianella pyramidalis* and *Senna macranthera*, were among the types identified, and these pollens were used as indicators of the geographical origin of the samples. The average values of the pollen niche breadth (H') and equitability (J') for Itaberaba (H' = 1.10; J' = 0.50) and Ruy Barbosa (H' = 1.11; J' = 0.52) indicated a generalist habit in the foraging of *T. angustula* as well as an equilibrium between the homogeneous and heterogeneous use of the floral resources by this native bee in the *caatinga*.

INTRODUCTION

Over the past several decades, emerging threats, such as deforestation, habitat loss, and the introduction of exotic species, have led to a decline in the populations of native pollinators. This phenomenon has led the international scientific community to attempt to understand the implications of this decline for global ecosystems and to propose mechanisms for attenuating it (Allen-Wardell et al., 1998; International Pollinators Initiative, 1999; Biesmeijer et al., 2006; Freitas et al., 2009; Burkle & Alarcón, 2011; Giannini et al., 2012). Considering the importance of the environmental services provided by native bees in particular, it is essential to understand the elements of their biology, behavior, and ecology, which will support conservation initiatives designed to maintain pollination (Allen-Wardell et al., 1998).

The pollinators are primarily female bees that collect pollen as the main protein source for themselves and the larvae (Michener, 2007). In the Neotropical region, however, continuous and systematic studies of the flora involved in the protein diet of native bees represent a challenge. In Brazil, these types of studies have been ongoing for decades; however, the studies are a long way from covering the entire Brazilian territory (Barth, 2004; Borges et al., 2006). Among the Brazilian biomes, the phytogeographic domain of the *caatinga* appears to represent the largest gap in botanical knowledge, largely because of the erroneous belief that this type of vegetation originated from the modification of another plant formation and exhibits low species diversity (Giulietti et al., 2004). Recent studies have indicated a surprising diversity of flora in the *caatinga* (Giulietti et al., 2002, 2004, 2009; Albuquerque et al., 2012), estimated at 4,320 species of angiosperms (Forzza et al., 2010), which are maintained by the relationships established with a range of pollinators including 187 species of native bees (Zanella & Martins, 2003). The predominantly dry vegetation in the *caatinga* establishes different ecosystem mosaics that are distributed over a total area of approximately 800,000 km², which covers practically the entire semiarid climate region of Brazil, from the northeast through a region north of the State of Minas Gerais (Prado, 2003; Giulietti et al., 2004).

Among the Meliponini reported in the Brazilian *caatinga*, *Tetragonisca angustula* (Latreille, 1811) (Hymenoptera, Apidae) is one of the most well-known and handled species. The geographical distribution of this stingless species goes beyond the Brazilian territory, extending from Mexico to Argentina (Camargo & Pedro, 2012). Although pollen studies have been performed with *T. angustula* in different Brazilian vegetation formations (Iwama & Melhem, 1979; Imperatriz-Fonseca et al., 1984; Carvalho et al., 1999; Morgado et al., 2011; Novais & Absy, 2013), there have been few studies of areas of the *caatinga*. Novais et al. (2006) performed a palynological study of honeys from this species in a hyperxerophytic *caatinga* region at the Canudos Biological Station in the northeastern microregion of Bahia State. Recently, the pollen contents of honeys from *T. angustula* originating from Itaberaba and Ruy Barbosa in Bahia State have been investigated (Novais et al., unpublished data). However, there are no reports of palynological studies using pollen stored by *T. angustula* in *caatinga* environments.

Because information regarding the floral spectrum foraged by *T. angustula* for the collection of pollen in the dry vegetation in the *caatinga* region of the Brazilian semiarid region is lacking, in this study, we asked the following questions: *i*) what pollen types reflect the floral preferences of *T. angustula* in the *caatinga* of Bahia?; *ii*) what pollen types function as regional geographical markers that participate in the composition of the pollen spectra of this species?, and *iii*) does the pattern of use of pollen resources in the areas of *caatinga* investigated indicate a homogeneous or heterogeneous use of local flora?

MATERIALS AND METHODS

Study areas

The study areas were located in the municipalities of Itaberaba (12º26'18.8"S, 40º13'12.7"W) and Ruy Barbosa (12º17'27.6"S, 40º30'03.0"W), a semiarid climate zone in the State of Bahia, Northeastern Brazil (Fig. 1). The annual precipitation in this area does not exceed 800 mm, and the average temperature is approximately 25 ºC (EMBRAPA, 2013).

The most diverse plant families in the region include Fabaceae, Euphorbiaceae, Apocynaceae, Orchidaceae, Rubiaceae, and Asteraceae, which comprise more than 20 recognized species (Cardoso & Queiroz, 2008). Depending on the altitude, various plant formations can be distinguished locally, from *caatinga* with palm trees at lower altitudes (up to 450 m), to vegetation similar to the savanna, to areas of rupestrian fields (at approximately 900 m) (Cardoso & Queiroz, 2008).

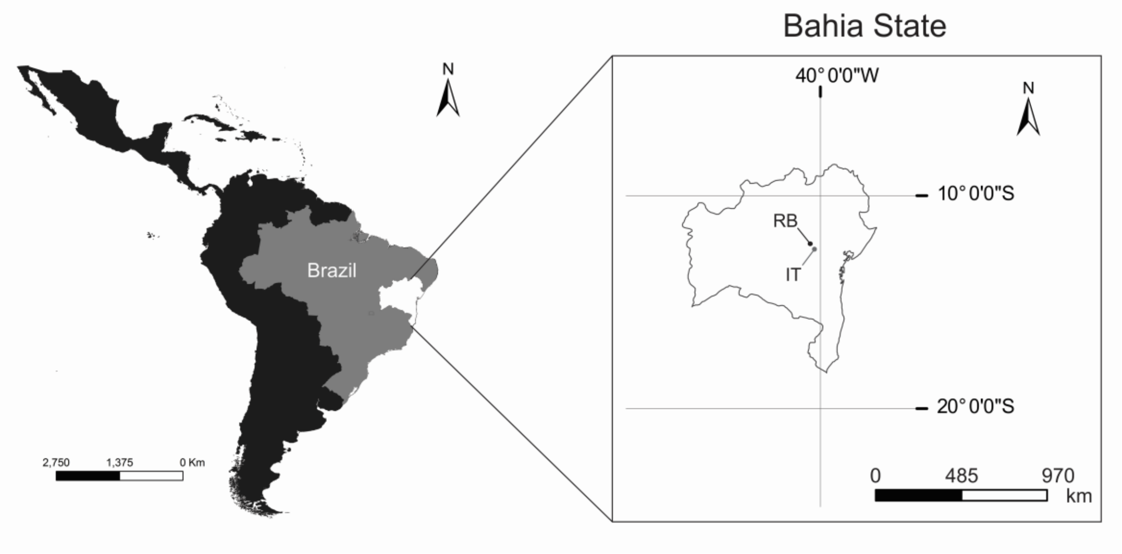


Fig. 1. The map on the left indicates the location of Brazil (light gray) in South America (black). The map on the right shows the State of Bahia, indicating the study areas Itaberaba (IT) and Ruy Barbosa (RB).

Sampling and laboratory processing

Samples of pollen (23 in total) stored in *T. angustula* colonies from the study areas were examined. In Itaberaba, the sample collection (n = 10) was performed monthly during 2011, with the exception of July and November because of the scarcity of food pots in the colonies. In Ruy Barbosa, the samples were collected monthly (n = 13) between October 2010 and December 2011, with the exception of June and November. Each month, the samples were collected preferentially from the same colony, giving priority to the pollen pots that had been sealed most recently by the bees. The material from the food pots was collected using pieces of disposable plastic straws (approximately 3 cm), which were packed in lidded pots, labeled, and preserved under refrigeration until used in the laboratory procedures.

The protocol used was in accordance with Novais and Absy (2013), which included drying the material in an oven at 40 ºC to stabilize the weight, dissolving in warm water and 95% ethanol, dehydrating in glacial acetic acid, and acetolysis (Erdtman, 1960).

For each sample, three slides were prepared using glycerin gelatin, and at least 500 pollen grains were quantified and were identified using optical microscopy. The botanical affinity of the pollen types was determined based on catalogues (Roubik & Moreno, 1991; Silva, 2007) and following consultation of the pollen library at the Laboratory of Plant Micromorphology of the Bahia State University at Feira de Santana. Because the pollen type represents a morphological entity that potentially includes various species or genera (Joosten & de Klerk, 2009), the author cited for each species refers to the first time the taxonomic entities are referred to in the text.

After the microscopic analysis, the classes of occurrence (C.O.) were established based on the presence or absence of each pollen type in the set of samples as follows: **r**, rare (<10%); **i**, infrequent (10–20%); **f**, frequent (21–50%); and **vf**, very frequent (>50%) (Jones & Bryant, 1996).

Ecological analysis

The pollen niche breadth of *T. angustula* in each sample was estimated using Shannon-Weaver's diversity index (H') (Shannon & Weaver, 1949) in accordance with the following formula:

$$H' = -\sum_{i}^{n} p_i . \ln p_i$$

In the above equation, p_i represents the proportion of each pollen type *i* found in the sample. This proportion is given by $\frac{n_i}{N}$, where n_i is the number of grains of each pollen type *i*, and *N* is the total number of pollen grains counted in the sample.

Pielou's equitability index (J') (Pielou, 1977) was used to indicate the dynamics of the use of pollen resources by the bees. The following formula was applied:

$$J' = \frac{H'}{H' \max}$$

In this equation, *H'* max represents the natural logarithm of the total number of pollen types (S_e) found in the sample; $H' \max = \ln S_e$. The J' index varies from 0 to 1. Values between 0 and 0.5 indicate the heterogeneous use of the local flora, and values between 0.5 and 1 indicate homogeneous use.

All analyses were performed using the *PAST* (Palaeontological Statistics) software version 2.16 (Hammer et al., 2001).

RESULTS

Our data demonstrated that *T. angustula* used a large number of plant species, reflected by the 45 pollen types listed in the spectra (Tables 1 and 2). Of these pollen types, 19 were common to both study areas, 10 were exclusive to the samples from Itaberaba, and 16 occurred only in Ruy Barbosa. In total, 29 pollen types belonging to 18 plant families were found in the samples from Itaberaba (Table 1), and 35 pollen types from 25 families were found in the spectrum of samples from Ruy Barbosa (Table 2). Fabaceae was the most represented family in the spectra, with eight morphologically differentiated pollen types (Tables 1 and 2).

The main plant association components of the pollen samples collected in Itaberaba included the following pollen types: *Brosimum*, *Prosopis juliflora*, *Senna macranthera* and *Solanum* (Table 1). In Ruy Barbosa, the strongest pollen associations included *Brosimum*, *Heteropterys*, *Prosopis juliflora*, *Schinus*, *Senna macranthera* and *Solanum* (Table 2). The pollen types from these species were recorded in more than 50% of the analyzed samples (“very frequent” class of occurrence), representing greater than 10% in at least one of the samples.

T. angustula demonstrated a significant preference for the pollen from *Prosopis juliflora* (Sw.) DC. In addition to being present in all of the analyzed pollen samples from both study areas (*n* = 23), *Prosopis juliflora* occurred with a frequency of greater than 10% in 20 of the samples (86.96%) (Tables 1 and 2). The second most represented pollen type in the spectra was *Solanum*, which occurred in 90% of the samples from Itaberaba and in 92.31% of the samples from Ruy Barbosa. The third most used pollen type in Itaberaba was *Senna macranthera*, which occurred in 80% of the samples from this municipality, followed by *Poincianella pyramidalis* (70%), *Mikania* (60%), *Brosimum* (60%), *Myrcia* (50%), and

Heteropterys (50%). In Ruy Barbosa, *Brosimum* and *Schinus* each occurred in 84.62% of the samples, followed by *Senna* (76.92%) and *Heteropterys* (61.54%).

In Itaberaba, the *Mikania* and *Poincianella pyramidalis* pollen types demonstrated a frequency lower than 10% in more than 50% of the samples (Table 1). In Ruy Barbosa, the pollen types included in the "very frequent" class of occurrence demonstrated a greater than 10% frequency in at least one sample (Table 2). Although a large number of pollen types were recorded in the spectra, less than 25% of these were found consistently at a high percentage (>10%) (Ramalho et al., 1985) in the *T. angustula* collections (Tables 1 and 2).

In 2011, eight pollen types were found in at least three consecutive months in Itaberaba, *Poincianella pyramidalis* (Jan – May), *Prosopis juliflora* (Jan – Dec), *Solanum* (Feb – Dec), *Senna macranthera* (Feb – Aug), *Zornia echinocarpa* (Apr – May), *Myrcia* (May – Aug), *Brosimum* (Jun – Dec), and *Mikania* (Sep – Dec). The occurrence of these pollen types in consecutive months was more evident in the second half of 2011 (Table 1).

In Ruy Barbosa, eight pollen types were also found in at least three consecutive months between Oct 2010 and Dec 2011 as follows: *Prosopis juliflora* (Oct 2010 – Dec 2011), *Solanum* (Oct – Dec 2010 and Feb – Dec 2011), *Poincianella pyramidalis* (Dec 2010 – Feb 2011), *Brosimum* (Jan – Oct 2011), *Geonoma* (Jan – Mar 2011), *Schinus* (Jan – Mar and May – Dec 2011), *Senna macranthera* (Apr – Dec 2011), and *Heteropterys* (Sep – Dec 2011) (Table 2).

In the months when the collections were performed at both study sites, the number of pollen types recognized in Itaberaba per month was slightly lower than in Ruy Barbosa (Fig. 4, Tables 1 and 2). Furthermore, in these months, the number of pollen types shared simultaneously by the spectra from the two areas varied from three (in Jan and Apr 2011) to eight (in Dec 2011) (an average of 4 ± 1.5 s.d., $n = 9$) (Fig. 4, Table 3). In total, eleven pollen types were shared by *T. angustula* in the same months in Itaberaba and Ruy Barbosa, representing the families Anacardiaceae, Arecaceae, Asteraceae, Fabaceae, Malpighiaceae, Malvaceae, Moraceae, Myrtaceae, and Solanaceae (Table 3, Fig. 3).

The ecological analysis demonstrated that the average trophic niche breadth of *T. angustula* in Itaberaba was 1.10 ± 0.46 s.d. ($n = 13$). The month with the smallest niche breadth was Jan

2011 (H' = 0.42), whereas Dec 2011 demonstrated the largest niche breadth (H' = 1.79) (Table 1). In Ruy Barbosa, the average H' index was 1.11 ± 0.35 s.d. (*n* = 10), with minimum and maximum values observed in the months of Sep 2011 (H' = 0.65) and Dec 2011 (H' = 1.76), respectively (Table 2).

The average equitability in Itaberaba was 0.50 ± 0.15 s.d. (*n* = 13), with a minimum and maximum observed in Jan 2011 (J' = 0.24) and Jun 2011 (J' = 0.69), respectively. In Ruy Barbosa, the average J' value was 0.52 ± 0.16 s.d. (*n* = 10), with a minimum and maximum observed in Sep 2011 (J' = 0.31) and Apr 2011 (J' = 0.81), respectively (Fig. 2, Tables 1 and 2).

The monthly H' and J' values for Itaberaba decreased or increased in parallel (Table 1). In Ruy Barbosa, however, this parallelism in behavior was not consistent. In 2011, in Feb-Mar and Mar-Apr, the H' and J' values demonstrated opposite trends: the H' index decreased when the J' value increased, and vice-versa (Table 2).

