

Valdeir Pereira Lima

**Current and future distribution of stingless bees in Brazil:
identifying potential threats to species conservation**

Dissertation presented to Programa de Pós Graduação em Ecossistemas Agrícolas e Naturais of Universidade Federal de Santa Catarina, as a requirement to obtain master degree.

Supervisor: Professor Dr. Cesar Augusto Marchioro

Curitibanos/SC

2018

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Lima, Valdeir Pereira
Current and future distribution of stingless
bees in Brazil: identifying potential threats to
species conservation / Valdeir Pereira Lima ;
orientador, Cesar Augusto Marchioro, 2018.
184 p.

Dissertação (mestrado) - Universidade Federal de
Santa Catarina, Campus Curitibanos, Programa de Pós
Graduação em Ecossistemas Agrícolas e Naturais,
Curitibanos, 2018.

Inclui referências.

1. Ecossistemas Agrícolas e Naturais. 2. Bee
conservation. 3. Climate shifts. 4. Conservation
biogeography. 5. Species Distribution Modeling. I.
Marchioro, Cesar Augusto. II. Universidade Federal
de Santa Catarina. Programa de Pós-Graduação em
Ecossistemas Agrícolas e Naturais. III. Título.



UNIVERSIDADE FEDERAL DE SANTA CATARINA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOSISTEMAS
AGRÍCOLAS E NATURAIS - PPGEAN

Termo de aprovação

**Current and future distribution of stingless bees in Brazil:
identifying potential threats to species conservation**

Por

VALDEIR PEREIRA LIMA

Dissertação aprovada como requisito parcial para a obtenção do Grau de Mestre em Ciências, área de concentração Ciências Agrárias, no Programa de Pós-Graduação em Ecossistemas Agrícolas e Naturais, Centro de Ciências Rurais da Universidade Federal de Santa Catarina, pela Comissão formada pelos membros:

Dr. Cesar Augusto Marchioro – UFSC
Presidente e orientador

Dr. Andreas Luis Schwarz Meyer – UFRR

Dra. Julia Carina Niemeyer – UFSC

Curitiba, 08 de fevereiro de 2018.

“I do not know what I may appear to the world, but to myself I seem to have been only like a boy playing on the sea-shore, and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.”

Isaac Newton

Aos meus pais,

Dedico

CONTENTS

| | |
|--|-----------|
| INTRODUCTION | 15 |
| CHAPTER 1 - PREDICTING THE CURRENT DISTRIBUTION OF STINGLESS BEES IN BRAZIL: LAND USE AND EFFECTIVENESS OF PROTECTED AREAS..... | 20 |
| ABSTRACT | 20 |
| INTRODUCTION..... | 21 |
| MATERIAL AND METHODS..... | 23 |
| RESULTS | 26 |
| DISCUSSION | 31 |
| ACKNOWLEDGMENTS..... | 35 |
| REFERENCES | 35 |
| CHAPTER 2 - IMPACTS OF CLIMATE CHANGE ON THE DISTRIBUTION OF STINGLESS BEES IN BRAZIL | 44 |
| ABSTRACT | 44 |
| INTRODUCTION..... | 45 |
| MATERIALS AND METHODS..... | 47 |
| RESULTS | 49 |
| DISCUSSION | 55 |
| ACKNOWLEDGMENTS..... | 58 |
| REFERENCES | 58 |
| FINAL CONSIDERATIONS | 64 |
| SUPPLEMENTARY MATERIAL | 66 |

RESUMO

O presente estudo teve como objetivo (i) estimar a distribuição de espécies de dez *Melipona* no Brasil, (ii) quantificar as mudanças recentes no uso da terra abrangendo as áreas estimadas como adequadas para essas abelhas, (iii) verificar a eficácia das áreas protegidas no Brasil (APs) para a conservação das mesmas, (iv) avaliar como as mudanças climáticas afetarão a distribuição geográfica das espécies, bem como (v) estimar as áreas climaticamente estáveis para as espécies em diferentes cenários de mudanças climáticas. Para isso utilizou-se modelos de nicho ecológico usando o algoritmo de entropia máxima implementado no *software* MaxEnt. Este algoritmo estima a probabilidade cumulativa de entropia máxima com base em registros de ocorrência de espécies e variáveis ambientais. Ademais, análises espaciais foram utilizadas para quantificar as recentes mudanças no uso da terra dentro das áreas de distribuição estimadas para as espécies de *Melipona*, bem como avaliar a eficácia das APs para a conservação das abelhas sem ferrão. Os modelos climáticos ajustados para as condições climáticas do presente foram projetados para condições futuras previstas para 2050 e 2070 usando dois cenários de mudança climática fornecidos pelo Painel Intergovernamental sobre Mudanças Climáticas (RCP 4.5 e RCP 8.5). As áreas preditas como adequadas para as espécies de *Melipona* estão distribuídas em diferentes regiões e biomas do Brasil. As espécies *Melipona melanoventer* Schwarz, 1932, *Melipona seminigra abunensis* Cockerell, 1912, *Melipona flavolineata* Friese, 1900, *Melipona fasciculata* Smith, 1854, *Melipona amazonica* Schulz, 1905, *Melipona subnitida* Ducke, 1910 e *Melipona paraensis* Ducke, 1916 estão distribuídas principalmente em áreas naturais, enquanto *Melipona scutellaris* Latreille, 1811, *Melipona quadrifasciata anthidioides* Lepeletier, 1836 e *Melipona quadrifasciata quadrifasciata* Lepeletier, 1836 ocorrem predominantemente em mosaicos de agricultura e remanescentes florestais. A espécie *M. paraensis* apresentou a maior porcentagem (31.54%) de suas áreas adequadas cobertas por APs e *M. scutellaris* a menor (6.54%). As mudanças recentes no uso da terra dentro da distribuição das espécies de *Melipona*, particularmente a conversão de áreas naturais para uso agrícola, indicam que isso pode afetar negativamente esses polinizadores e consequentemente os serviços ecossistêmicos promovidos por eles. As APs brasileiras apresentaram pouca eficácia para a conservação das espécies estudadas. Os modelos predizem que sete das dez espécies irão enfrentar uma redução nas suas áreas climaticamente adequadas e três encontrarão um

aumento em suas áreas nos cenários climáticos futuros avaliados. Dado o papel fundamental que essas espécies desempenham como polinizadores nos ecossistemas agrícolas e naturais, isso pode gerar graves consequências para a produção de alimento e conservação de espécies de plantas nativas.

PALAVRAS-CHAVE: Conservação de abelhas, Mudanças climáticas, Biogeografia da conservação, *Melipona*, Modelagem de Distribuição de Espécies, Conservação de polinizadores.