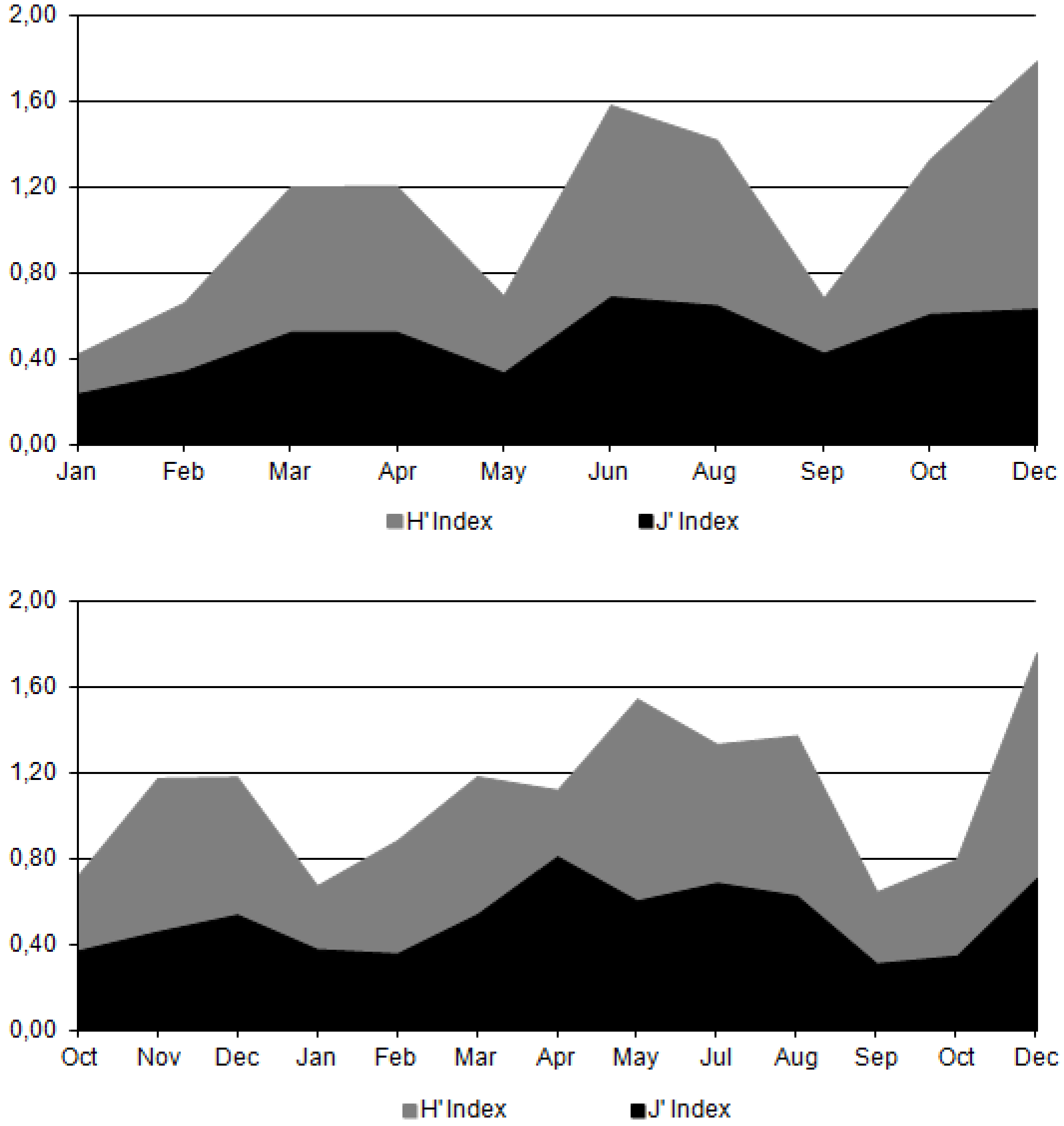


Fig. 2. Monthly variation in pollen niche breadth (H' index) and equitability (J' index) in pollen samples from *Tetragonisca angustula* colonies in the municipalities of Itaberaba (upper graph) and Ruy Barbosa (lower graph), in the semiarid region of Bahia, Northeastern Brazil.

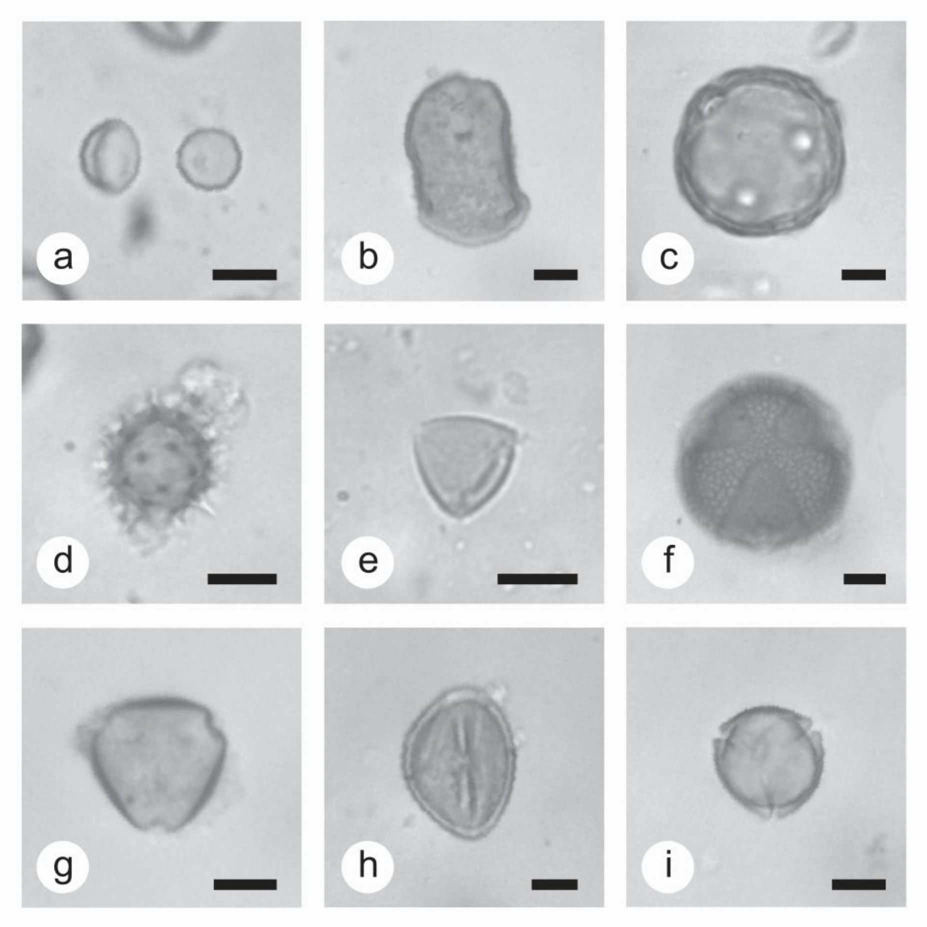


Fig. 3. Photomicrographs of some pollen types found in pollen provisions of *Tetragonisca angustula* in *caatinga* (seasonally dry tropical forest) vegetation from Northeastern Brazil. a, *Brosimum*, Moraceae. b, *Geonoma*, Arecaceae. c, *Heteropterys*, Malpighiaceae. d, *Mikania*, Asteraceae. e, *Myrcia*, Myrtaceae. f, *Poincianella pyramidalis*, Fabaceae. g, *Prosopis juliflora*, Fabaceae. h, *Senna macranthera*, Fabaceae. i, *Solanum*, Solanaceae. Bars = 10 µm.

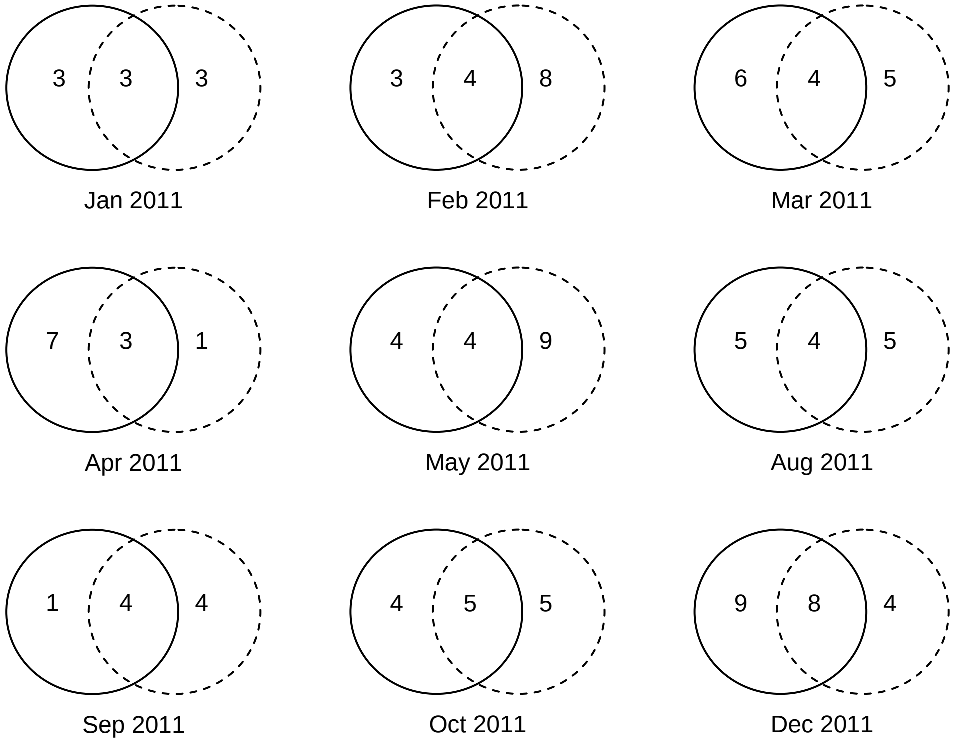


Fig. 4. Diagrams comparing the number of exclusive and shared pollen types per month in the municipalities of Itaberaba (solid circles) and Ruy Barbosa (dashed circles) stored by *Tetragonisca angustula* in *caatinga* vegetation in Northeastern Brazil. Only months in which material was collected from both locations were considered for analysis.

Table 1. Pollen spectrum showing monthly frequency (%), classes of occurrence (C.O.) and total number of pollen types in pollen samples stored by *Tetragonisca angustula* in 2011 in Itaberaba, located in the semiarid region of Bahia in Northeastern Brazil. Values from Shannon-Weaver's diversity Index (H') and Pielou's equitability index (J') are shown. C.O.: R, rare; I, infrequent; F, frequent; and VF, very frequent.

Plant Family	Pollen Type	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Dec	C.O.
Amaranthaceae	*Alternanthera brasiliana*	–	–	–	–	–	–	0,19	–	–	–	I
	Gomphrena demissa	–	–	–	0,78	–	–	–	–	0,17	–	I
Anacardiaceae	*Schinus*	–	–	–	–	–	–	–	0,74	–	0,71	I
Arecaceae	*Geonoma*	–	–	–	–	–	–	–	–	–	3,91	I
Asteraceae	Asteraceae type	–	–	–	0,58	–	–	–	–	–	–	I
	Mikania	0,18	–	0,37	–	0,57	–	–	0,18	0,17	0,53	VF
Cactaceae	*Cereus*	–	–	–	–	–	–	–	–	–	0,36	I
Capparaceae	*Capparis*	–	–	–	–	–	–	–	–	–	1,60	I
Cucurbitaceae	*Cayaponya*	–	–	–	–	–	–	–	–	–	0,18	I
Euphorbiaceae	*Alchornea*	–	3,86	2,38	–	–	–	0,38	–	–	–	F
Fabaceae	Caesalpinioideae 1	90,57	–	–	–	–	–	–	–	–	–	I
	Caesalpinioideae 2	–	5,33	–	–	–	7,90	–	–	–	–	I
	Copaifera langsdorfii	–	–	–	0,19	–	–	–	–	–	–	I
	Poincianella pyramidalis	0,18	0,18	1,47	0,78	1,13	–	–	–	2,43	1,78	VF
	Prosopis juliflora	4,62	1,29	12,82	15,92	2,27	43,75	14,34	24,58	21,66	46,98	VF
	Senna macranthera	–	84,56	1,47	0,97	0,38	7,54	2,45	–	1,21	4,80	VF
	Senna rizzinni	–	–	–	–	–	–	–	–	–	1,07	I
	Zornia echinocarpa	–	–	–	0,97	0,57	0,92	–	–	–	0,18	F
Malpighiaceae	*Byrsonima*	–	–	–	–	–	0,37	–	–	–	–	I
	Heteropterys	–	3,68	–	2,91	–	–	4,15	–	18,37	2,31	F
Malvaceae	*Quararibea*	2,59	–	–	–	–	–	–	–	–	11,74	I
	Waltheria	–	–	60,62	16,50	–	–	–	–	3,47	–	F
Melastomataceae	*Clidemia hirta*	–	–	–	–	–	–	–	–	–	0,71	I
Moraceae	*Brosimum*	1,85	–	–	–	–	19,49	50,00	73,01	50,95	4,27	VF
Myristicaceae	*Virola*	–	–	–	–	–	1,29	20,00	–	–	–	I
Myrtaceae	*Myrcia*	–	–	0,18	–	5,10	2,02	0,19	–	–	1,25	F
Phytolaccaceae	*Microtea*	–	–	1,28	–	–	–	–	–	–	–	I

Table 1 (Continuation)

Plant Family	Pollen Type	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Dec	C.O.
Solanaceae	*Solanum*	–	1,10	19,05	60,39	83,55	16,54	8,30	1,48	1,56	16,90	VF
Urticaceae	*Cecropia*	–	–	0,37	–	6,43	0,18	–	–	–	–	F
Undetermined	–	–	–	–	–	–	–	–	–	–	0,71	I
	TOTAL	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	–
	Number of pollen types	6	7	10	10	8	10	9	5	9	17	–
	H' Index	0,42	0,66	1,20	1,21	0,70	1,58	1,42	0,68	1,33	1,79	–
	J' Index	0,24	0,34	0,52	0,52	0,33	0,69	0,65	0,43	0,61	0,63	–

Table 2. Pollen spectrum showing monthly frequency (%), classes of occurrence (C.O.), and total number of pollen types in the pollen samples stored by *Tetragonisca angustula* from October 2010 to December 2011 in Ruy Barbosa, located in the semiarid region of Bahia in Northeastern Brazil. Values from Shannon-Weaver’s diversity index (H') and Pielou’s equitability index (J') are shown. C.O.: R, rare; I, infrequent; F, frequent; and VF, very frequent.

Plant Family	Pollen Type	2010			2011										C.O.
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jul	Aug	Sep	Oct	Dec	
Amaranthaceae	Amaranthaceae type	–	–	–	–	1,57	–	–	–	–	–	–	–	–	R
	Gomphrena demissa	–	–	1,25	–	–	–	–	–	–	–	–	–	–	R
Anacardiaceae	*Schinus*	2,98	6,35	–	2,48	0,52	2,12	–	2,96	47,96	17,03	4,03	8,23	29,06	VF
Annonaceae	*Annona*	–	–	–	–	–	–	–	0,17	–	–	–	–	–	R
Apiaceae	Apiaceae type	0,35	0,69	–	–	–	–	–	–	0,53	1,79	–	0,16	0,75	F
Arecaceae	*Geonoma*	–	0,34	–	0,18	0,17	0,39	–	–	–	0,54	–	–	1,32	F
Asteraceae	Asteraceae type	–	–	0,71	–	–	–	–	–	–	–	–	–	–	R
	Mikania	–	–	–	–	0,52	0,19	–	0,17	–	–	–	–	–	F
Burseraceae	*Protium*	–	–	0,18	–	–	–	–	–	–	–	–	–	–	R
Capparaceae	*Capparis*	–	–	0,18	–	–	–	–	–	–	–	–	–	–	R
Convolvulaceae	*Evolvulus*	–	–	–	–	–	–	–	–	–	–	0,18	–	–	R
Euphorbiaceae	*Croton*	–	–	–	–	–	–	–	–	–	–	–	0,47	–	R
	Euphorbia	–	0,17	–	–	–	–	–	–	–	–	–	–	–	R
Fabaceae	Caesalpinioideae 1	–	0,34	–	–	–	–	–	0,52	–	–	–	–	–	I
	Poincianella pyramidalis	0,18	–	0,71	0,35	0,17	–	–	–	–	–	–	–	6,60	F
	Prosopis juliflora	80,74	71,01	17,97	80,53	76,66	49,33	54,91	12,37	28,77	53,41	85,11	81,06	11,51	VF
	Senna macranthera	2,28	1,20	–	3,19	–	–	14,15	5,05	1,95	5,38	5,78	4,50	0,75	VF
	Zornia echinocarpa	–	–	–	–	13,94	0,77	–	–	–	–	–	–	–	I
Lamiaceae	*Hyptis*	–	–	–	–	–	–	–	–	–	–	0,18	–	–	R
Lythraceae	Lythraceae type	–	–	–	–	–	–	–	6,97	–	–	–	–	–	R
Malpighiaceae	*Heteropterys*	–	3,95	19,57	–	2,61	36,61	–	11,67	–	–	0,70	0,47	35,47	VF
Malvaceae	*Pseudobombax*	–	–	–	–	–	–	–	–	–	–	–	–	1,13	R
	Quararibea	–	0,17	–	–	–	–	–	0,52	–	–	–	–	–	I
	Waltheria	–	0,86	–	–	1,92	0,19	–	–	–	–	–	–	–	F
Melastomataceae	*Clidemia hirta*	–	–	–	–	–	–	–	0,87	–	–	–	–	–	R
Meliaceae	*Trichilia hirta*	–	–	–	–	–	–	–	–	–	–	–	1,09	–	R

Table 2 (Contnuation)

Plant Family	Pollen Type	2010			2011										C.O.
		Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jul	Aug	Sep	Oct	Dec	
Moraceae	*Brosimum*	11,56	6,35	–	13,27	0,35	6,55	6,04	2,44	10,66	16,67	1,93	1,24	–	VF
Myrtaceae	*Myrcia* 1	–	–	–	–	–	–	–	–	–	–	–	–	2,26	R
	Myrcia 2	–	–	–	–	–	–	–	–	1,95	0,72	–	–	–	I
Phyllanthaceae	*Phyllanthus*	–	–	–	–	0,52	–	–	1,39	–	–	–	–	–	I
Plantaginaceae	*Scoparia dulcis*	–	–	–	–	–	–	–	–	–	–	–	1,09	–	R
Rubiaceae	*Borreria verticillata*	–	–	–	–	–	–	–	–	–	0,18	–	–	0,57	I
Rutaceae	*Citrus*	–	5,49	–	–	–	–	–	–	–	–	–	–	6,04	I
Solanaceae	*Solanum*	1,93	3,09	57,12	–	1,05	3,85	24,91	54,88	8,17	4,30	2,10	1,71	4,53	VF
Urticaceae	*Cecropia*	–	–	2,31	–	–	–	–	–	–	–	–	–	–	R
	TOTAL	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	–
	Number of pollen types	7	13	9	6	12	9	4	13	7	9	8	10	12	–
	H' Index	0,72	1,18	1,18	0,68	0,89	1,19	1,12	1,55	1,34	1,38	0,65	0,80	1,76	–
	J' Index	0,37	0,46	0,54	0,38	0,36	0,54	0,81	0,60	0,69	0,63	0,31	0,35	0,71	–

Table 3. Botanical discrimination and total monthly number (2011) of pollen types shared simultaneously in pollen spectra obtained from two semiarid regions in Bahia in Northeastern Brazil. The data are derived from the palynological analysis of the pollen stored by *Tetragonisca angustula*.

Plant Family	Pollen Type	Jan	Feb	Mar	Apr	May	Aug	Sep	Oct	Dec	Local plants with taxonomical affinity to pollen types
Anacardiaceae	*Schinus*							o		o	*Anacardium occidentale* L.
Arecaceae	*Geonoma*									o	*Geonoma pauciflora* Mart. *G. pohliana* Mart.
Asteraceae	*Mikania*			o		o					*Mikania cordifolia* (L.f.) Willd. *M. elliptica* DC. *M. obovata* DC.
Fabaceae	*Poincianella pyramidalis*	o	o							o	*Poincianella pluviosa* (DC.) L.P.Queiroz
Fabaceae	*Prosopis juliflora*	o	o	o	o	o	o	o	o	o	*Prosopis juliflora* (Sw.) DC.
Fabaceae	*Senna macranthera*				o	o	o		o	o	*Senna macranthera* var. *micans* (Nees) H.S.Irwin
Malpighiaceae	*Heteropterys*		o						o	o	*Heteropterys* aff. *fluminensis* (Griseb.) W.R.Anderson *H. macrostachya* A.Juss. *H. perplexa* W.R.Anderson
Malvaceae	*Waltheria*			o							*Waltheria indica* L.
Moraceae	*Brosimum*	o					o	o	o		*Brosimum gaudichaudii* Trécul *B. guianense* (Aubl.) Huber
Myrtaceae	*Myrcia* sp. 1									o	*Myrcia blanchetiana* (O.Berg.) Mattos *M. guianensis* (Aubl.) DC. *M. rostrata* DC. *M. splendens* (Sw.) DC.
Solanaceae	*Solanum*		o	o	o	o	o	o	o	o	*Solanum caavurana* Vell. *S. crinitum* Lam. *S. depauperatum* Dunal *S. jabrense* Agra & M.Nee *S. palinacanthum* Dunal *S. paniculatum* L.
	Total number of pollen types	3	4	4	3	4	4	3	5	8	

DISCUSSION AND CONCLUSIONS

This study demonstrated that *T. angustula* foraged on a wide spectrum of flowers and exhibited a preference for species such as *Prosopis juliflora* (Fabaceae) and *Solanum* spp. (Solanaceae), which predominated in the pollen spectrum during the majority of the period studied. The consistent use of certain floral sources by the bees and other pollinators reflects the ability of these insects to “learn” or “memorize” floral characteristics, such as colors, odors, sizes, and patterns, which function as indicators of rewards, such as nectar, pollen, or resin (Gonzalez et al., 1995; Chittka et al., 1999; Glover, 2007; Nicolson, 2007). Although the search for preferential flower sources can often be inferred by the pollen spectra, this fact does not necessarily imply that these species provide a greater amount of resources than other species. Chittka et al. (1999) suggested that in the search for a preferred species, bees could neglect flowers from other plant species that offer as much or more resources than the preferred plants. Additionally, pollen is not always a reliable indicator of a nectar source because the availability of resources varies even within the same genus, and in-depth studies of the floral and reproductive biology of a large number of plant species in areas such as *caatinga* are lacking (Iwama & Melhem, 1979; Machado & Lopes, 2004; Santos et al., 2010; Roubik & Moreno, 2013). Therefore, it is essential that more field studies be performed to ratify or rectify the inferences made based on the pollen spectra (Roubik & Moreno, 2013).

The pollen grains contained in bee products provide clues to the geographical origin of these raw materials because the key plant species that characterize the production region can then be identified (Maurizio, 1975; Louveaux et al., 1978). Giulietti et al. (2002) listed 318 species endemic to areas of *caatinga* in Northeastern Brazil. Of the genera identified in the study, 13 were represented in the pollen spectra obtained in Itaberaba and Ruy Barbosa; however, few of the pollen types were considered geographical indicators of this vegetation type, such as *Poincianella pyramidalis*, *Senna macranthera*, and *Zornia echinocarpa* (Giulietti et al., 2004).

Queiroz (2009) reported that *Poincianella pyramidalis* (Tul.) L.P. Queiroz var. *pyramidalis* marks the physiognomy of areas of *stricto sensu caatinga*, where a small-sized tree stratum predominates without forming a continuous canopy, trees and bushes exhibit xerophytic characteristics, and an ephemeral herbaceous stratum is limited to the rainy season. *Poincianella pyramidalis* var. *pyramidalis* is typical of the State of Bahia and adjacent regions of *caatinga* in Pernambuco and Alagoas States, mainly occurring in arboreal *caatinga*. The majority of the floral visitors of *P. pyramidalis* seek nectar, although the volume of this resource per flower is limited, which can cause the visitor to forage from a larger number of flowers, thereby increasing the chance of effectively pollinating the species (Leite & Machado, 2009).

Meanwhile, *Senna macranthera* (Collad.) H.S. Irwin & Barneby exhibits three different varieties occurring in areas of *caatinga* (Queiroz, 2009), of which only *S. macranthera* var. *micans* (Nees) H.S. Irwin & Barneby was reported by Cardoso and Queiroz (2008) in the region of the Serra do Orobó [Orobó Mountains] in the municipalities of Itaberaba and Ruy Barbosa. Pollen from the genus *Senna* has been recorded in various palynological studies performed in areas of *caatinga* (Novais et al., 2009; Oliveira et al., 2010; Silva et al., 2012), and *S. macranthera* represents an important source of pollen used by the bees in this type of vegetation (Maia-Silva et al., 2012). It is likely that the bee *T. angustula* takes advantage of the residual pollen in the flowers of this species after the vibration of the anthers by larger bees, such as the genera *Xylocopa* and *Bombus* (Machado & Lopes, 2004; Maia-Silva et al., 2012).

Queiroz (2009) reported that the *Zornia echinocarpa* (Moric.) Benth. species occurs in *restinga* (coastal vegetation) and *caatinga* on sandy soil only in the State of Bahia. Cardoso and Queiroz (2008) confirmed the presence of this species in the Serra do Orobó. Pollen from *Zornia echinocarpa* was among the dominant types identified by Novais et al. (2010) for pollen loads of *Apis mellifera* Linnaeus, 1758 in the *caatinga* region of Canudos, Bahia. In our study, *Zornia echinocarpa* was represented at a low level in the spectra.

In contrast, the increased observation of pollen types indicating genera and species markedly important to the bees in the *caatinga* region were observed, both for collection of nectar (e.g., *Prosopis juliflora* (Fabaceae) and *Waltheria* (Malvaceae)) and pollen (e.g., *Solanum* (Solanaceae)) (Machado & Lopes, 2004; Santos et al., 2006; Maia-Silva et al., 2012). The *Prosopis juliflora* pollen type exhibited the highest occurrence in the studied samples. This species is not native to the *caatinga*; however, it occurs spontaneously in various regions where agricultural activities have been abandoned (Queiroz, 2009). The adaptation of

Prosopis juliflora to the *caatinga* may be associated with its rapid growth and resistance to drought (Sajjad et al., 2012). In the study areas, this species flowered practically throughout the entire year, constituting a continuous source of floral resources for local bees.

Other pollen sources for the bees in the study areas were indicated by the pollen types related to genera such as *Brosimum*, which is common in pollen spectra although it comprises predominantly anemophilous species (Martins & Batalha, 2006), and *Virola* (Lena & Oliveira, 2006). Cesário and Gaglianone (2008) reported that *Schinus* is a source of pollen and nectar for various insect species because it exhibits a simple floral morphology, allowing the foraging by many visitors. *Heteropterys*, although it is considered a source of oil for Centridini bees in areas of *caatinga* (Aguiar et al., 2003), was observed with high frequency during a number of months in Itaberaba and Ruy Barbosa; therefore, this plant represents a pollen source (Rocha-Filho et al., 2012).

When compared with studies of other Meliponini, the trophic niche of *T. angustula* demonstrated a relatively small breadth ($H' < 1.5$) in the 2 study areas (Carvalho et al., 1999; Oliveira et al., 2009; Ferreira et al., 2010). However, values close to the values demonstrated in our study were obtained for *T. angustula* in other Brazilian locations. Novais and Absy (2013) investigated the pollen stored by *T. angustula* in Belterra ($H' = 1.04$) and Santarém ($H' = 0.59$) in the State of Pará; Carvalho et al. (1999) analyzed corbicular pollen stored by this species in Piracicaba, São Paulo ($H' = 2.70$); and Morgado et al. (2011) investigated corbicular pollen stored by *T. angustula* from Ilha Grande, Rio de Janeiro ($H' = 0.43$).

In general, H' and J' are complementary and follow equivalent trend of rise or fall. However, in some cases, these patterns are subject to inversion, as we observed from November to December 2010, in Ruy Barbosa. Although H' has reached the same value (1.18), the index J' had modest increase (from 0.46 to 0.54), caused by the decrease of the dominance of a single pollen type — while in November 2010 *Prosopis juliflora* occurred as predominant pollen (71.01%), the most dominant pollen in the spectrum in December 2010 was the *Solanum* pollen type (57.12%), but less than that value obtained by *Prosopis juliflora* in the previous month. In contrast, in December 2010, *P. juliflora* had frequency equal to 17.97%. Thus, the codominance of the *Solanum* and *Prosopis juliflora* pollen types in December 2010 may explain the increase in uniformity recorded in the spectrum (J'). Another example occurred from April to May 2011. Although there has been a rise in the H' index, there was a decrease in J'. This decline was due to the dominance of *Solanum* pollen type (54.88%). While in April 2010 *Prosopis juliflora* dominated in the spectrum (54.91%), followed by *Solanum* (24.91%) and *Senna macranthera* (14.15%), in May 2010 the *Solanum* pollen type was followed by *Prosopis juliflora* (12 , 37%) and *Heteropterys* (11.67%) pollen types. The lowest values of these last two types, compared to the frequencies of *Solanum* and *Senna macranthera* in April 2010, reflected the lower uniformity in the use of pollen resources in May 2010.

The uniform use of pollen sources was slightly lower in Itaberaba than in Ruy Barbosa. Carvalho et al. (1999) observed that *T. angustula* demonstrated lower uniformity among *Apis mellifera* and three species of Meliponini of the genera *Nannotrigona*, *Partamona*, and *Plebeia*, in Piracicaba (São Paulo). The diversity of floral sources used by *T. angustula*, together with the consistency exhibited by this species in the use of these resources, confirmed the generalist habit of this species. The small size of this insect results in reduced energy expenditure (Imperatriz-Fonseca et al., 1984), making various plants equally attractive for supplying food rewards. This characteristic can be an advantage if there are competitors in the same foraging radius and can increase the chances of *T. angustula* pollinating a larger number of the plant species visited when collecting resources.

Therefore, we concluded that *T. angustula* exploits a significant number of plant species in the study areas, confirming the polylectic strategy of the species. A number of the plant species functioned as indicators of *caatinga* vegetation, such as *Poincianella pyramidalis* and *Senna macranthera*. The *Prosopis juliflora* and *Solanum* were the most represented pollen types in the samples, demonstrating their prioritization for the supply of pollen by *T. angustula* in Itaberaba and Ruy Barbosa. The ecological analyses indicated an homogeneous use of floral resources by *T. angustula* in the areas of *caatinga* studied.

ACKNOWLEDGMENTS. The authors thank Prof. MSc Carleandro de Souza Dias for contacting the bee keepers who provided samples from their private apiary; the regional office of the Bahia Company of Agricultural Development (EBDA, Empresa Baiana de Desenvolvimento Agrícola S.A.) in Itaberaba for their logistic support; the board of directors of the Agricultural Family School Mãe Jovina for access to the apiary at the institution in Ruy Barbosa; the beekeepers Alex and Manoel for providing samples for the study; Bruno Henrique Andrade-Silva for his help in the field and laboratory; MSc Leilton Santos

Damascena for generating the map used for this study; and the National Council of Scientific and Technological Development (CNPq, Conselho Nacional de Desenvolvimento Científico e Tecnológico) for partially financing this study and for the grants (processes 575747/2008-0, 143084/2009-7, 303557/2010-9, and 477127/2011-8).

REFERENCES

Aguiar C.M.L., Zanella F.C.V., Martins C.F. & Carvalho C.A.L. 2003: Plantas visitadas por *Centris* spp. (Hymenoptera: Apidae) na caatinga para obtenção de recursos florais. — *Neotrop. Entomol.* **32**(2): 247–259.

Albuquerque U.P., Araújo E.L., El-Deir A.C.A., Lima A.L.A., Souto A., Bezerra B.M., Ferraz E.M.N., Freire E.M.X., Sampaio E.V.S.B., Las-Casas F.M.G., Moura G.J.B., Pereira G.A., Melo J.G., Ramos M.A., Rodal M.J.N., Schiel N., Lyra-Neves R.M., Alves R.R.N., Azevedo-Júnior S.M., Telino Júnior W.R., Severi W. 2012: Caatinga revisited: ecology and conservation of an important seasonal dry forest. — *The Scientific World Journal* **2012**(Article ID 205182). doi: 10.1100/2012/205182

Allen-Wardell G., Bernhardt P., Bitner R., Burquez A., Buchmann S., Cane J., Cox P.A., Dalton V., Feinsinger P., Inouye D., Ingram M., Jones C.E., Kennedy K., Nabham G.P., Pavlik B., Tepedino V., Torchio P. & Walker S. 1998: The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. — *Conserv. Biol.* **12**: 8–17.