RESUMO EXPANDIDO

Introdução

As abelhas são os principais polinizadores nos ecossistemas agrícolas e naturais (Breeze et al., 2016; Garibaldi et al., 2016; Potts et al., 2016), atuando ativamente no equilíbrio e manutenção da vegetação (Giannini et al., 2012). Nos agroecossistemas, mais de 90% das 107 principais culturas agrícolas globais cultivadas atualmente são dependentes da polinização por abelhas (Klein et al., 2007). Além disso, os serviços de polinização aumentam a produção agrícola em até 577 bilhões de dólares por ano (Lautenbach et al., 2012), sendo estimada uma perda de 5 a 8% na produção mundial sem os serviços de polinização (Potts et al., 2016).

Nos últimos anos, populações de abelhas têm sofrido um significativo declínio em diferentes partes do mundo, gerando uma grande preocupação com a conservação desse grupo (Allen-Wardell et al., 1998; Buchmann & Nabhan, 1996; Kearns et al., 1998; Kevan & Viana, 2003). Cinco fatores antropogênicos são mencionados como causas desse declínio, a saber: (i) mudança de uso da terra e intensidade de manejo, (ii) mudanças climáticas, (iii) uso indiscriminado de pesticidas e organismos geneticamente modificados OGMs, (iv) manejo inadequado de polinizadores e (v) disseminação de patógenos e espécies exóticas invasoras (Potts et al., 2016). O presente estudo avaliou a vulnerabilidade de dez espécies de abelhas sem ferrão do gênero *Melipona* distribuídas no Brasil considerando dois dos cinco fatores listados: mudança de uso da terra e mudanças climáticas. Neste contexto, dividimos nosso estudo em dois capítulos. No primeiro capítulo abordamos as recentes mudanças no uso da terra,

especificamente áreas agrícolas, áreas naturais e mosaicos de áreas agrícolas e remanescentes naturais, dentro das áreas climaticamente adequadas para as espécies de *Melipona*. Em seguida, para avaliar a eficácia das áreas protegidas no Brasil para a conservação das espécies, quantificamos todas as áreas protegidas que abrangem regiões preditas como adequadas para as abelhas sem ferrão estudadas. No segundo capítulo, avaliamos como as mudanças climáticas podem afetar a distribuição dessas abelhas em diferentes anos e cenários futuros. As informações aqui geradas podem servir como subsídio para o desenvolvimento de estratégias de conservação destas importantes espécies por órgãos ambientais responsáveis.

Objetivos

O presente estudo teve como objetivos (i) estimar a distribuição de espécies de *Melipona* no Brasil, (ii) quantificar as mudanças recentes no uso da terra dentro das áreas previstas como adequadas para essas abelhas, (iii) avaliar a eficácia das Áreas Protegidas no Brasil (APs) para a conservação das espécies, (iv) avaliar como a mudança climática afetará a distribuição geográfica dessas espécies, bem como (v) estimar as áreas climaticamente estáveis para as espécies em diferentes cenários de mudanças climáticas.

Material e Métodos

Os registros de ocorrência para *Melipona scutellaris* Latreille, 1811, *Melipona quadrifasciata anthidioides* Lepeletier, 1836, *Melipona quadrifasciata quadrifasciata* Lepeletier, 1836, *Melipona melanoventer* Schwarz, 1932, *Melipona seminigra abunensis* Cockerell, 1912, *Melipona flavolineata* Friese, 1900, *Melipona fasciculata* Smith, 1854, *Melipona amazonica* Schulz, 1905, *Melipona subnitida* Ducke, 1910 e *Melipona paraensis* Ducke, 1916 foram obtidos a partir da literatura e bancos de dados on-line, como o Global Information Biodiversity Facility (<http://www.gbif.org>) e SpeciesLink (<http://splink.cria.org.br>). Todos os dados de ocorrência foram analisados usando o *software* ArcGIS 10.3 e os registros que não estavam dentro da distribuição geográfica conhecida das espécies foram excluídos. A informação sobre as áreas de ocorrência de cada espécie foi obtida no Catálogo Moure (<http://www.moure.org.br>).

Foram utilizados dados de altitude e 19 variáveis bioclimáticas na resolução de 5 arc-min obtidas no site Worldclim version 1.4. (<http://worldclim.org>) para caracterizar o nicho climático das espécies em estudo. As variáveis bioclimáticas derivam de medidas mensais de temperatura e dados de precipitação. De acordo com Slater & Michael (2012), essas variáveis capturam informações de grande relevância para a modelagem de nicho ecológico, como variações anuais e limites bem definidos de temperatura e precipitação que restringem a distribuição das espécies.

Os modelos de distribuição de espécies foram construídos usando um algoritmo que estima a probabilidade cumulativa de entropia máxima através de registros de ocorrências e variáveis ambientais (Elith, et al., 2011; Phillips et al., 2006; Phillips; Dudík, 2008), implementado no *software* MaxEnt v. 3.3.3k (Phillips et al., 2006). O MaxEnt é considerado um dos métodos atuais de modelagem de nicho ecológico de presença que apresentam melhor desempenho, mesmo quando poucos registros de ocorrências estão disponíveis (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008; Phillips et al., 2006).

O MaxEnt permite aos usuários selecionar diferentes funções: linear (L), quadratic (Q), product (P), hinge (H) e threshold (T), e multiplicadores de regularização (*regularization multiplier*). Essas configurações podem ser alteradas com o objetivo de construir modelos mais parcimoniosos (Merow et al., 2013). Dado este fato, quinze modelos distintos foram construídos para cada uma das espécies estudadas, utilizando diferentes combinações de funções (L; H; LQ; LQH e LQHPT) e multiplicadores de regularização (1, 3 e 5). Este procedimento foi realizado para selecionar modelos menos complexos e que apresentam boa capacidade preditiva. A seleção dos melhores modelos foi realizada usando o Critério de Informação Akaike corrigido (AICc). O AICc é um método comumente usado para comparar modelos levando em consideração sua complexidade e desempenho, sendo que valores mais baixos de AICc indicam modelos de melhor ajuste (Warren et al., 2010). O cálculo de AICc foi conduzido com o *software* ENM Tools v. 1.3 (Warren et al., 2010). O desempenho dos modelos selecionados foi avaliado usando a área sob a curva (AUC) da característica operativa do receptor (ROC), que analisa a comissão versus erros de omissão (Fielding & Bell, 1997). Os valores de AUC variam de 0 a 1, sendo que valores entre 0,5 e 0,7 indicam um

desempenho fraco, entre 0,7 a 0,9 indicam desempenho moderado e maiores que 0,9 indicam um alto desempenho (Peterson et al., 2011).

Os modelos finais obtidos no presente para cada espécie foram sobrepostos a mapas de Unidades de Conservação (UC) e uso e cobertura da terra (LULC) com objetivo avaliar a eficácia das UCs e vulnerabilidade dessas espécies frente ao uso e cobertura da terra. Este procedimento foi realizado com o *software* ArcGIS 10.3.