Barth O.M. 2004: Melissopalynology in Brazil: a review of pollen analysis of honeys, propolis and pollen loads of bees. — *Sci. Agric.* **61**(3): 342–350.

Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemüller R., Edward M., Peeters T., Schaffers A.P., Potts S.G., Kleukers R., Thomas C.D., Settele J. & Kunin W.E. 2006: Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. — *Science* **313**: 351–354.

Borges R.L.B., Lima L.C.L., Oliveira P.P., Silva F.H.M., Novais J.S., Dórea M.C. & Santos F.A.R. 2006: O pólen no mel do semi-árido brasileiro. In Santos F.A.R. (ed): *Apium Plantae*. IMSEAR, Recife, PE, pp. 103–118.

Burkle L.A. & Alarcón R. 2011: The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. — *Am. J. Bot.* **98**: 528–538.

Camargo J.M.F. & Pedro S.R.M. 2012: Meliponini Lepeletier, 1836. In Moure J.S., Urban D. & Melo G.A.R. (orgs): *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region* - online version. Available at http://www.moure.cria.org.br/catalogue. Accessed on 16 Apr 2013.

Cardoso D.B.O.S. & Queiroz L.P. 2008: Floristic composition of seasonally dry tropical forest fragments in Central Bahia, Northeastern Brazil. — *J. Bot. Res. Inst. Texas* **2**(1): 551–573.

Carvalho C.A.L., Marchini L.C. & Ros PB. 1999: Fontes de pólen utilizadas por *Apis mellifera* L. e algumas espécies de Trigonini (Apidae) em Piracicaba (SP). — *Bragantia* **58**: 49–56.

Cesário L.F. & Gaglianone M.C. 2008: Biologia floral e biologia reprodutiva de *Schinus terebinthifolius* Raddi (Anacardiaceae) em restinga do Norte Fluminense. — *Acta bot. bras*. **22**(3): 828–833.

Chittka L., Thomson J.D. & Waser N.M. 1999: Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* **86**: 361–377.

EMBRAPA — Monitoramento por Satélite. 2013: *Banco de Dados Climáticos do Brasil*. Available on http://www.bdclima.cnpm.embrapa.br/resultados/index.php?UF=ba. Accessed on 17 Apr 2013.

Erdtman G. 1960: The acetolysis method – a revised description. — *Sv. Bot. Tidskr.* **54**(4): 561–564.

Ferreira M.G., Manente-Balestieri F.C.D. & Balestieri J.B.P. 2010: Pólen coletado por *Scaptotrigona depilis* (Moure) (Hymenoptera, Meliponini), na região de Dourados, Mato Grosso do Sul, Brasil. — *Rev. Bras. Entomol.* **54**(2): 258–262.

Forzza R.C., Baumgratz J.F.A., Bicudo C.E.M., Canhos D.A.L., Carvalho Jr A.A., Costa A., Costa D.P., Hopkins M., Leitman P.M., Lohmann L.G., Lughadha E.N., Maia L.C., Martinelli G., Menezes M., Morim M.P., Coelho M.A.N., Peixoto A.L., Pirani J.R., Prado J., Queiroz L.P., Souza S., Souza V.C., Stehmann J.R., Sylvestre L.S., Walter B.M.T. & Zappi D. 2010: Síntese da diversidade brasileira. In Forzza R.C. [et al.] (orgs): *Catálogo de Plantas e Fungos do Brasil*. v.1. Andrea Jakobsson Estúdio, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, RJ, pp. 21–42.

Freitas B.M., Imperatriz-Fonseca V.L., Medina L.M., Kleinert A.M.P., Galetto L., Nates-Parra G. & Quezada-Euán J.J.G. 2009: Diversity, threats and conservation of native bees in the Neotropics. *Apidologie* — **40**: 332–346.

Giannini T.C., Acosta A.L., Garófalo C.A., Saraiva A.M., Alves-dos-Santos I. & Imperatriz-Fonseca V.L. 2012: Pollination services at risk: bee habitats will decrease owing to climate change in Brazil. — *Ecol. Model.* **244**: 127–131.

Giulietti A.M., Harley R.M., Queiroz L.P., Barbosa M.R.V., Du Bocage Neta A.L. & Figueiredo M.A. 2002: Espécies endêmicas da caatinga. In Sampaio E.V.S.B., Giulietti A.M., Virgínio J. & Gamarra-Rojas C.F.L. (eds): *Vegetação e Flora da Caatinga*. APNE/CNIEB, Recife, PE, pp. 103–108.

Giulietti A.M., Du Bocage Neta A.L., Castro A.A.J.F., Gamarra-Rojas C.F.L., Sampaio E.V.S.B., Virgínio J.F., Queiroz L.P., Figueiredo M.A., Rodal M.J.N., Barbosa M.R.V. & Harley R.M. 2004: Diagnóstico da vegetação nativa do bioma caatinga. In Silva J.M.C., Tabarelli M., Fonseca M.T. & Lins L.V. (orgs): *Biodiversidade da Caatinga: Áreas e Ações Prioritárias para a Conservação*. MMA, Brasília, DF, pp. 47–90.

Giulietti A.M., Rapini A., Andrade M.J.G., Queiroz L.P., Silva J.M.C. (orgs) 2009: *Plantas Raras do Brasil*. Conservação Internacional, Universidade Estadual de Feira de Santana, Belo Horizonte, MG, 496 pp.

Glover B. 2007: Do pollinators discriminate between different floral forms? In Glover B. *Understanding Flowers and Flowering: An Integrated Approach*. Oxford University Press, Oxford, pp. 181–191.

Gonzalez A., Rowe C.L., Weeks P.J., Whittle D., Gilbert F.S. & Barnard C.J. 1995: Flower choice by honey bees (*Apis mellifera* L.): sex-phase of flowers and preferences among nectar and pollen foragers. — *Oecologia* **101**: 258–264.

Hammer Ø., Harper D.A.T. & Ryan P.D. 2001: PAST: Palaeontological Statistics software package for education and data analysis. — *Palaeontologia Electronica* **4**(1). Available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm. Accessed on 17 Apr 2013.

Imperatriz-Fonseca V.L., Kleinert-Giovannini A., Cortopassi-Laurino M. & Ramalho M. 1984: Hábitos de coleta de *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). — *Bolm. Zool. Univ. S. Paulo* **8**: 115–131.

International Pollinators Initiative. 1999: *The São Paulo Declaration on Pollinators. Report on the Recommendations of the Workshop on the Conservation and Sustainable Use of Pollinators in Agriculture with Emphasis on Bees*. Brazilian Ministry of the Environment (MMA), Brasília, DF, 66 pp. Available at http://www.cbd.int/doc/case-studies/agr/cs-agr-pollinator-rpt.pdf. Accessed on 16 Apr 2013.

Iwama S. & Melhem T.S. 1979: The pollen spectrum of the honey of *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). — *Apidologie* **10**(3): 275–295.

Jones G.D. & Bryant Jr V.M. 1996: Melissopalynology. In Jansonius J. & McGregor D.C. (eds): *Palynology: Principles and Applications*. v. 3. AASP Foundation, Dallas, pp. 933–938.

Joosten H. & de Klerk P. 2002: What's in a name? Some thoughts on pollen classification, identification, and nomenclature in Quaternary palynology. — *Rev. Palaeobot. Palynol.* **122**: 29-45.

Leite A.V. & Machado I.C. 2009: Biologia reprodutiva da "catingueira" (*Caesalpinia pyramidalis* Tul., Leguminosae-Caesalpinioideae), uma espécie endêmica da caatinga. — *Revista Brasil. Bot*. **32**: 79–88.

Lena E. & Oliveira P.E. 2006: Biologia reprodutiva e fenologia de *Virola sebifera* Aubl. (Myristicaceae) em mata mesofítica de Uberlândia, MG, Brasil. — *Revista Brasil. Bot.* **29**(3): 443–451.

Louveaux J., Maurizio A. & Vorwohl G. 1978: Methods of melissopalynology. — *Bee World* **59**(4): 139–157.

Machado I.C. & Lopes A. V. 2004: Floral traits and pollination systems in the caatinga, a Brazilian tropical dry forest. — *Ann. Bot.* **94**: 365–376.

Maia-Silva C., Silva C.I., Hrncir M., Queiroz R.T. & Imperatriz-Fonseca V.L. 2012: *Guia de Plantas Visitadas por Abelhas na Caatinga*. Fundação Brasil Cidadão, Fortaleza, CE, 191 pp.

Martins F.Q. & Batalha M.A. 2006: Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (Central Brazil). — *Braz. J. Biol.* **66**(2A): 543–552.

Maurizio A. 1975: Microscopy of honey. In Maurizio A. (ed): *Honey: A Comprehensive Survey*. William Heinemann, London, pp. 240–257.

Michener C.D. 2007: *The Bees of the World*. 2nd. ed. The Johns Hopkins University Press, Baltimore, MD, 953 pp.

Morgado L.N., Andrade R.C., Lorenzon M.C.A. & Gonçalves-Esteves V. 2011: Padrão polínico utilizado por *Tetragonisca angustula* Latreille (Apidae: Meliponina). — *Acta bot. bras.* **25**(4): 932–934.

Nicolson S.W. 2007: Nectar consumers. In Nicolson S.W., Nepi M. & Pacini E. (eds): *Nectaries and Nectar*. Springer, Dordrecht, The Netherlands, pp. 289–342.

Novais J.S. & Absy M.L. 2013: Palynological examination of the pollen pots of native stingless bees from the Lower Amazon region in Pará, Brazil. — *Palynology* doi: http://dx.doi.org/10.1080/01916122.2013.787127

Novais J.S., Lima L.C.L. & Santos F.A.R. 2006: Espectro polínico de méis de *Tetragonisca angustula* Latreille, 1811 coletados na caatinga de Canudos, Bahia, Brasil. — *Magistra* **18**(4): 257–264.

Novais J.S., Lima L.C.L. & Santos F.A.R. 2009: Botanical affinity of pollen harvested by *Apis mellifera* L. in a semi-arid area from Bahia, Brazil. — *Grana* **48**(3): 224–234.

Novais J.S., Lima L.C.L. & Santos F.A.R. 2010: Bee pollen loads and their use in indicating flowering in the caatinga region of Brazil. — *J. Arid Environ*. **74**(10): 1355–1358.

Oliveira F.P.M., Absy M.L. & Miranda I.S. 2009: Recurso polínico coletado por abelhas sem ferrão (Apidae, Meliponinae) em um fragmento de floresta na região de Manaus – Amazonas. — *Acta Amaz.* **39**(3): 505–518.

Oliveira P.P., van den Berg C. & Santos F.A.R. 2010: Pollen analysis of honeys from caatinga vegetation of the state of Bahia, Brazil. — *Grana* **49**(1): 66–75.

Pielou E.C. 1977: *Mathematical Ecology*. 2nd ed. Willey-Interscience Publication, John Willey & Sons, New York, NY, 385 pp.

Prado D. 2003: As caatingas da América do Sul. In Leal I.R., Tabarelli M. & Silva J.M.C. (eds): *Ecologia e Conservação da Caatinga*. Ed. Universitária da UFPE, Recife, PE, pp.. 3–73.

Queiroz L.P. 2009: *Leguminosas da Caatinga*. UEFS, Feira de Santana, BA, 467 pp.

Ramalho M., Imperatriz-Fonseca V.L., Kleinert-Giovannini A. & Cortopassi-Laurino M. 1985: Exploitation of floral resources by *Plebeia remota* Holmberg (Apidae, Meliponinae). — *Apidologie* **16**(3): 307–330.

Rocha-Filho L.C., Krug C., Silva C.I. & Garófalo C.A. 2012: Floral resource used by Euglossini bees (Hymenoptera: Apidae) in coastal ecosystems of the Atlantic forest. — *Psyche* **2013**(Article ID 934951). doi:10.1155/2012/934951

Roubik D.W. & Moreno P. J.E. 1991: *Pollen and Spores of Barro Colorado Island*. MBG Press, St. Louis, MO, 286 pp.

Roubik D.W. & Moreno P. J.E. 2013: How to be a bee-botanist using pollen spectra. In Vit P., Pedro S.R.M. & Roubik D. (eds): *Pot-Honey: A Legacy of Stingless Bees*. Springer, New York, NY, pp. 295–314.

Sajjad A., Saeed S. & Bashir M.A. 2012: Spatial variation in pollinator communities and reproductive performance of *Prosopis juliflora* (Fabaceae). — *J. Poll. Ecol*. **8**(9): 59–66.

Santos F.A.R., Oliveira J.M., Oliveira P.P., Leite K.R.B. & Carneiro C.E. 2006: Plantas do semi-árido importantes para as abelhas. In Santos F.A.R. (ed): *Apium Plantae*. IMSEAR, Recife, PE, pp. 61–86.

Santos A.P.M., Romero R. & Oliveira P.E.A.M. 2010: Biologia reprodutiva de *Miconia angelana* (Melastomataceae), endêmica da Serra da Canastra, Minas Gerais. — *Revista Brasil. Bot.* **33**: 333–341.

Shannon C.E. & Weaver W. 1949: *The Mathematical Theory of Communication*. Univ. of Illinois Press, Urbano, IL, 117 pp.

Silva A.P.C., Lima Á.S. & Santos F.A.R. 2012: Botanical biodiversity in honey samples from the semiarid region of Sergipe state, Brazil. — *Magistra* **24**: 158–171.

Silva F.H.M. 2007: *Contribuição à Palinologia das Caatingas*. Bahia State Univ. at Feira de Santana, Feira de Santana, BA, 182 pp.

Zanella F.C.V. & Martins C.F. 2003: Abelhas da caatinga: biogeografia, ecologia e conservação. In Leal I.R., Tabarelli M. & Silva J.M.C. (eds): *Ecologia e Conservação da Caatinga*. Ed. Universitária da UFPE, Recife, PE, pp. 75–134.

3 Síntese

3 SÍNTESE

A diversidade de tipos polínicos reconhecidos no conteúdo dos potes de mel e pólen de *Tetragonisca angustula* confirma o hábito generalista desse meliponíneo, ao passo que assinala, ainda, a riqueza florística encontrada nas zonas amazônicas e semiáridas brasileiras.

Os méis de *T. angustula* procedentes do Baixo Amazonas destacaram-se pela presença de tipos polínicos como *Borreria verticillata* (Rubiaceae), *Byrsonima* (Malpighiaceae), *Cecropia* (Urticaceae), *Clidemia* (Melastomataceae), *Eriope* (Lamiaceae), *Microtea* (Phytolaccaceae), *Myrcia* (Myrtaceae), *Solanum* (Solanaceae), *Tapirira guianensis* (Anacardiaceae) e *Warszewiczia coccinea* (Rubiaceae). Nesse méis, a concentração polínica variou entre 20.000 e 500.000 grãos de pólen em cada 10 g de mel. Em contrapartida, os méis oriundos da *caatinga* foram caracterizados pela presença dos tipos polínicos *Heteropterys* (Malpighiaceae), *Mikania* (Asteraceae), *Mimosa tenuiflora* (Fabaceae), *Myrcia*, *Prosopis juliflora* (Fabaceae), *Schinus* (Anacardiaceae), *Senna macranthera* (Fabaceae), *Solanum*, *Syagrus coronata* (Arecaceae) e *Solanum*.