Resultados e Discussão

As áreas preditas como adequadas para *M. paraensis*, *M. melanoventer*, *M. s. abunensis* e *M. amazonica* estão na região norte do Brasil, predominantemente na região amazônica. As espécies *M. subnitida* e *M. scutellaris* ocorrem na região nordeste do país, cobrindo áreas de Caatinga e Mata Atlântica. Os modelos estimam áreas adequadas para *M. flavolineata* e *M. fasciculata* na região norte e nordeste, incluindo os biomas Amazonia, Cerrado, Caatinga e Pantanal. E *M. q. anthidioides* e *M. q. quadrifasciata* foram previstas em toda a costa leste do Brasil, incluindo regiões do Nordeste, Sul e Sudeste na Mata Atlântica, Cerrado e Caatinga. As espécies *M. melanoventer*, *M. s. abunensis*, *M. flavolineata*, *M. fasciculata*, *M. amazonica*, *M. subnitida* e *M. paraensis* estão distribuídas predominantemente em áreas de vegetação natural, enquanto *M. scutellaris*, *M. q. anthidioides* e *M. q. quadrifasciata* ocorrem predominantemente em mosaicos de agricultura e remanescentes florestais. As mudanças no uso da terra, principalmente em relação à conversão da vegetação natural em áreas urbanas e agrícolas, são frequentemente citadas como uma das causas mais importantes do declínio das populações de polinizadores (Ollerton et al., 2014; De Palma et al., 2016). A espécie *M. paraensis* apresentou a maior porcentagem (31.54%) de suas áreas adequadas cobertas por APs e *M. scutellaris* a menor (6.54%). As APs brasileiras apresentam pouca eficácia para a conservação das espécies estudadas (Oliveira et al., 2017; Rayner et al., 2013). Os modelos predizem que sete das dez espécies analisadas irão enfrentar uma redução nas suas áreas ambientalmente adequadas enquanto três irão encontrar um aumento em suas áreas adequadas nos cenários climáticos avaliados. Diversos estudos relacionados a essa temática têm apontando as mudanças climáticas como uma das principais causas do declínio das abelhas polinizadoras (Biesmeijer et al., 2006; Dupont et al., 2011, Giannini et al., 2012), fato este corroborado pelos resultados do presente estudo.

Considerações Finais

Os resultados indicam que o uso da terra necessita ser considerado nos planejamentos de estratégias de conservação, especialmente ao criar novas Áreas Protegidas no país. Destacamos ainda a necessidade de discutir práticas agrícolas e serviços de polinização para garantir os serviços ecossistêmicos fornecidos pelos polinizadores no futuro e sugerimos que as estratégias favoráveis à biodiversidade, como a meliponicultura, sejam consideradas para assegurar os serviços ecossistêmicos e aumentar a renda econômica e bem-estar das populações locais. Nosso estudo fornece uma significativa contribuição para o conhecimento da vulnerabilidade das abelhas sem ferrão, podendo este ser utilizado por tomadores de decisões para o desenvolvimento de estratégias de conservação destas espécies.

PALAVRAS-CHAVE: Conservação de abelhas, Mudanças climáticas, Biogeografia da conservação, *Melipona*, Modelagem de Distribuição de Espécies, Conservação de polinizadores.

ABSTRACT

The present study aimed to (i) predict the potential distribution of ten *Melipona* species in Brazil, (ii) quantify the recent changes in land use within the predicted suitable ranges for the stingless bees, (iii) assess the efficacy of Brazilian Protected Areas (PAs) for conservation of the studied species, (iv) evaluate whether climate change will affect the distribution of these species, as well as (v) estimate the climatically stable areas for the species in different years and scenarios of climate change. We applied Ecological Niche Modeling using the maximum entropy algorithm implemented in the software MaxEnt. This algorithm estimates the cumulative probability of maximum entropy based on species occurrence records and environmental data. Additionally, we used Geographic Information System analysis to quantify recent land use changes within the distribution ranges of the *Melipona* species and assess the efficacy of PAs for the conservation of the stingless bees. The models fitted to the current climatic conditions were projected onto the future climatic conditions predicted for 2050 and 2070 using two different climate change scenarios (RCP 4.5 and RCP 8.5) provided by the Intergovernmental Panel on Climate Change. The areas predicted as suitable for *Melipona* species are distributed in different regions and biomes of Brazil. The species *Melipona melanoventer* Schwarz, 1932,

Melipona seminigra abunensis Cockerell, 1912, *Melipona flavolineata* Friese, 1900, *Melipona fasciculata* Smith, 1854, *Melipona amazonica* Schulz, 1905, *Melipona subnitida* Ducke, 1910 and *Melipona paraensis* Ducke, 1916 are mostly distributed in areas with natural vegetation, while *Melipona scutellaris* Latreille, 1811, *Melipona quadrifasciata anthidioides* Lepeletier, 1836 and *Melipona quadrifasciata quadrifasciata* Lepeletier, 1836 occurs predominantly in areas with mosaic of agriculture and forest remnants. The species *M. melanoventer*, *M. s. abunensis*, *M. flavolineata*, *M. fasciculata*, *M. amazonica*, *M. subnitida* and *M. paraensis* are mostly distributed in natural areas while the species *M. scutellaris*, *M. q. anthidioides* and *M. q. quadrifasciata* occur predominantly in areas with mosaic between agriculture and forest remnants. The species *M. paraensis* presented the highest percentage (31.54%) of their suitable range covered by PAs and *M. scutellaris* the lowest (6.54%). The recent changes in land use within the distribution ranges of *Melipona* species, particularly conversion of natural areas for agricultural use, indicates that it might negatively affect these pollinators, and consequently the ecosystem services they provide. Brazilian protected areas presented poor effectiveness for the conservation of the studied species. Our models predicted that seven out of ten species will face a reduction in their suitable areas and three species will find an increase in the available suitable areas in the different climate change scenarios evaluated. Given the key role the stingless bees play as pollinators in natural and agroecosystems, this may have serious consequences for the food production and conservation of the native plant species.

KEYWORDS: Bee conservation, Climate shifts, Conservation biogeography, *Melipona*, Species Distribution Modeling, Pollinator conservation.

Introduction

The global biodiversity is fundamental to ecological processes, economic practices and human well-being (Millennium Ecosystem Assessment, 2005). Over the years, biodiversity has been threatened by conflicts between conservation and human development. A large number of species have been considered endangered (IUCN, 2009), mainly due to environmental changes resulted from the increase in human population growth (United Nations, 2008) and per capita consumption (Myers & Kent, 2003). In this context, conservation biology plays an urgent role, seeking to understand the causes of biodiversity losses at individual, ecosystemic and genetic levels, as well as proposing tools to minimize these losses.

Pollination is among the ecological services that have severe impact on economic activities, food production and, as a consequence on human well-being. Bees are the main pollinators in agricultural and natural ecosystems (Breeze et al., 2016; Garibaldi et al., 2016; Potts et al., 2016; Ollerton et al., 2011), playing an important role on both conservation of natural vegetation and food production. In recent years, the decline of these pollinators has been recorded in different regions of the world (Allen-Wardell et al., 1998; Buchmann & Nabhan, 1996; Kearns et al., 1998; Kevan & Viana, 2003). This situation has prompted a global demand for studies aiming to understand the causes of this decline and promote conservation strategies for these species. An example that illustrates this perception is the recent Brazilian government decision of funding studies involving the conservation of insect pollinators in Brazil. The National Council for Scientific and Technological Development (CNPq) and The Brazilian Bee Studies Association (ABELHA) have issued a call for proposals for financial support for research projects regarding to pollinating insects involving the following five research lines: (i) research on pathogens and parasites in native bees and *Apis mellifera*, (ii) monitoring and evaluation of the situation of native bees in Brazil, (iii) evaluation of ecotoxicity of pesticides for selected native species, (iv) quantification and characterization of environmental resources collected by species of native bees and (v) bioeconomic evaluation of the service of pollination in the agricultural productivity by relevant culture.

The species from genus *Melipona* Illiger, 1806 (Meliponini tribe) are important pollinators of plants in the Neotropical region,

having the greater diversity in South America. These advanced eusocial bees are characterized by forming their perennial nests with a single fertile and active female, and a large number of worker bees which provide food and care for the reproductive males and the hive (Michener, 1974). Additionally, they construct their nests in pre-existent cavities such as hollows of trees (Roubik, 2006), holes in the ground, anthills or termite mounds or in other natural cavities (Kerr et al., 1967; Alves et al., 2006), using waxes, cerumes and batumes for these constructions (Nogueira-Neto, 1970). *Melipona* species act on the maintenance of tropical forests in different biomes such as Atlantic Forest (Ramalho, 2004) and Cerrado (Silva et al., 2017). They play an indispensable role in agricultural ecosystems, pollinating a variety of crops (Giannini et al., 2015). Furthermore many of these species have been used by beekeepers as a supplementary income for smallholders in Brazil (Pereira, 2003). Due to the socioeconomic and socioecological importance of these species, their conservation should be considered of high priority.

Five anthropogenic drivers have been reported as the causes of worldwide decline of bees: land-use change and management intensity, climate change, indiscriminate use of pesticides and genetically modified organisms, inadequate pollinator management, dissemination of pathogens and invasive alien species (Potts et al, 2016). In this study we evaluated the vulnerability of ten stingless bees from the genus *Melipona* distributed in Brazil considering two of these drivers: land use change and climate change. In this context, we divided our study into two main chapters. In the first chapter we used ecological niche models to predict the potential distribution of the species under study and evaluated the recent land use changes within the estimated climatically suitable areas. Then, in order to evaluate the effectiveness of protected areas in Brazil, we quantified all protected areas that were within the suitable range of the *Melipona* species. In the second chapter, we evaluated the effects of climate change on the distribution of these stingless bees in different years and future climate scenarios. Together, such information can be used as subsidies in the development of conservation strategies by decision-makers aiming to protect the stingless bees as well as the ecosystem services they provide.

References

- Allen-Wardell, G., Bernhardt, P., Bitner, R.; Burquez, A., Buchmann, S., Cane, J., Cox, P. A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C. E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, 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. *Conservation Biology*, 12, 8-17.
- Alves, J. E., Freitas, B. M., Lima-Verde, L. W., Ribeiro, M. F. (2006). A uruçu-do-chão (*Melipona quinquefasciata*) no Nordeste: extrativismo de mel e esforços para a preservação da espécie. *Mensagem doce*, 85: 1-4.
- Breeze, T. D., Gallai, N., Garibaldi, L. A., & Li, X. S. (2016). Economic Measures of Pollination Services: Shortcomings and Future Directions. *Trends in Ecology & Evolution*, 31, 927-939.
- Buchmann, S., & Nabhan, G. (1996). *The Forgotten Pollinators*. Island Press, Washington.
- Giannini, T. C., Cordeiro, G. D., Freitas, B., Saraiva, A. M., & Imperatriz-Fonseca, V. L. (2015). The dependence of crops for pollinators and the economic value of pollination in Brazil. *Journal of Economic Entomology*, 108, 839-848.
- Garibaldi, L. et al. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, 351, 388-391.
- International Union for Conservation of Nature. IUCN red list of threatened species. 2009. Disponível em < <http://www.iucnredlist.org> > Acesso em: 17/09/16.
- Kerr, W. E., Sakagami, S. F., Zucchi, R., Portugal-Araújo, V., Camargo, J. M. F. (1967). Observações sobre a arquitetura dos ninhos e comportamento de algumas espécies de abelhas sem ferrão das vizinhanças de Manaus, Amazonas (Hymenoptera, Apoidea). *Atas do Simpósio sobre a Biota Amazônica*, 5: 255-309.

Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology, Evolution, and Systematics*, 29, 83-112.

Kevan, P. G., & Viana, B. F. (2003). The Global decline of Pollination Services. *Tropical Conservancy*, 4, 3-8.

Michener, C. D. (1974). *The Social Behavior of the Bees. A Comparative Study*. Harvard University Press, Cambridge, Massachusetts, 404 pp.

Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: scenarios*, vol 2. Island Press, Washington, DC.

Myers, N., & Kent, J. (2003). New consumers: the influence of affluence on the environment. *Proceedings of the National Academy of Sciences*, 100, 4963-4968.

Nogueira-Neto. (1970). *Vida e Criação de abelhas indígenas sem ferrão (Meliponinae)*. 2da. Edição. Editora Chácaras e Quintais. São Paulo, Brasil, 365 p.

Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, 346, 1360-1362.

Pereira, J. C., Vincenzi, M. L., Lovato, P. E. (2003). Roland Ristow: uma contribuição ao estudo da agricultura sustentável. *Eisforia*, 1, 63-97.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220-229.

Ramalho, M. (2004). Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a Tight Relationship. *Acta Botânica Brasileira*, 18, 37-47.

Roubik, D.W. (2006). Stingless bee nesting biology. *Apidologie*, 37: 124-143.

Silva, D. P., Nogueira, D. S., De Marco Jr., P. (2017). Pollen resources used by *Melipona quadrifasciata anthidioides* Lepeletier in an urban forest in Rio de Janeiro city, Brazil. *Neotropical Entomology*, 46, 264-274.

United Nations. Population division. World Population Prospects: The 2008 Revision. Disponível em < <http://www.un.org/esa/population> > Acesso em: 17/09/16.