Por sua vez, os potes de pólen de *Tetragonisca angustula* procedentes da Amazônia destacaram-se por apresentarem os tipos polínicos *Acalypha* (Euphorbiaceae), *Byrsonima*, *Brosimum paraense* (Moraceae), *Borreria verticillata*, *Cecropia*, *Clidemia hirta*, *Davilla kunthii* (Dilleniaceae), *Eriope*, *Lindackeria paludosa* (Achariaceae), *Myrcia*, *Schefflera morototoni* (Araliaceae), *Tabebuia* (Bignoniaceae), *Tapirira guianensis* e *Vismia guianensis* (Hypericaceae). Na *caatinga*, os tipos polínicos mais destacados foram *Prosopis juliflora* e *Solanum*, apresentando ainda *Poincianella pyramidalis* (Fabaceae) e *Senna macranthera* como indicadores deste tipo vegetacional.

Quando considerados os tipos polínicos mais representativos (>10%), os méis da Amazônia e da *caatinga* apresentaram 23 e 16 tipos polínicos, respectivamente, com destaque para as famílias Fabaceae, Solanaceae e Urticaceae. Nas amostras de pólen, 18 e 11 tipos polínicos foram encontrados, respectivamente.

A família Fabaceae destacou-se em todas as análises palinológicas realizadas, especialmente no que diz respeito ao número de tipos polínicos reconhecidos nos produtos meliponícolas, demonstrando ser uma importante mantenedora das populações de meliponíneos em diferentes regiões brasileiras.

A amplitude de nicho trófico nos méis foi superior à dos potes de pólen tanto na Amazônia quanto na *caatinga*, geralmente com valor médio do índice de diversidade de Shannon-Weaver (H') em torno de 1,5. A equitabilidade apontou, na maioria das amostras, para um uso homogêneo dos recursos florais por *Tetragonisca angustula*.

As análises de cluster apresentaram resultados mais consistentes quando foram efetuadas com os espectros polínicos dos méis, agrupando as amostras analisadas por região geográfica. Por outro lado, os dados de precipitação pluviométrica não permitiram um consistente agrupamento geográfico das amostras.

Estudos palinológicos adicionais devem ser estimulados e fomentados, especialmente gerando espectros polínicos comparativos entre *T. angustula* e outras espécies de abelhas indígenas sem ferrão que compartilham os mesmos ecossistemas na Amazônia e na *caatinga* brasileiras. Com isso, será possível avalia o grau de sobreposição de nicho entre tais espécies, bem como ampliar a lista de flores que servem aos meliponíneos no Brasil.

Referências

REFERÊNCIAS

Absy, M.L.; Kerr, W.E. 1977. Algumas plantas visitadas para obtenção de pólen por operárias de *Melipona compressipes merrillae* em Manaus. *Acta Amazonica*, 7(3): 309-315.

Absy, M.L.; Bezerra, E.B.; Kerr, W.E. 1980. Plantas nectaríferas utilizadas por duas espécies de *Melipona* da Amazônia. *Acta Amazonica*, 10(2): 271-281.

Absy, M.L.; Camargo, J.M.F.; Kerr, W.E.; Miranda, I.P.A. 1984. Espécies de plantas visitadas por Meliponinae (Hymenoptera; Apoidea), para coleta de pólen na região do médio Amazonas. *Revista Brasileira de Biologia*, 44(2): 227-237.

Aguiar, C.M.L.; Zanella, F.C.V.; Martins, C.F.; Carvalho, C.A.L. 2003. Plantas visitadas por *Centris* spp. (Hymenoptera: Apidae) na caatinga para obtenção de recursos florais. *Neotropical Entomol*ogy, 32(2): 247–259.

Aires, E.R.B.; Freitas, B.M. 2001. Caracterização palinológica de algumas amostras de mel do Estado do Ceará. *Ciência Agronômica*, 32(1/2): 22–29.

Albuquerque, M.F.; Souza, E.B.; Oliveira, M.C.F.; Souza Júnior, J.A. 2010. Precipitação nas mesorregiões do estado do Pará: climatologia, variabilidade e tendências nas últimas décadas (1978-2008). *Revista Brasileira de Climatologia*, 6(6): 151-168.

Albuquerque, U.P.; Araújo, E.L.; El-Deir, A.C.A.; Lima, A.L.A.; Souto, A.; Bezerra, B.M.; *et al*. 2012. Caatinga revisited: ecology and conservation of an important seasonal dry forest. *The Scientific World Journal*, 2012: Article ID 205182. DOI: 10.1100/2012/205182

Allen-Wardell, G.; Bernhardt, P.; Bitner, R.; Burquez, A.; Buchmann, S.; Cane, J.; *et al*. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* 12(1): 8–17.

Almeida, A.M.M.; Carvalho, C.A.L.; Abreu, R.D.; Santos, F.A.R.; Araújo, R.C.M.S.; Oliveira, P.P. 2005. Espectro polínico de amostras de mel de *Apis mellifera* L. provenientes de Nova Soure, Bahia. *Revista de Agricultura*, 80(2): 131–147.

Alvarado, J.L.; Delgado R., M. 1985. Flora apicola en Uxpanapa, Veracruz, Mexico. *Biotica*, 10: 257–275.

Alves, R.M.O.; Souza, B.A.; Carvalho, C.A.L. 2006. Espectro polínico de amostras de mel de *Melipona mandacaia* Smith. 1863 (Hymenoptera - Apidae). *Acta Scientiarum. Biological Sciences*, 28(1): 33–38.

Andrada, A.; Valle, A.; Aramayo, E.; Lamberto, S.; Cantamutto, M. 1998. Analisis polinico de las mieles de las sierras australes de la provincia de Buenos Aires, Argentina. *Investigación Agraria. Producción y Protección Vegetales*, 13(3): 265-275.

Bagnouls, F.; Gaussen, H. 1962. Estação seca e índice xerotérmico. *Boletim Geográfico*, XX(169): 338–369. (traduzido para o Português por R.S.B. Santos)

Barbier, E. 1958. Examen pollinique de quelques miels unifloraux. *Annales de l'Abeille*, 1(2): 73-76. DOI: 10.1051/apido:19580201

Barbier, E.; Pangaud, C.-Y. 1961. Origine botanique et caractéristiques physicochimiques des miels. *Annales de l'Abeille*, 4(1): 51-65. DOI: 10.1051/apido:19610103

Barth, O.M. 2004. Melissopalynology in Brazil: a review of pollen analysis of honeys, propolis and pollen loads of bees. *Scientia Agricola*, 61(3): 342–350.

Barth, O.M. 2013. Palynology serving bees. In: Vit, P.; Pedro, S.R.M.; Roubik D. (Ed.). *Pot-honey: a legacy of stingless bees*. Springer, New York, p.285-294.

Battesti, M.-J.; Goeury, C. 1992. Efficacité de l'analyse mélitopalynologique quantitative pour la certification des origines géographique et botanique des miels: le modèle des miels corses. *Review of Palaeobotany and Palynology*, 75: 77-102. DOI: 10.1016/0034-6667(92)90151-6

Benninghof, W.S. 1962. Calculation of pollen and spore density in sediments by addition of exotic pollen in known quantities. *Pollen et Spores*, 4: 332-333.

Biesmeijer, J.C.; Roberts, S.P.M.; Reemer, M.; Ohlemüller, R.; Edward, M.; Peeters, T.; *et al*. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313: 351–354.

Borges, R.L.B.; Lima, L.C.L.; Oliveira, P.P.; Silva, F.H.M.; Novais, J.S.; Dórea, M.C.; Santos, F.A.R. 2006. O pólen no mel do semi-árido brasileiro. In: Santos, F.A.R. (Ed.). *Apium plantae*. IMSEAR, Recife, Pernambuco, p.103–118.

Bryant Jr., V.M. 2001. Pollen contents of honey. *CAP Newsletter*, 24(1): 10-24.

Burkle, L.A.; Alarcón, R. 2011. The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. *American Journal of Botany*, 98: 528–538.

Cabral, E.; Salas, R. 2011. *Borreria*. In: *Lista de Espécies da Flora do Brasil*. Jardim Botânico do Rio de Janeiro. (http://floradobrasil.jbrj.gov.br/2011/FB020712). Acesso em 25/09/2012.

Caccavari, M.; Fagúndez, G. 2010. Pollen spectra of honeys from the Middle Delta of the Paraná River (Argentina) and their environmental relationship. *Spanish Journal of Agricultural Research*, 8(1): 42-52. DOI:10.5424/1142

Camargo, J.M.F.; Pedro, S.R.M. 2012. Meliponini Lepeletier, 1836. In: Moure, J.S.; Urban, D.; Melo, G.A.R. (Org.). *Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region - online version*. (http://www.moure.cria.org.br/catalogue). Acesso em 24/09/2012.

Cardoso, D.B.O.S.; Queiroz, L.P. 2008. Floristic composition of seasonally dry tropical forest fragments in Central Bahia, Northeastern Brazil. *Journal of the Botanical Research Institute of Texas*, 2(1): 551–573.

Carreira, L.M.M.; Lopes, J.R.C.; Silva, M.F.; Nascimento, L.A.S. 1996. *Catálogo de pólen das leguminosas da Amazônia brasileira*. Museu Paraense Emílio Goeldi, Belém, 137p.

Carvalho, C.A.L.; Marchini, L.C.; Ros, P.B. 1999. Fontes de pólen utilizadas por *Apis mellifera* L. e algumas espécies de Trigonini (Apidae) em Piracicaba (SP). *Bragantia*, 58(1): 49-56. DOI: 10.1590/S0006-87051999000100007

Carvalho, C.A.L.; Nascimento, A.S.; Pereira, L.L.; Machado, C.S.; Clarton, L. 2006. Fontes nectaríferas e poliníferas utilizadas por *Melipona quadrifasciata* (Hymenoptera: Apidae) no Recôncavo Baiano. *Magistra*, 18: 249–256.

Carvalho, J.O.P.; Silva, J.N.M.; Lopes, J.C.A.; Montagner, L.H.; Carvalho, M.S.P. 1986. Composição florística de uma mata secundária no planalto de Belterra no Pará. In: I Simpósio do Trópico Úmido. *Anais*... v.2. EMBRAPA-CPATU, Belém, p.197205.

Cesário, L.F.; Gaglianone, M.C. 2008. Biologia floral e biologia reprodutiva de *Schinus terebinthifolius* Raddi (Anacardiaceae) em restinga do Norte Fluminense. *Acta Botanica Brasilica*. 22(3): 828–833.

Chittka, L.; Thomson, J.D.; Waser, N.M. 1999. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften*, 86: 361–377.

Cortopassi-Laurino, M.; Gelli, G.S. 1991. Analyse pollinique, propriétés physico-chimiques et action antibactérienne des miels d'abeilles africanisées *Apis mellifera* et de Méliponinées du Brésil. *Apidologie*, 22: 61-73. DOI: 10.1051/apido:19910108

Cortopassi-Laurino, M.; Ramalho, M. 1988. Pollen harvest by *Apis mellifera* and *Trigona spinipes* in São Paulo: Botanical and ecological views. *Apidologie*, 19(1): 1-24. DOI: 10.1051/apido:19880101

Dardón, M.J.; Maldonado-Aguilera, C.; Enríquez, E. 2013. The pot-honey of Guatemalan bees. In: Vit, P.; Pedro, S.R.M.; Roubik, D. (Ed.). *Pot-honey: a legacy of stingless bees*. Springer, New York, p.395–408.

de Klerk, P.; Joosten, H. 2007. The difference between pollen types and plant taxa: a plea for clarity and scientific freedom. *Eiszeitalter und Gegenwart*, 56(3): 162-171.

Demianowicz, Z. 1964. Charakteristik der einartenhonige. *Annales de l'Abeille*, 7(4): 273-288. DOI: 10.1051/apido:19640401

Dias, B.S.F.; Raw, A.; Imperatriz-Fonseca, V.L. 1999. *Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees*. Brazilian Ministry of the Environment, Brasília, 79p.

Dutra, V.F.; Vieira, M.F.; Garcia, F.C.P.; Lima, H.C. 2009. Fenologia reprodutiva, síndromes de polinização e dispersão em espécies de Leguminosae dos campos rupestres do Parque Estadual do Itacolomi, Minas Gerais, Brasil. *Rodriguésia*, 60(2): 371–387.

EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária. 2012. *Banco de dados climáticos do Brasil*. (http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=pa&COD=121) Acesso em 5/10/2012.

Erdtman, G. 1952. *Pollen morphology and plant taxonomy. Angiosperms*. Almqvist & Wiksell, Stockholm, 539p.

Erdtman, G. 1960. The acetolysis method - a revised description. *Svensk Botanisk Tidskrift*, 54(4): 561-564.

Fægri, K.; van der Pijl, L. 1979. *The principles of pollination biology*. 3rd ed. Pergamon Press, Oxford, 244p.

FAO - Food and Agriculture Organisation. 2010. *Global forest resources assessment 2010 – main report*. Food and Agriculture Organization of the United Nations, Rome, 340p.

Fearnside, P.M. 2001. Soybean cultivation as a threat to the environment in Brazil. *Environmental Conservation*, 28(1): 23-38. DOI: 10.1017/S0376892901000030.

Ferreira, M.G.; Manente-Balestieri, F.C.D.; Balestieri, J.B.P. 2010. Pólen coletado por *Scaptotrigona depilis* (Moure) (Hymenoptera, Meliponini), na região de Dourados, Mato Grosso do Sul, Brasil. *Revista Brasileira de Entomologia*, 54(2): 258–262.

Fisch, G.; Marengo, J.A.; Nobre, C.A. 1998. Uma revisão geral sobre o clima da Amazônia. *Acta Amazonica*, 28(2): 101–126.

Forzza, R.C.; Baumgratz, J.F.A.; Costa, A.; Hopkins, M.; Leitman, P.M.; Lohmann, L.G.; *et al*. 2010. As angiospermas do Brasil. In: Forzza, R.C. *et al*. (Org.). *Catálogo de plantas e fungos do Brasil*. v.1. Andrea Jakobsson Estúdio/Instituto de Pesquisas Jardim Botânico do Rio de Janeiro; Rio de Janeiro, p.78–89.

Freitas, B.M. 1991. *Potencial da caatinga para produção de pólen e néctar para a exploração apícola*. Dissertação de Mestrado, Universidade Federal do Ceará, Fortaleza, Ceara. 140p.

Freitas, B.M.; Silva, E.M.S. 2006. Potencial apícola da vegetação do Semi-Árido brasileiro. In: Santos, F.A.R. (Ed.). *Apium plantae*. v.3. IMSEAR, Recife, p.19–32.

Freitas, B.M.; Imperatriz-Fonseca, V.L.; Medina, L.M.; Kleinert, A.M.P.; Galetto, L.; Nates-Parra, G.; Quezada-Euán, J.J.G. 2009. Diversity, threats and conservation of native bees in the Neotropics. *Apidologie*, 40(3): 332–346. DOI: 10.1051/apido/2009012

Fonseca, M.T.; Lins, L.V. (Org.). 2004. *Biodiversidade da caatinga: áreas e ações prioritárias para a conservação*. Ministério do Meio Ambiente, Brasília, p.47–90.

Giannini, T.C.; Acosta, A.L.; Garófalo, C.A.; Saraiva, A.M.; Alves-dos-Santos, I.; Imperatriz-Fonseca, V.L. 2012. Pollination services at risk: bee habitats will decrease owing to climate change in Brazil. *Ecological Modelling*, 244: 127–131. DOI: 10.1016/j.ecolmodel.2012.06.035

Giulietti, A.M.; Rapini, A.; Andrade, M.J.G.; Queiroz, L.P.; Silva, J.M.C. (Org.). 2009. *Plantas Raras do Brasil*. Conservação Internacional, Universidade Estadual de Feira de Santana, Belo Horizonte, 496p.

Giulietti, A.M.; Harley, R.M.; Queiroz, L.P.; Barbosa, M.R.V.; Du Bocage Neta, A.L.; Figueiredo, M.A. 2002. Espécies endêmicas da caatinga. In: Sampaio, E.V.S.B.; Giulietti, A.M.; Virgínio, J.; Gamarra-Rojas, C.F.L. (Ed.). 2002. *Vegetação e flora da caatinga*. APNE/CNIEB, Recife, p.103–108.