Chapter 1 - Predicting the current distribution of stingless bees in Brazil: land use and effectiveness of protected areas

Abstract

The study aimed to predict the potential geographic distributions of ten *Melipona* species found in Brazil and quantify the recent changes in land use within the predicted stingless bees suitable ranges. Additionally, we assessed the efficacy of Brazilian Protected Areas (PAs) for conservation of the studied species. We employed ecological niche modeling approaches using the maximum entropy algorithm implemented in the software MaxEnt v. 3.3.3k. This algorithm estimates the cumulative probability of maximum entropy based on species occurrence records and environmental data. Further, we used Geographic Information System analysis to quantify recent land use changes within the distribution ranges of the *Melipona* species and assess the efficacy of PAs of the stingless bees. The areas predicted as suitable for *Melipona* species are distributed in different regions and biomes of Brazil. The species *Melipona melanoventer* Schwarz, 1932, *Melipona seminigra abunensis* Cockerell, 1912, *Melipona flavolineata* Friese, 1900, *Melipona fasciculata* Smith, 1854, *Melipona amazonica* Schulz, 1905, *Melipona subnitida* Ducke, 1910 and *Melipona paraensis* Ducke, 1916 are mostly distributed in natural areas, while *Melipona scutellaris* Latreille, 1811, *Melipona quadrifasciata anthidioides* Lepeletier, 1836 and *Melipona quadrifasciata quadrifasciata* Lepeletier, 1836 occurs predominantly in mosaic of agriculture with natural remnants. The species *M. paraensis* presented the highest percentage (31.54%) of their suitable range covered by PAs and *M. scutellaris* the lowest (6.54%). The recent changes in land use within the distribution ranges of *Melipona* species, in particular conversion of natural areas for agricultural use, indicate that it might negatively affect these pollinators, and consequently crop production. Brazilian protected areas present poor effectiveness for the conservation of the studied species of stingless bees.

KEYWORDS: Environmental drivers, *Melipona*, Species Distribution Modeling, Pollinator conservation.

Introduction

Bees are the main pollinators in natural and agricultural ecosystems (Breeze et al., 2016; Garibaldi et al., 2016; Potts et al., 2016). They are important visitors in the tropics and actively participate in the maintenance of the vegetation (Giannini et al., 2012). In agroecosystems, more than 90% of the 107 main known global agricultural crops are dependent of bees as pollinators (Klein et al., 2007). Furthermore, pollination services increase world crop production by up to 577 billion US dollars annually (Lautenbach et al., 2012), and it is estimated a loss of 5 to 8% in the worldwide crop production in the absence of pollination services (Potts et al., 2016).

The stingless bees belonging to the genus *Melipona* Illiger, 1806 (Meliponini tribe) are important floral visitors of plants in tropical regions, playing a key role in the maintenance of tropical forests, including the highly threatened Brazilian hotspots Atlantic Forest (Ramalho, 2004) and Cerrado (Silva et al., 2017). Also, stingless bees are commonly found in agroecosystems visiting several crops used as food source by humans (Giannini et al., 2015). Further, many species of *Melipona* are economically important because they are used in meliponiculture, a sustainable activity that contributes to the conservation of ecosystems and production of income for smallholders in Brazil (Pereira, 2003). Given the ecological and economic importance of these species, their conservation should have high priority.

Similarly to other pollinators, the stingless bees are threatened by human-induced changes such as habitat loss due to land use changes and climate change (Ashraf et al., 2017; Senapathi et al., 2017). Land use is considered the most direct driver of terrestrial biodiversity loss in the last decades in most ecosystems (Millennium Ecosystem Assessment, 2005). Changes in land use include destruction, degradation and fragmentation of natural vegetation for different uses such as urbanization and agriculture. The conversion of natural vegetation or diversified agricultural systems into conventional agriculture, which is characterized by extensive homogeneous areas and the indiscriminate use of pesticides have severe effects on biodiversity, particularly on pollinators (Potts et al., 2016). In fact, several studies have demonstrated the impact of hahacurrent changes in landscape and land use on pollinators (Bates et al., 2011; Cariveau et al., 2013; Jha & Kremen, 2013), as well as the negative impacts of pesticides on several species of

bees (Henry et al., 2012; Woodcock et al., 2017; Mitchell et al., 2017). Despite our increasing understanding of how human-induced change affects pollinators, there is still a lack of knowledge on the quantification of habitat losses on pollinator biodiversity (Senapathi et al., 2017).

Brazil is considered a priority country for conservation due to its high diversity of endemic species (Oliveira et al., 2017). In this context, public policies related to the conservation of species have been carried out, such as the creation of Protected areas (PAs) by the Brazilian Protected Areas System (SNUC), which include two main categories: strictly protected and sustainable use (Silva, 2005; Soares-Filho et al., 2010). Although vegetation remnants still cover about 60% of the country (Soares-Filho et al., 2014), few attempts to evaluate the efficacy of these areas for species conservation are known (Oliveira et al., 2017). In addition, there are few ecological criteria used for the creation of PAs, since previous assessments of biodiversity in Brazil focus on specific taxonomic groups, such as amphibians and birds instead of the whole biota, thus disregarding the majority of endemic species (Oliveira et al., 2017).

Ecological niche models (ENM) have become one of the most employed tools to estimate species distribution based on occurrence records and environmental variables (Almpanidou et al., 2016). These models are important because they allow estimation of diversity patterns, determining potential areas of persistence, extinction and colonization (Assis et al., 2017). ENMs can be integrated with Geographic Information System (GIS) information to provide valuable information with respect to the development of conservation strategies, including the determination of priority areas for conservation and the understanding of biodiversity patterns (Balram et al., 2004). Here, we applied ENM and GIS approaches to answer a number of questions regarding to stingless bees conservation. First, we used ENM to estimate the geographical distributions of *Melipona* species. Then, we quantified the recent land use changes within the suitable distributions of *Melipona* in order to shed light on the threats on their conservation. Finally, we analyzed the efficacy of PAs from Brazil as a refuge for the studied species.

Material and methods

Species occurrence data

The study was conducted with ten species of the genus *Melipona* found in Brazil (Table 1). The occurrence records for each species were obtained from the literature and online databases such as Global Biodiversity Information Facility (<http://www.gbif.org/>) and SpeciesLink (<http://splink.cria.org.br/>). When the locations were not geo-referenced, geographic coordinates were obtained through Google Earth software. All occurrence points were analyzed using the software ArcGIS 10.3 and those records that were not within the known geographical distribution of the species were excluded. Information on the occurrence range of each species was obtained from the Moure Catalog (<http://moure.cria.org.br/>).

Environmental data

We used altitude data and 19 bioclimatic variables in the resolution of 5 arc-min obtained from the Worldclim version 1.4. (<http://worldclim.org>) to characterize the climatic species requirements. The bioclimatic variables derive from monthly measures of temperature and precipitation data. According to Slater & Michael (2012), these variables capture information of great relevance for ecological niche modeling, such as annual variations and well-defined limits of temperature and precipitation that is known to constraint the distribution of species.

Species distribution models

ENMs were developed using an algorithm that estimates the cumulative probability of maximum entropy through occurrence records and environmental variables (Elith, et al., 2011; Phillips et al., 2006; Phillips; Dudík, 2008) implemented in the software MaxEnt v.3.3.3k (Phillips et al., 2006). MaxEnt is one of the current presence-only ecological niche modeling methods that presents better performance, even when few occurrence records are available (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008 (Phillips et al., 2006). The development of models with an appropriate level of complexity is fundamental to achieve satisfactory results and avoid under- and over-fitting (Warren & Seifert, 2011; Merow et al., 2013). Therefore, in order

to build more parsimonious models we adopted the following steps: (1) spatially filtering of occurrence data, (2) reducing the number of environmental predictors by means of an *a priori* selection of uncorrelated variables, (3) delimiting the study area, and (4) using different combinations of feature classes and regulation multiplier values.

Spatial filtering has been used to reduce spatial auto-correlation and consequently improve the performance of ENMs (Boria et al., 2014, Fourcade et al., 2017). The species occurrence data were spatially filtered at a distance of 2 km, based on the known flight capability distance for the genus *Melipona* (Araújo et al., 2004). This procedure was performed using the toolkit SDMtoolbox incorporated into the software ArcGIS 10.3 (Brown, 2014).

Studies have shown that *a priori* selection of variables and the exclusion of highly correlated variables are important steps in the development of less complex models (Fourcade et al., 2017, West et al., 2015). Firstly we selected the following variables based on their biological significance: annual mean temperature (Bio1), temperature seasonality (Bio4), maximum temperature of warmest month (Bio5), minimum temperature of coldest month (Bio6), temperature annual range (Bio7), annual precipitation (Bio12), precipitation of wettest (Bio13) and driest month (Bio14), precipitation seasonality (Bio15) and altitude. Secondly we used the Pearson's correlation test to assess multicollinearity among the selected variables. When two or more variables were correlated ($r > 0.85$), the preference was given to the one with the highest biological significance (Elith et al., 2010). The correlation tests were performed with the software ENM Tools v1.3 (Warren et al., 2010).

Ideally, the study area should cover all regions where species could occur in a recent evolutionary past (Elith et al., 2011). Here, the study area was determined primarily based on biomes (Rutherford, 1997), including in some cases adjacent areas to the known historical distribution of the species (Anderson & Raza, 2010; Elith et al., 2010; Meyer et al., 2013). This approach has been shown to improve the performance of ENM, especially when the models are projected to other regions or different scenarios of climate change (Anderson & Raza, 2010; Elith et al., 2010; Meyer et al., 2014).

MaxEnt allows users to select different feature classes: linear (L), quadratic (Q), product (P), hinge (H) and threshold (T), and regularization multiplier values. These configurations can be used to build parsimonious models (Merow et al, 2013). We built fifteen distinct models for each species using different MaxEnt combinations of feature classes (L; H; LQ; LQH and LQHPT) and regularization multiplier values (1, 3 and 5). This procedure was accomplished to select less complex models that present good predictive ability (Merow et al., 2013; Morales et al., 2017; Radosavljevic & Anderson, 2014). The selection of the best models was performed using the corrected Akaike Information Criterion (AICc). AICc is a method commonly used to compare models taking into consideration their complexity and performance. Lower values of AICc indicate best-fit models (Warren et al., 2010). The calculation of AICc was conducted with ENM Tools v 1.3 (Warren et al., 2010).

The final models selected based on AICc were run with the following changes in the MaxEnt default settings: (1) allowed response curves to evaluate species response to each predictor variable, (2) performed jackknife analysis to measure variable importance, (3) set 80% of the occurrence records for training and 20% for test the model, (4) set replicated run-type as bootstrap with 100 replicates, and (6) disabled the option write output grids. The performance of the final models was evaluated using the area under the curve (AUC) of the receiver-operating characteristic (ROC), which analyzes commission versus omission errors (Fielding & Bell, 1997, Peterson et al., 2011). AUC values range from 0 to 1; values ranging from 0.5 to 0.7 indicate a poor performance, AUC values from 0.7 to 0.9 indicate moderate performance and higher than 0.9 indicates high performance (Peterson et al., 2011).

MaxEnt models were generated with logistic outputs with a scale varying between 0 (unsuitable) and 1 (highly suitable). In order to quantify the land use within the climatically suitable areas for each species, binary maps were created indicating the suitable and unsuitable areas using the *Maximum training sensitivity plus specificity logistic threshold* available in MaxEnt. This threshold maximizes the sensitivity and specificity of the model and has been suggested for studies aiming to determine areas for conservation (Bean et al., 2011, Meyer et al., 2014); because it diminish false-positives, which generally lead to errors in determining priority areas of conservation (Loiselle et al., 2003).

Geospatial analysis

Maps with Brazilian land use for 2000, 2010 and 2014, as well as maps with protected areas were obtained from the Brazilian Institute of Geography and Statistics (IBGE, <https://www.ibge.gov.br/>). These GIS-based data were intersected with the binary maps generated for each species in order to quantify the different land uses within their distribution range, as well as the percentage of the distribution range within conservation units.

Results

Model selection

A total of 794 occurrence records were obtained for *Melipona* species from the literature and online databases. Models for all species performed better than random, with average test AUC values ranging from 0.76 to 0.97. The best models were LQ1 for *M. subnitida*, *M. scutellaris*, *M. q. anthidioides*, *M. q. quadrifasciata*, *M. amazonica* and *M. melanoventer*; L3 for *M. paraensis* and *M. flavolineata*; LQHPT1 for *M. s. abunensis* and LQHPT3 for *M. fasciculata* (Supplementary material).

Species distribution

The predicted distribution ranges for the ten studied species in Brazil are shown in Figure 1. The areas predicted as suitable for *M. paraensis*, *M. melanoventer*, *M. s. abunensis* and *M. amazonica* are in the northern region of Brazil, predominantly in the Amazon region. Suitable areas for *M. subnitida* and *M. scutellaris* were predicted in northeastern Brazil, comprising Caatinga and Atlantic forest areas. The models estimated suitable areas for *M. flavolineata* and *M. fasciculata* in northern and northeastern regions, including Amazon, Cerrado, Caatinga and Pantanal biomes. For *M. q. anthidioides* and *M. q. quadrifasciata* suitable areas were predicted throughout the east coast of Brazil, including northeastern, southern and southeastern regions in Atlantic forest, Cerrado and Caatinga biomes. While the species *M. scutellaris* and *M. subnitida* have the most restricted distribution, occurring predominantly in the Caatinga biome and in small areas of Atlantic forest, the remaining species have comparatively larger

distribution ranges, occupying more extensive biomes (Amazon) or more than one biome (Figure 1).

Land use and efficacy of Brazilian protected areas

The areas estimated as suitable for *Melipona* species comprise different land use as shown in Figure 2. The species *M. melanoventer*, *M. s. abunensis*, *M. flavolineata*, *M. fasciculata*, *M. amazonica*, *M. subnitida* and *M. paraensis* are mostly distributed in areas with natural vegetation while the species *M. scutellaris*, *M. q. anthidioides* and *M. q. quadrifasciata* occur predominantly in areas with mosaic of agriculture and forest remnants. We also observed that agricultural areas increased and natural areas decreased within the distribution range of all species over time. The areas with mosaics of agriculture with forest remnants increased, except for *M. scutellaris*. On the other hand, for *M. q. anthidioides* these areas remained similar over the fourteen years assessed.