Giulietti, A.M.; Du Bocage Neta, A.L.; Castro, A.A.J.F.; Gamarra-Rojas, C.F.L.; Sampaio, E.V.S.B.; Virgínio, J.F.; *et al*. 2004a. Diagnóstico da vegetação nativa do bioma caatinga. In: Silva, J.M.C.; Tabarelli, M.; Fonseca, M.T.; Lins, L.V. (Org.). 2004. *Biodiversidade da caatinga: áreas e ações prioritárias para a conservação*. Ministério do Meio Ambiente, Brasília, p.47-90.

Giulietti, A.M.; Du Bocage Neta, A.L.; Paula, D.C.; Barbosa, D.C.; Nogueira, E.; Sampaio, E.V.S.B.; *et al*. 2004b. Vegetação: áreas e ações prioritárias para a conservação da caatinga. In: Silva, J.M.C.; Tabarelli, M.; Fonseca, M.T.; Lins, L.V. (Org.). 2004.

Biodiversidade da caatinga: áreas e ações prioritárias para a conservação. Ministério do Meio Ambiente, Brasília, p.113–131.

Glover, B. 2007. Do pollinators discriminate between different floral forms? In Glover B. *Understanding flowers and flowering: an integrated approach*. Oxford University Press, Oxford, p.181–191.

Gonzalez, A.; Rowe, C.L.; Weeks, P.J.; Whittle, D.; Gilbert, F.S.; Barnard, C.J. 1995. Flower choice by honey bees (*Apis mellifera* L.): sex-phase of flowers and preferences among nectar and pollen foragers. *Oecologia*, 101: 258–264.

Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. 2001. PAST: Palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1): 9p. (http://palaeo-electronica.org/2001_1/past/issue1_01.htm). Acessado em 4/05/2013.

Heinrich, B. 1976a. Resource partitioning among some eusocial insects: bumblebees. *Ecology*, 57: 874–889.

Heinrich, B. 1976b. The foraging specializations of individual bumblebees. *Ecological Monographs*, 46: 105–128.

Hopkins, M.J.G. 2007. Modelling the known and unknown plant biodiversity of the Amazon Basin. *Journal of Biogeography*, 34: 1400-1411. DOI: 10.1111/j.1365-2699.2007.01737.x

IBGE — Instituto Brasileiro de Geografia e Estatística. 1990. *Divisão regional do Brasil em mesorregiões e microrregiões geográficas*. v.I. Fundação IBGE, Rio de Janeiro, 135p.

IBGE — Instituto Brasileiro de Geografia e Estatística. 2004. *Mapa dos biomas brasileiros*. IBGE, Rio de Janeiro. (http://www.ibge.gov.br). Acessado em 2/05/2013.

Imperatriz-Fonseca, V.L.; Kleinert-Giovannini, A.; Cortopassi-Laurino, M.; Ramalho, M. 1984. Hábitos de coleta de *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Boletim de Zoologia da Universidade de São Paulo*, 8: 115-131.

INMET — Instituto Nacional de Meteorologia. 2013. *Banco de dados meteorológicos para ensino e pesquisa* (http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep). Acessado em 21/04/2013.

INPE — Instituto Nacional de Pesquisas Espaciais. 2012. *Taxas anuais do desmatamento - 1998 até 2011*. (http://www.obt.inpe.br/prodes/prodes_1988_2011.htm). Acessado em 5/10/2012.

International Pollinators Initiative. 1999. *The São Paulo declaration on pollinators. report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees*. Brazilian Ministry of the Environment, Brasília, 66p. (http://www.cbd.int/doc/case-studies/agr/cs-agr-pollinator-rpt.pdf). Acessado em 16/04/2013.

Iwama, S.; Melhem, T.S. 1979. The pollen spectrum of the honey of *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Apidologie*, 10(3): 275-295. DOI: 10.1051/apido:19790305

Jones, G.D.; Bryant Jr., V.M. 1996. Melissopalynology. In: Jansonius, J.; McGregor, D.C. (Ed.). *Palynology: principles and applications*. v.3. AASP Foundation, Dallas, p.933–938.

Jones, G.D.; Bryant Jr., V.M. 2001. Is one drop enough? In: Goodman, D.K.; Clarke, R.T. (Ed.). *Proceedings of the 9th International Palynological Congress, 1996*. AASP Foundation, Houston, p.483–487.

Jones, G.D.; Bryant Jr., V.M. 2004. The use of ETOH for dilution of honey. *Grana*, 43(3): 174-182. DOI: 10.1080/00173130410019497

Joosten, H.; de Klerk, P. 2002. What's in a name? Some thoughts on pollen classification, identification, and nomenclature in Quaternary palynology. *Review of Palaeobotany and Palynology*, 122: 29-45. DOI: 10.1016/S0034-6667(02)00090-8

Kerr, W.E.; Absy, M.L.; Marques-Souza, A.C. 1986/1987. Espécies nectaríferas e poliníferas utilizadas pela abelha *Melipona compressipes fasciculata* (Meliponinae, Apidae) no Maranhão. *Acta Amazonica*, 16/17: 145-156.

Laurance, W.F.; Albernaz, A.K.M.; Fearnside, P.M.; Vasconcelos, L.V.; Ferreira, L.V. 2004. Deforestation in Amazonia. *Science*, 304: 1109-1111. DOI: 10.1126/science.304.5674.1109b

Leite, A.V.; Machado, I.C. 2009. Biologia reprodutiva da "catingueira" (*Caesalpinia pyramidalis* Tul., Leguminosae-Caesalpinioideae), uma espécie endêmica da caatinga. *Revista Brasileira de Botânica*, 32: 79–88.

Lena, E.; Oliveira, P.E. 2006. Biologia reprodutiva e fenologia de *Virola sebifera* Aubl. (Myristicaceae) em mata mesofítica de Uberlândia, MG, Brasil. *Revista Brasileira de Botânica*, 29(3): 443–451.

Lieux, M.H. 1980. Acetolysis applied to microscopical honey analysis. *Grana*, 19: 57–61.

Lieux, M.H. 1981. An analysis of Mississipi (U.S.A.) honey: pollen, color and moisture. *Apidologie*, 12(2): 137-158. DOI: 10.1051/apido:19810205

Lima, L.C.L. 2007. *Espécies de* Mimosa *L. (Leguminosae) do semi-árido nordestino: palinologia, fenologia, biologia floral e potencial apícola*. Tese de Doutorado, Universidade Estadual de Feira de Santana; Feira de Santana, Bahia. 96p.

Lima, L.C.L.; Santos, F.A.R.; Silva, F.H.M. 2006. Morfologia polínica de espécies de *Mimosa* L. (Leguminosae) apícolas do semi-árido. In: Santos, F.A.R. (Ed.). *Apium plantae*. IMSEAR, Recife, p.87–102.

Lindauer, M.; Kerr, W.E. 1960. Communication between the workers of stingless bees. *Bee World*, 41: 29-41.

Louveaux, J.; Maurizio, A.; Vorwohl, G. 1970. Methods of mellissopalynology. *Bee World*, 51: 125-138.

Louveaux, J.; Maurizio, A.; Vorwohl, G. 1978. Methods of melissopalynology. *Bee World*, 59: 139-153.

Ludwig, J.A.; Reynolds, J.F. 1988. *Statistical ecology: a primer on methods and computing*. John Wiley & Sons, New York, 337p.

Lutier, P.M.; Vaissière, B.E. 1993. An improved method for pollen analysis of honey. *Review of Palaeobotany and Palynology*, 78: 129-144. DOI: 10.1016/0034-6667(93)90019-Q

Machado, I.C.; Lopes, A.V. 2003. Recursos florais e sistemas de polinização e sexuais em caatinga. In: Leal, I.R.; Tabarelli, M.; Silva, J.M.C. (Ed.). *Ecologia e conservação da caatinga*. Editora Universitária da UFPE, Recife, p.515–563.

Machado, I.C.; Lopes, A.V. 2004. Floral traits and pollination systems in the caatinga, a Brazilian tropical dry forest. *Annals of Botany*, 94: 365–376.

Machado, I.C.S.; Barros, L.M.; Sampaio, E.V.S.B. 1997. Phenology of caatinga species at Serra Talhada, PE, Northeastern Brazil. *BIOTROPICA*, 29(1): 57–68.

Maia-Silva, C.; Silva, C.I.; Hrncir, M.; Queiroz, R.T.; Imperatriz-Fonseca, V.L. 2012. *Guia de plantas visitadas por abelhas na caatinga*. Fundação Brasil Cidadão, Fortaleza, 191p.

Mamede, M.C.H. 2011. *Byrsonima*. In: *Lista de Espécies da Flora do Brasil*. Jardim Botânico do Rio de Janeiro. (http://floradobrasil.jbrj.gov.br/2011/FB008827). Acessado em 25/09/2012.

Marques, L.J.P.; Muniz, F.H; Lopes, G.S.; Silva, J.M. 2011. Levantamento da flora apícola em Santa Luzia do Paruá, Sudoeste da Amazônia, Maranhão. *Acta Botanica Brasilica*, 25(1): 141-149.

Marques-Souza, A.C. 1996. Fontes de pólen exploradas por *Melipona compressipes manaosensis* (Apidae: Meliponinae), abelha da Amazônia Central. *Acta Amazonica,* 26(1/2): 77-86.

Marques-Souza, A.C. 2010. Ocorrência do pólen de *Podocarpus* sp. (Podocarpaceae) nas coletas de *Frieseomelitta varia* Lepeletier 1836 (Apidae: Meliponinae) em uma área de Manaus, AM, Brasil. *Acta Botanica Brasilica*, 24: 558–566.

Marques-Souza, A.C.; Absy, M.L.; Kerr, W.E. 2007. Pollen harvest features of the Central Amazonian bee *Scaptotrigona fulvicutis* Moure 1964 (Apidae: Meliponinae), in Brazil. *Acta Botanica Brasilica*, 21(1): 11-20. DOI: 10.1590/S0102-33062007000100002

Marques-Souza, A.C.; Moura, C.O.; Nelson, B.W. 1996. Pollen collected by *Trigona williana* (Hymenoptera: Apidae) in Central Amazonia. *Revista de Biología Tropical*, 44: 567–573.

Marques-Souza, A.C.; Absy, M.L.; Condé, P.A.A.; Coelho, H.A. 1993. Dados da obtenção do pólen por operárias de *Apis mellifera* no município de Ji-Paraná (RO), Brasil. *Acta Amazonica*, 23(1): 59-76.

Marques-Souza, A.C.; Absy, M.L.; Kerr, W.E.; Aguilera-Peralta, F.J. 1995. Pólen coletado por duas espécies de meliponíneos (Hymenoptera: Apidae) da Amazônia. *Revista Brasileira de Biologia*, 55: 855–864.

Marques-Souza, A.C.; Miranda, I.P.A.; Moura, C.O.; Rabelo, A.; Barbosa, E.M. 2002. Características morfológicas e bioquímicas do pólen coletado por cinco espécies de meliponíneos da Amazônia Central. *Acta Amazonica*, 32(2): 217-229.

Martins, A.C.L.; Rêgo, M.M.C.; Carreira, L.M.M.; Albuquerque, P.M.C. 2011. Espectro polínico de mel de tiúba (*Melipona fasciculata* Smith, 1854, Hymenoptera, Apidae). *Acta Amazonica*, 41(2): 183-190.

Martins, F.Q.; Batalha, M.A. 2006. Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (Central Brazil). *Brazilian Journal of Biology*, 66(2A): 543–552.

Maurizio, A. 1958. Beitraege zur quantitativen pollenanalyse des honigs. 3. - Absoluter gehalt pflanzlicher bestandteile in esparsette-, luzerne-, orangen- und rapshonigen. *Annales de l'Abeille*, 1(2): 93-106. DOI: 10.1051/apido:19580204

Maurizio, A. 1975. Microscopy of honey. In: Maurizio, A. (Ed.). *Honey: a comprehensive survey*. William Heinemann, London, p.240–257.

McCune, B.; Grace, J. 2002. *Analysis of ecological communities*. MjM Software, Gleneden Beach, 300p.

Medeiros, S.S.; Cavalcante, A.M.B.; Marin, A.M.P.; Tinôco, L.B.M.; Salcedo, I.H.; Pinto, T.F. 2012. *Sinopse do censo demográfico para o semiárido brasileiro*. INSA, Campina Grande, 103p.

Michener, C.D. 2007. *The bees of the world*. 2nd. ed. The Johns Hopkins University Press, Baltimore, 953p.

Michener, C.D. 2013. The Meliponini. In: Vit, P.; Pedro, S.R.M.; Roubik, D. (Ed.). *Pot-honey: a legacy of stingless bees*. Springer, New York, p.3–17.

Moar, N.T. 1985. Pollen analysis of New Zealand honey. *New Zealand Journal of Agricultural Research*, 28: 39-70. DOI: 10.1080/00288233.1985.10426997

Molan, P. 1998. The limitations of the methods of identifying the floral source of honeys. *Bee World*, 79: 59-68.

Morgado, L.N.; Andrade, R.C.; Lorenzon, M.C.A.; Gonçalves-Esteves, V. 2011. Padrão polínico utilizado por *Tetragonisca angustula* Latreille (Apidae: Meliponina). *Acta Botanica Brasilica*, 25: 932–934.

Murphy, P.G.; Lugo, A.E. 1986. Ecology of tropical dry forest. *Annual Review of Ecology, Evolution, and Systematics*, 17: 67–88.

Nepstad, D.; Soares-Filho, B.S.; Merry, F.; Lima, A.; Moutinho, P.; Carter, J.; *et al*. 2009. The end of deforestation in the Brazilian Amazon. *Science*, 326: 1350-1451. DOI: 10.1126/science.1182108

Nicolson, S.W. 2007. Nectar consumers. In: Nicolson, S.W.; Nepi, M.; Pacini, E. (Ed.). *Nectaries and nectar*. Springer, Dordrecht, p.289–342.

Nimer, E. 1972. Climatologia da região Nordeste do Brasil: introdução à climatologia dinâmica – subsídios à geografia regional do Brasil. *Revista Brasileira de Geografia*, 34(2): 3–51.

Novais, J.S.; Absy, M.L. 2013. First melissopalynological records in honeys from *Tetragonisca angustula* (Latreille, 1811) in Lower Amazon, Brazil: pollen spectrum and concentration. *Journal of Apicultural Research*. (submetido)

Novais, J.S.; Navarro, E.D.M. 2012. A flowering calendar of plants growing near hives of native bees in the Lower Amazon region, Pará State, Brazil. *Uludağ Bee Journal*, 12(3): 83-88.

Novais, J.S.; Lima, L.C.L.; Santos, F.A.R. 2006. Espectro polínico de méis de *Tetragonisca angustula* Latreille, 1811 coletados na caatinga de Canudos, Bahia, Brasil. *Magistra* 18(4): 257-264.

Novais, J.S.; Lima, L.C.L.; Santos, F.A.R. 2008. Uso de marcador exótico em investigações palinológicas de amostras de mel e pólen coletadas na caatinga de Canudos, Nordeste do Brasil. In: *Anais eletrônicos da 60ª. Reunião Anual da SBPC, Campinas, Brazil, 13-18 July 2008*. (http://www.sbpcnet.org.br/livro/60ra). Acessado em 5/11/2012.

Novais, J.S.; Lima, L.C.L.; Santos, F.A.R. 2009. Botanical affinity of pollen harvested by *Apis mellifera* L. in a semi-arid area from Bahia, Brazil. *Grana*, 48: 224–234.

Novais, J.S.; Lima, L.C.L.; Santos, F.A.R. 2010. Bee pollen loads and their use in indicating flowering in the caatinga region of Brazil. *Journal of Arid Environments*, 74(10): 1355–1358.

Obregón, D.; Rodríguez-C., Á.; Chamorro, F.J.; Nates-Parra, G. 2013. Botanical origin of pot-honey from *Tetragonisca angustula* Latreille in Colombia. In: Vit, P.; Pedro, S.R.M.; Roubik, D. (Ed.). *Pot-honey: a legacy of stingless bees*. Springer, New York, p.337–346.