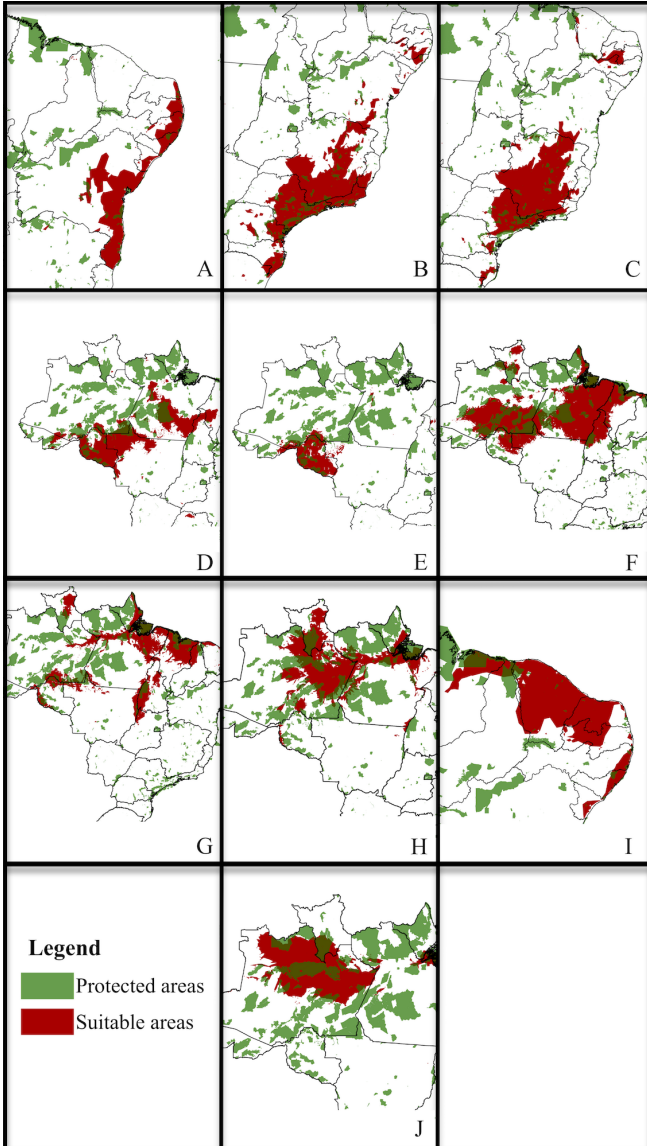
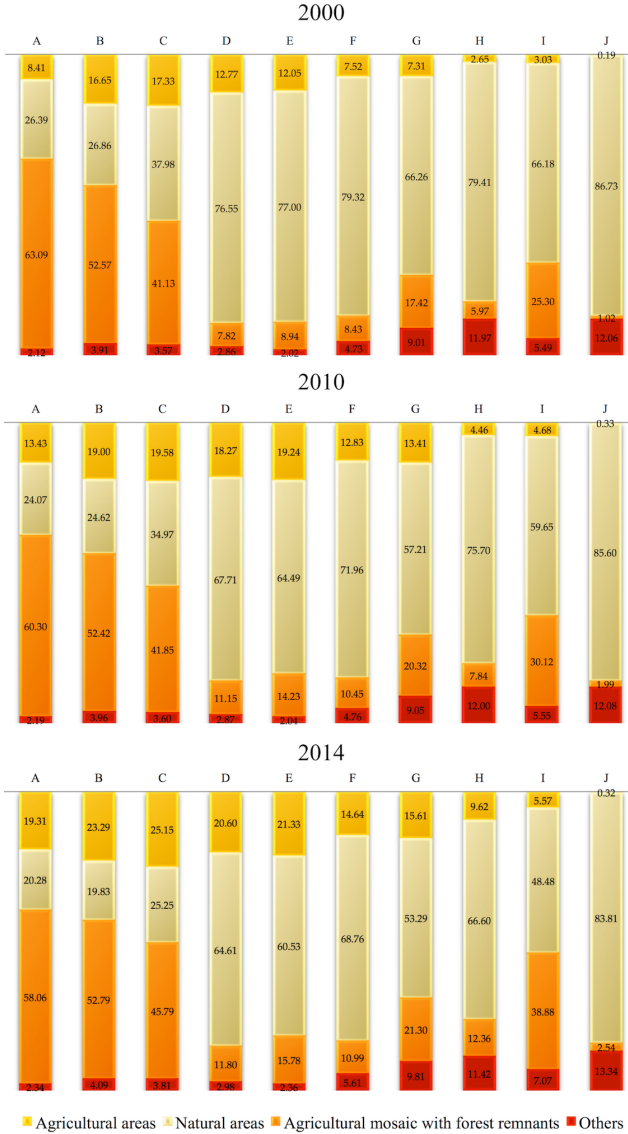


Figure 1. Current geographic distributions and potential climatic niches for *Melipona* species in Brazil. **A.** *M. scutellaris*, **B.** *M. q. anthidioides*, **C.** *M. q. quadrifasciata*, **D.** *M. melanoventer*, **E.** *M. s. abunensis*, **F.** *M. flavolineata*, **G.** *M. fasciculata*, **H.** *M. amazonica*, **I.** *M. subnitida* and **J.** *M. paraensis*.

The percentages of the suitable ranges for *Melipona* species within PAs in Brazil vary according to the species (Figure 3). The species *M. paraensis* presented the highest percentage (31.54%) of their suitable range covered by PAs and *M. scutellaris* the lowest (6.54%). In general, the species with distribution in the Amazon region have the highest percentage of their suitable range covered by PAs, reflecting the higher proportion of PAs in this biome.

Figure 2.



Percentage of land use within the suitable range of *Melipona* species in Brazil. **A.** *M. scutellaris*, **B.** *M. q. anthidioides*, **C.** *M. q. quadrifasciata*, **D.** *M. melanoventer*, **E.** *M. s. abunensis*, **F.** *M. flavolineata*, **G.** *M. fasciculata*, **H.** *M. amazonica*, **I.** *M. subnitida* and **J.** *M. paraensis*.

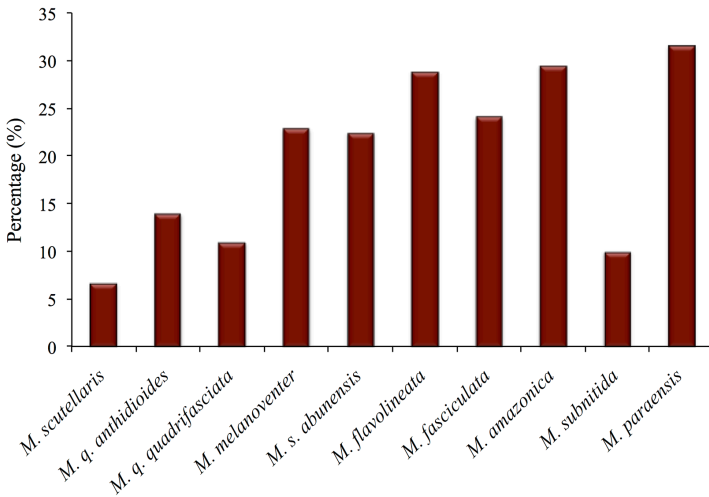


Figure 3. Percentage of protected areas within the suitable range of *Melipona* species in Brazil.