Oliveira, F.P.M.; Absy, M.L.; Miranda, I.S. 2009. Recurso polínico coletado por abelhas sem ferrão (Apidae, Meliponinae) em um fragmento de floresta na região de Manaus - Amazonas. *Acta Amazonica*, 39(2): 505-518. DOI: 10.1590/S0044-59672009000300004

Oliveira, F.P.M.; Carreira, L.M.M.; Jardim, M.A.G. 1998. Carcaterização polínica do mel de *Apis mellifera* L. em área de floresta secundária no muncípio de Igarapé-Açu - Pará. *Boletim do Museu Paraense Emílio Goeldi, série Botânica*, 14(2): 157-176.

Oliveira, P.P. 2009. *Análise palinológica de amostras de mel de* Apis mellifera *L. produzidas no estado da Bahia*. Tese de Doutorado, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia. 192p.

Oliveira, P.P.; van den Berg, C.; Santos, F.A.R. 2010.) Pollen analysis of honeys from Caatinga vegetation of the state of Bahia, Brazil. *Grana*, 49(1): 66–75. DOI: 10.1080/00173130903485122

Opler, P.A.; Frankie, G.W.; Baker, H.G. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography*, 3: 231–236.

Pielou, E.C. 1977. *Mathematical ecology*. John Wiley & Sons, New York, 385p.

Poinar Jr., G.O.; Danforth, B.N. 2006. A fossil bee from Early Cretaceous burmese amber. *Science*, 134: 614.

Prado, D. 2003. As caatingas da América do Sul. In: Leal, I.R.; Tabarelli, M.; Silva, J.M.C. (Ed.). *Ecologia e conservação da caatinga*. Editora Universitária da UFPE, Recife, PE, pp 3–73

Proctor, M.; Yeo, P.; Lack, A. 1996. *The natural history of pollination*. Harper Collins, London, 479p.

Queiroz, L.P. 2006. The Brazilian Caatinga: phytogeographical patterns inferred from distribution data of the Leguminosae. In: Pennington, R.T.; Lewis, G.P.; Ratter, J.A. (Org.). *Neotropical savannas and dry forests: diversity, biogeography, and conservation*. Taylor & Francis, CRC Press, Boca Raton, p.113–149.

Queiroz, L.P. 2009. *Leguminosas da caatinga*. UEFS, Feira de Santana, 467p.

Ramalho, M.; Imperatriz-Fonseca, V.L.; Kleinert-Giovannini, A.; Cortopassi-Laurino, M. 1985. Exploitation of floral resources by *Plebeia remota* Holmberg (*Apidae, Meliponinae*). *Apidologie*, 16(3): 307-330. DOI: 10.1051/apido:19850306

Ramalho, M.; Kleinert-Giovannini, A.; Imperatriz-Fonseca, V.L. 1990. Important bee plants for stingless bees (*Melipona* and Trigonini) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. *Apidologie*, 21: 469-488. DOI: 10.1051/apido:19900508

Ramírez-Arriaga, E.; Martínez-Hernández, E. 2007. Melitopalynological characterization of *Scaptotrigona mexicana* Guérin (Apidae: Meliponini) and *Apis mellifera* L. (Apidae: Apini) honey samples in Northern Puebla State, Mexico. *Journal of The Kansas Entomological Society*, 80(4): 377-391.

Ramírez-Arriaga, E.; Navarro-Calvo, L.A.; Díaz-Carbajal, E. 2011. Botanical characterisation of Mexican honeys from a subtropical region (Oaxaca) based on pollen analysis. *Grana*, 50(1): 40-54. DOI: 10.1080/00173134.2010.537767

Rech, A.R.; Absy, M.L. 2011a. Pollen sources used by species of Meliponini (Hymenoptera: Apidae) along the Rio Negro channel in Amazonas, Brazil. *Grana*, 50(2): 150-161. DOI: 10.1080/00173134.2011.579621

Rech, A.R.; Absy, M.L. 2011b. Pollen storages in nests of bees of the genera *Partamona*, *Scaura* and *Trigona* (Hymenoptera, Apidae). *Revista Brasileira de Entomologia*, 55(3): 361-372. DOI: 10.1590/S0085-56262011005000026

Rêgo, M.M.C.; Albuquerque, P.M.C.; Ramos, M.C.; Carreira, L.M. 2006. Aspectos da biologia de nidificação de *Centris flavifrons* (Friese) (Hymenoptera: Apidae, Centridini), um dos principais polinizadores do murici (*Byrsonima crassifolia* L. Kunth, Malpighiaceae), no Maranhão. *Neotropical Entomology*, 35: 579–587.

Ribeiro, J.E.L.S.; Hopkins, M.J.G.; Vicentini, A.; Sothers, C.A.; Costa, M.A.S.; Brito, J.M.; *et al*. 2002. *Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central*. Instituto Nacional de Pesquisas da Amazônia, Manaus, 816p.

Rocha-Filho, L.C.; Krug, C.; Silva, C.I.; Garófalo, C.A. 2012. Floral resource used by Euglossini bees (Hymenoptera: Apidae) in coastal ecosystems of the Atlantic forest. *Psyche*, 2013(Article ID 934951). DOI:10.1155/2012/934951

Roubik, D. (Ed.). 1995. *Pollination of cultivated plants in the tropics*. Food and Agriculture Organization of the United Nations, Rome, 196p.

Roubik, D.W.; Moreno P., J.E. 1991. *Pollen and spores of Barro Colorado Island*. Missouri Botanical Garden; St. Louis, 268p.

Roubik, D.W.; Moreno P., J.E. 2009. *Trigona corvina*: an ecological study based on unusual nest structure and pollen analysis. *Psyche*, 2009(Article ID 268756). DOI:10.1155/2009/268756.

Roubik, D.W.; Moreno P., J.E. 2013. How to be a bee-botanist using pollen spectra. In: Vit, P.; Pedro, S.R.M.; Roubik, D. (Ed.). *Pot-honey: a legacy of stingless bees*. Springer, New York, p.295–314.

Sajjad, A.; Saeed, S.; Bashir, M.A. 2012. Spatial variation in pollinator communities and reproductive performance of *Prosopis juliflora* (Fabaceae). *Journal of Pollination Ecology*, 8(9): 59–66.

Sampaio, E.V.S.B. 2002. Uso das plantas da caatinga. In: Sampaio, E.V.S.B.; Giulietti, A.M.; Virgínio, J.; Gamarra-Rojas, C.F.L. (Ed.). *Vegetação e flora da caatinga*. APNE, Recife, p.49–90.

Santana, A.L.A.; Fonseca, A.A.O.; Alves, R.M.O.; Carvalho, C.A.L.; Melo, P.A.; Silva, E.S.; Souza, B.A.; Jesus, J.N.; Sodré, G.S. 2011. Tipos polínicos em amostras de méis de abelhas sem ferrão de municípios do semiárido baiano. *Magistra*, 23(3): 134–139.

Santos, A.P.M.; Romero, R.; Oliveira, P.E.A.M. 2010. Biologia reprodutiva de *Miconia angelana* (Melastomataceae), endêmica da Serra da Canastra, Minas Gerais. *Revista Brasileira de Botânica*, 33: 333–341.

Santos, F.A.R.; Oliveira, A.V.; Lima, L.C.L.; Barros, R.F.M.; Schlindwein, C.P.; Martins, C.F.; Camargo, R.C.R.; Freitas, B.M.; Kiill, L.H.P. 2005. Apícolas. In: Sampaio, E.V.S.B.; Pareyn, F.G.C.; Figueroa, J.M.; Santos Jr., A.G. (Ed.). *Espécies da flora nordestina com importância econômica potencial*. APNE, Recife, p.15–26.

Santos, F.A.R; Oliveira, J.M.; Oliveira, P.P.; Leite, K.R.B.; Carneiro, C.E. 2006. Plantas do semi-árido importantes para as abelhas. In: Santos, F.A.R. (Ed.). *Apium plantae*. IMSEAR, Recife, p.61–86.

Santos, R.F.; Kiill, L.H.P.; Araújo, J.L.P. 2006. Levantamento da flora melífera de interesse apícola no município de Petrolina - PE. *Caatinga*, 19(3): 221–227.

Santos Jr., M.C.; Santos, F.A.R. 2003. Espectro polínico de amostras de méis coletadas na microrregião do Paraguassu, Bahia. *Magistra*, 15(1): 79–85.

SEI — Superintendência de Estudos Econômicos e Sociais da Bahia. 2013. *Informações geográficas. Sistema de dados estatísticos*. (http://www.sei.ba.gov.br/side/consulta_frame.wsp?tmp.codpai=gr1&tmp.pesquisa=false). Acessado em 19/03/2013.

Shannon, C.E.; Weaver, W. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbano, 117p.

Silva, A.P.C.; Lima, Á.S.; Santos, F.A.R. 2012. Botanical biodiversity in honey samples from the semiarid region of Sergipe state, Brazil. *Magistra*, 24: 158–171.

Silva, F.H.M. 2007. *Contribuição à palinologia das caatingas*. Tese de Doutorado, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia. 182p.

Silva, M.F.F.; Secco, R.S.; Lobo, M.G.A. 1996. Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. *Acta Amazonica*, 26(1/2): 17-44.

Silva, S.J.R.; Absy, M.L. 2000. Análise do pólen encontrado em amostras de mel de *Apis mellifera* L. (Hymenoptera, Apidae) em uma área de savana de Roraima, Brasil. *Acta Amazonica*, 30(4): 579-588.

Silva, S.J.R.; Rebouças, M.A.P. 1998. Plantas melíferas de Roraima - Parte II. *Boletim do Museu Integrado de Roraima*, 4: 31-38.

Silveira, F.A. 1991. Influence of pollen grains volume on the estimation of the relative importance of its source to bees. *Apidologie*, 22: 495–502.

Silveira, F.A.; Melo, G.A.R.; Almeida, E.A.B. 2002. *Abelhas brasileiras: sistemática e identificação*. Fernando A. Silveira, Belo Horizonte, 253p.

Silveira, T.A. 2012. *Caracterização sazonal do pólen apícola quanto à origem botânica, aspectos físico-químicos e elementos traços como bioindicadora de poluição ambiental*. Dissertação de Mestrado, Universidade de São Paulo Escola Superior de Agricultura "Luiz de Queiroz", Piracicaba, São Paulo. 66p.

Sodré, G.S.; Marchini, L.C.; Carvalho, C.A.L.; Moreti, A.C.C.C. 2007. Pollen analysis in honey samples from the two main producing regions in the Brazilian northeast. *Anais da Academia Brasileira de Ciências*, 79(3): 381–388.

Sorkun, K.; Doğan, C. 2002. The importance of the total number of pollen types in 10 gr of honey in distinguishing between natural honey and artificial honey produced in Turkey. *Mellifera*, 2-3: 34-38.

Sosa-Nájera, M.S.; Martínez-Henández, E.; Lozano-García, M.S.; Cuadriello-Aguiar, J.I. 1994. Nectaropolliniferous sources used by *Trigona* (*Tetragonisca*) *angustula* in Chiapas, southern México. *Grana*, 33(4): 225–230. DOI: 10.1080/00173139409429003

Stehmann, J.R.; Mentz, L.A.; Agra, M.F.; Vignoli-Silva, M.; Giacomin, L. 2013. Solanaceae. In: *Lista de espécies da flora do Brasil*. (http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB14716). Acessado em 29/03/2013.

Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, 13(4): 615-621.

Symon, D.E. 1979. Sex forms in *Solanum* (Solanaceae) and the role of pollen collecting insects. In: Hawkes, J.G.; Lester, R.N.L.; Skelding, A.D. (Ed.). *The biology and taxonomy of the Solanaceae*. Academic Press, London, p.385–397.

Teixeira, L.A.G.; Machado, I.C. 2000. Sistema de polinização e reprodução de *Byrsonima sericea* DC. (Malpighiaceae). *Acta Botanica Brasilica*, 14: 347–357.

Veloso, H.P.; Rangel Filho, A.L.R.; Lima, J.C.A. 1991. *Classificação da vegetação brasileira, adaptada a um sistema universal*. IBGE, Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro, 123p.

Vergeron, P. 1964. Interprétation statistique des résultats en matière d'analyse pollinique des miels. *Annales de l'Abeille*, 7(4): 349-364. DOI: 10.1051/apido:19640407

Young, W.J. 1908. *A microscopical study of honey pollen*. Bulletin 110. United States Bureau of Chemistry, Washington, 93p.

Zalamea, P.-C.; Heuret, P.; Sarmiento, C.; Rodríguez, M.; Berthouly, A.; Guitet, S.; Nicolini, E.; Delnatte, C.; Barthélémy, D.; Stevenson, P.R. 2012. The genus *Cecropia*: a biological clock to estimate the age of recently disturbed areas in the Neotropics. *PLoS ONE*, 7: e42643. DOI:10.1371/journal.pone.0042643

Zanella, F.C.V.; Martins, C.F. 2003. Abelhas da caatinga: biogeografia, ecologia e conservação. In: Leal, I.R.; Tabarelli, M.; Silva, J.M.C. (Ed.). *Ecologia e conservação da caatinga*. Editora Universitária da UFPE, Recife, p.75–134.

Anexos

ANEXO A — *Links* para as normas de formatação dos capítulos

Observação: A formatação dos capítulos anteriores seguiu as **instruções para autores** apresentadas pelos periódicos listados abaixo e as "Normas para Apresentação de Trabalhos de Conclusão" do INPA, edição de janeiro 2011. Os *hiperlinks* direcionam para as *homepages* nas quais as instruções dos periódicos podem ser acessadas.

Capítulo I – ***Journal of Apicultural Research*** - ISSN: 0021-8839
Disponível em: <http://www.ibra.org.uk>.
Acesso em: 3 maio 2013
Fator de impacto (*JCR* 2011): 1,531

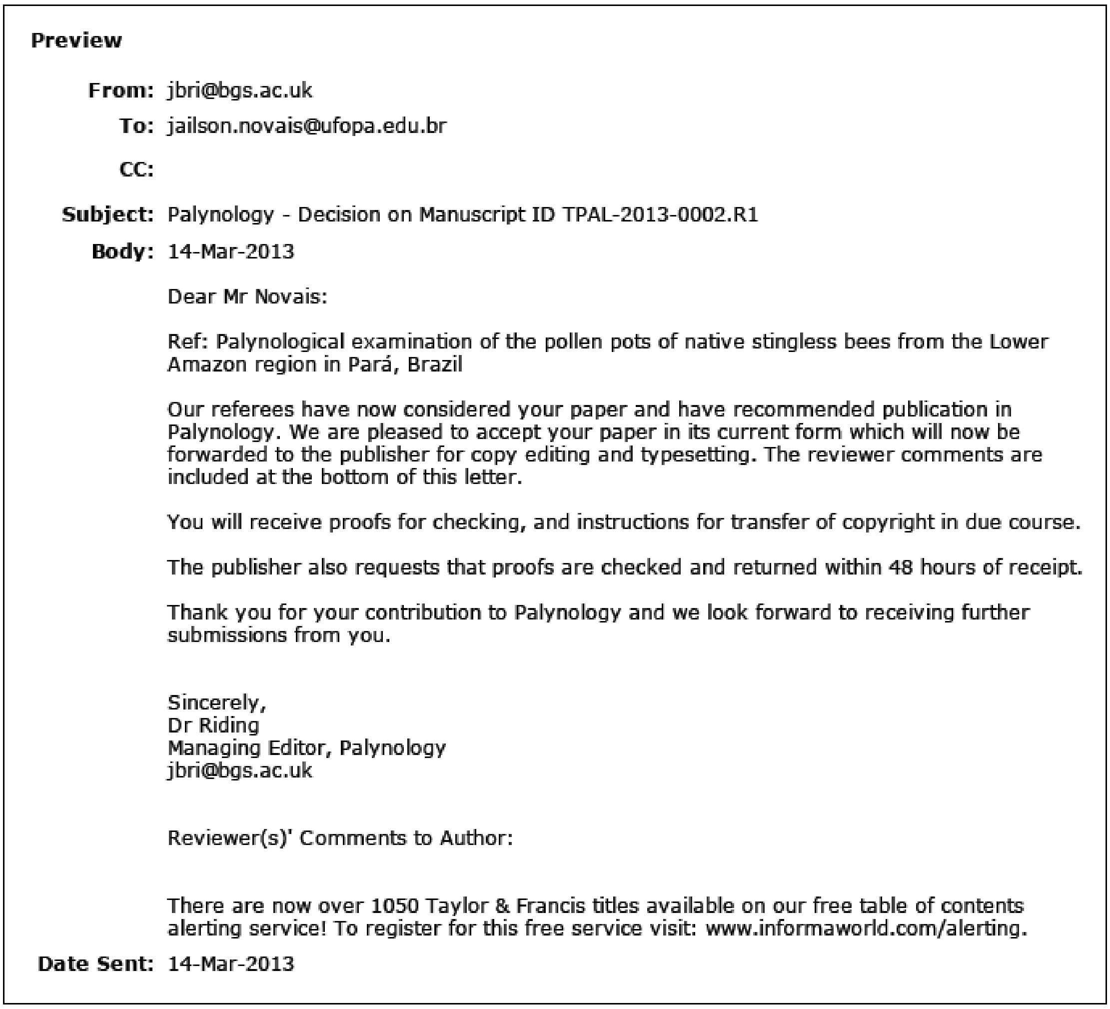
Capítulo II – ***Palynology*** - ISSN: 0191-6122
Disponível em: <http://www.tandfonline.com>.
Acesso em: 3 maio 2013
Fator de impacto (*JCR* 2011): 0,943

Capítulo III – ***Arthropod-Plant Interactions*** - ISSN: 1872-8855
Disponível em: <http://www.springer.com>.
Acesso em: 3 maio 2013
Fator de impacto (*JCR* 2011): 1,309

Capítulo IV – ***European Journal of Entomology*** - ISSN: 1210-5759
Disponível em: <http://www.eje.cz>
Acesso em: 3 maio 2013
Fator de impacto (*JCR* 2011): 1,061

Capítulo V – ***Apidologie*** - ISSN: 0044-8435
Disponível em: <http://www.springer.com>.
Acesso em: 3 maio 2013
Fator de impacto (*JCR* 2011): 2,266

ANEXO B — Aceite de artigo submetido ao periódico *Palynology*



Preview

From: jbri@bgs.ac.uk
To: jailson.novais@ufopa.edu.br
CC:
Subject: Palynology - Decision on Manuscript ID TPAL-2013-0002.R1
Body: 14-Mar-2013

Dear Mr Novais:

Ref: Palynological examination of the pollen pots of native stingless bees from the Lower Amazon region in Pará, Brazil

Our referees have now considered your paper and have recommended publication in Palynology. We are pleased to accept your paper in its current form which will now be forwarded to the publisher for copy editing and typesetting. The reviewer comments are included at the bottom of this letter.

You will receive proofs for checking, and instructions for transfer of copyright in due course.

The publisher also requests that proofs are checked and returned within 48 hours of receipt.

Thank you for your contribution to Palynology and we look forward to receiving further submissions from you.

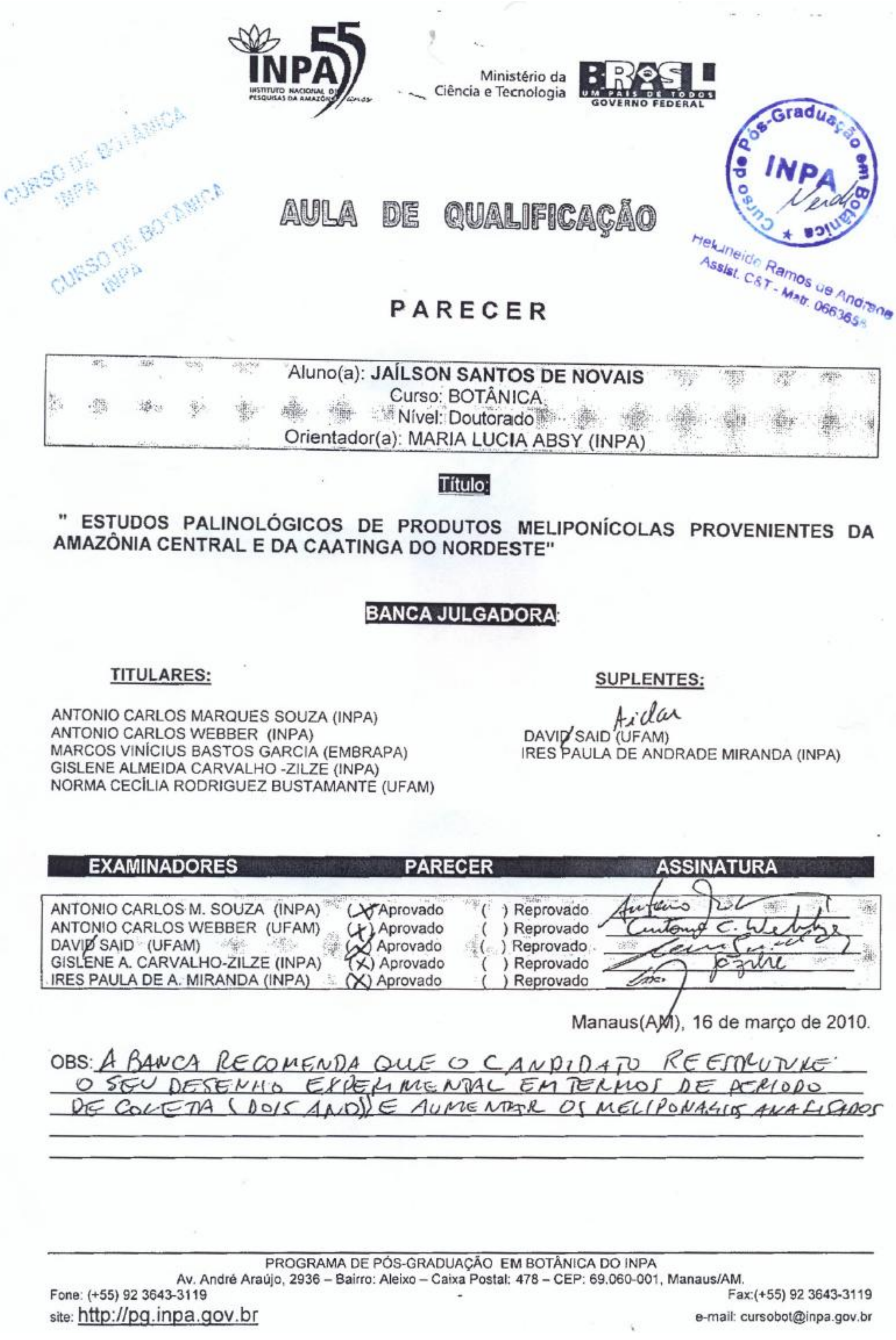
Sincerely,
Dr Riding
Managing Editor, Palynology
jbri@bgs.ac.uk

Reviewer(s)' Comments to Author:

There are now over 1050 Taylor & Francis titles available on our free table of contents alerting service! To register for this free service visit: www.informaworld.com/alerting.

Date Sent: 14-Mar-2013

ANEXO C — Cópia do Parecer da Aula de Qualificação



INPA 55 INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Ministério da Ciência e Tecnologia

BRASIL UM PAÍS DE TODOS GOVERNO FEDERAL

CURSO DE BOTÂNICA INPA

CURSO DE BOTÂNICA INPA

Heluneide Ramos de Andrade
Assist. C&T - Matr. 0663658

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): **JAÍLSON SANTOS DE NOVAIS**
Curso: BOTÂNICA
Nível: Doutorado
Orientador(a): MARIA LUCIA ABSY (INPA)

Título:

" ESTUDOS PALINOLÓGICOS DE PRODUTOS MELIPONÍCOLAS PROVENIENTES DA AMAZÔNIA CENTRAL E DA CAATINGA DO NORDESTE"

BANCA JULGADORA:

TITULARES:	SUPLENTES:
ANTONIO CARLOS MARQUES SOUZA (INPA)	Aidar DAVID SAID (UFAM)
ANTONIO CARLOS WEBBER (INPA)	IRES PAULA DE ANDRADE MIRANDA (INPA)
MARCOS VINÍCIUS BASTOS GARCIA (EMBRAPA)	
GISLENE ALMEIDA CARVALHO -ZILZE (INPA)	
NORMA CECÍLIA RODRIGUEZ BUSTAMANTE (UFAM)	

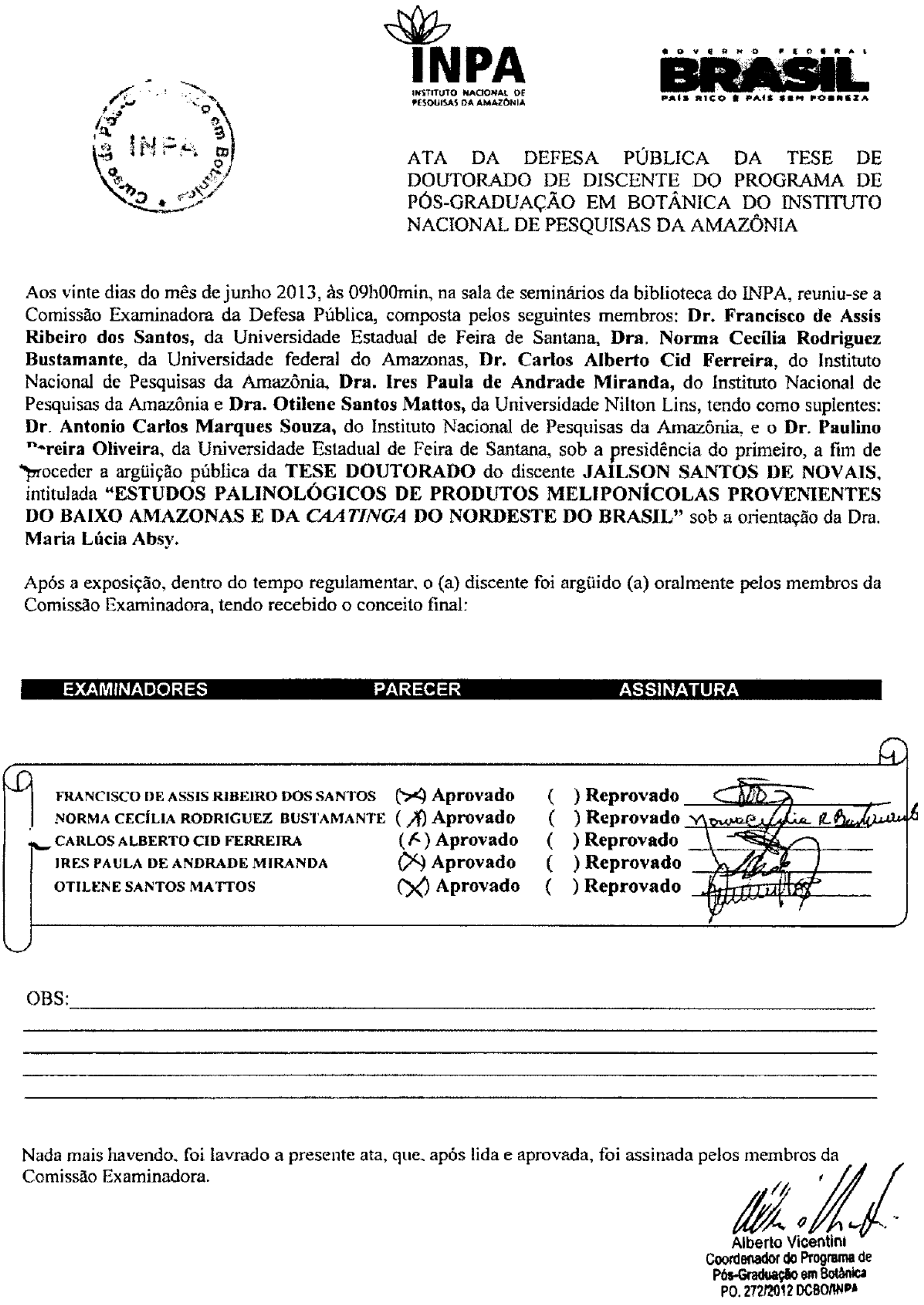
EXAMINADORES	PARECER		ASSINATURA
ANTONIO CARLOS M. SOUZA (INPA)	(X) Aprovado	( ) Reprovado	
ANTONIO CARLOS WEBBER (UFAM)	(X) Aprovado	( ) Reprovado	Antonio C. Webber
DAVID SAID (UFAM)	(X) Aprovado	( ) Reprovado	
GISLENE A. CARVALHO-ZILZE (INPA)	(X) Aprovado	( ) Reprovado	
IRES PAULA DE A. MIRANDA (INPA)	(X) Aprovado	( ) Reprovado	

Manaus(AM), 16 de março de 2010.

OBS: A BANCA RECOMENDA QUE O CANDIDATO REESTRUTURE O SEU DESENHO EXPERIMENTAL EM TERMOS DE PERIODO DE COLETA (DOIS ANOS) E AUMENTAR OS MELIPONARIOS ANALISADOS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA DO INPA
Av. André Araújo, 2936 – Bairro: Aleixo – Caixa Postal: 478 – CEP: 69.060-001, Manaus/AM.
Fone: (+55) 92 3643-3119
Fax:(+55) 92 3643-3119
site: http://pg.inpa.gov.br
e-mail: cursobot@inpa.gov.br

ANEXO D — Cópia do Parecer e Ata da Defesa Oral do Trabalho de Conclusão



INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

GOVERNO FEDERAL
BRASIL
PAÍS RICO É PAÍS SEM POBREZA

INPA

ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DE DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos vinte dias do mês de junho 2013, às 09h00min, na sala de seminários da biblioteca do INPA, reuniu-se a Comissão Examinadora da Defesa Pública, composta pelos seguintes membros: **Dr. Francisco de Assis Ribeiro dos Santos,** da Universidade Estadual de Feira de Santana, **Dra. Norma Cecília Rodriguez Bustamante**, da Universidade federal do Amazonas, **Dr. Carlos Alberto Cid Ferreira**, do Instituto Nacional de Pesquisas da Amazônia, **Dra. Ires Paula de Andrade Miranda,** do Instituto Nacional de Pesquisas da Amazônia e **Dra. Otilene Santos Mattos,** da Universidade Nilton Lins, tendo como suplentes: **Dr. Antonio Carlos Marques Souza,** do Instituto Nacional de Pesquisas da Amazônia, e o **Dr. Paulino Pereira Oliveira**, da Universidade Estadual de Feira de Santana, sob a presidência do primeiro, a fim de proceder a argüição pública da **TESE DOUTORADO** do discente **JAILSON SANTOS DE NOVAIS**, intitulada **"ESTUDOS PALINOLÓGICOS DE PRODUTOS MELIPONÍCOLAS PROVENIENTES DO BAIXO AMAZONAS E DA *CAATINGA* DO NORDESTE DO BRASIL"** sob a orientação da Dra. **Maria Lúcia Absy.**

Após a exposição, dentro do tempo regulamentar, o (a) discente foi argüido (a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

EXAMINADORES	PARECER		ASSINATURA
FRANCISCO DE ASSIS RIBEIRO DOS SANTOS	(X) Aprovado	( ) Reprovado	
NORMA CECÍLIA RODRIGUEZ BUSTAMANTE	(X) Aprovado	( ) Reprovado	Norma Cecília R Bustamante
CARLOS ALBERTO CID FERREIRA	(X) Aprovado	( ) Reprovado	
IRES PAULA DE ANDRADE MIRANDA	(X) Aprovado	( ) Reprovado	
OTILENE SANTOS MATTOS	(X) Aprovado	( ) Reprovado	

OBS:____

Nada mais havendo, foi lavrado a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Alberto Vicentini
Coordenador do Programa de Pós-Graduação em Botânica
PO. 272/2012 DCBO/INPA