Discussion

In this study we used ecological niche modeling to estimate the distribution range of ten species of the genus *Melipona* in Brazil. Our results showed that the areas predicted as suitable for *Melipona* species are distributed in different regions and biomes of Brazil and occupying different land uses. While some species occurs predominantly in natural areas (7 spp.) others occur in areas of mosaic of agriculture with natural remnants (3 spp.). Also, our results also showed that most species have a small portion of its suitable range protected by Brazilian conservation units, demonstrating that protected areas have poor effectiveness of for the conservation of the studied species.

Following the recommendations in the literature (Morales et al., 2017), we built 15 models for each species using different MaxEnt configurations. In fact, the results showed that model performance varied according to the changes made in the MaxEnt configuration, echoing other studies demonstrating that the default settings of MaxEnt generate models with lower performance when compared to those developed using different settings (Radosavljevic & Anderson, 2014; Syfert et al., 2013; Warren et al., 2014).

Several human-induced environmental changes have been causing declines in pollinator populations around the world. Land use changes, mainly as a result of conversion of natural vegetation into urban and agricultural areas, are frequently cited as one of the most important cause of pollinator population decline (Ollerton et al., 2014; De 3Palma et al., 2016). In this study we applied ENM and GIS in order to assess the recent land use changes within the predicted distribution ranges of the *Melipona* species studied. Our study is the first to quantify stingless bees habitat losses based on land use in three different years encompassing fourteen years in Brazil.

Our findings show a significant increase in agricultural areas within the predicted distribution range of the species between 2000 and 2014. This result has important consequences for provision of ecosystem services as well as for species conservation. One of these consequences is related to food production, considering that the *Melipona* species play an important role as pollinator of several agricultural crops, and therefore their presence in these agroecosystems may be fundamental for maximizing yield (Potts et al., 2016). It is recognized that bee pollination improves crop quality, shelf life and commercial value of agricultural products in comparison to self-pollination or wind-pollinated species. Klatt et al. (2015) recorded in their experiment that strawberries pollinated by bees presented heavier fruits with higher commercial grades and reduced the level of sugar and acids, thus providing a more useful commercial life through reduction of fruit loss by at least 11%.

Unfortunately, most of the conventional agricultural areas in Brazil rely on large amount of pesticides to promote disease and pest control (Kulay et al., 2016). Several studies have demonstrated the negative effect of pesticides on native species of pollinator bees (Henry et al., 2012; Woodcock et al., 2017; Mitchell et al., 2017). Mitchell et al. (2017) noted in their study that neonicotinoid pesticides are suspected of causing the decline of global pollinators. They evaluated the exposure of pollinators to five neonicotinoids (acetamiprid, clothianidin, imidacloprid, thiacloprid, and thiamethoxam) and found at least one component in 75% of all samples analyzed. Woodcock et al. (2017) also found the same result when evaluating native bee species in Hungary, Germany, and the United Kingdom. The authors observed that neonicotinoid residues negatively affected *Bombus terrestris* Linnaeus, 1758 and *Osmia bicornis* Linnaeus, 1758. In this context, the increase in

the areas used by agriculture confers greater vulnerability to these species (De Palma et al., 2016; Pisa et al., 2015; Slaa et al., 2006; Van der Sluijs et al., 2015). Further, *Melipona* species can nest in soil cavities, ant mounds, termite mounds and bird nests, and preferably in tree trunks. However, large areas of agriculture may not provide suitable conditions for species to nest, causing local biodiversity loss (Villas-Bôas, 2012).

The recorded decrease areas with natural vegetation within the species suitable range aggravates this situation, as it diminishes the habitats to nest and take refuge (Biesmeijer et al., 2006; Scheper et al., 2014). The natural areas currently available for the species shall be related to the pressure suffered by the different biomes where these species occur. The Atlantic Forest and Cerrado have suffered a great pressure regarding to urbanization and agriculture (Oliveira et al., 2017; Uuemaa et al., 2009), and for this reason it is expected that these biomes have comparatively smaller areas of forest remnants. On the other hand, Amazon biome still presents comparatively a greater percentage of preserved area (Oliveira et al., 2017). In this sense, it is possible to argue that the species that occur in Atlantic forest and Cerrado are more vulnerable.

The increase in the mosaic of agriculture with natural remnants recorded in this study indicates a process of habitat fragmentation resulted from the conversion of native vegetation to agricultural use. We emphasize that this process has been occurred more significantly in threatened biomes, such as the Cerrado and Atlantic forest. Thus, it is possible to relate the highest occurrence of Amazonian species in natural areas with the highest conservation of this biome in comparison to the species that occur in the Cerrado and Atlantic forest (Oliveira et al., 2017). Although habitat fragmentation is harmful for stingless bees, the presence of fragments might be used as a shelter for species such nesting, thus maintaining the provision of ecosystem services in agroecosystems (Senapathi et al., 2017).

The decline of the studied bee pollinators can have serious consequences for several crops cultivated in Brazil, such as Açaí palm (*Euterpe oleracea*), eggplant (*Solanum melongena*), cashew (*Anacardium occidentale*), tomato (*Lycopersicon esculentum*), annatto (*Bixa orellana*), pumpkin (*Cucurbita moschata*), capsicum (*Capsicum annum*), malagueta pepper (*Capsicum frutescens*), guava (*Psidium*

guajava), sunflower (*Helianthus annuus*), avocado (*Persea americana*), pitanga (*Eugenia uniflora*) and guarana (*Paullinia cupana*) (Silva et al., 2014). Further, several of these crops are used as income for family farming, thus resulting in socio-economic consequences for some communities (Krishnamurthy et al., 2017). Nevertheless, some studies have shown that these losses can be offset by the existence of heterogeneous landscapes, which include semi-natural environments such as mosaics of agriculture with natural remnants, which provide resources for nesting as well as forage (Nicholls & Altieri, 2013; Osgathorpe et al., 2012; Senapathi et al., 2017). Landscape heterogeneity is an important aspect of conservation efforts because it demonstrates that landscape must be considered entirely and not just specific areas (Senapathi et al., 2017; Westrich, 1996).

To estimate the efficacy of PAs on *Melipona* species, we quantified the proportion of the suitable ranges of each species that is within Brazilian PAs. The species, *M. melanoventer*, *M. s. abunensis*, *M. fasciculata*, *M. amazonica*, and *M. paraensis*, which are distributed mainly in the northern region of Brazil, presented the higher percentages of their distribution ranges protected by conservation units when compared to the others species. This is possibly related to the greater amounts of PAs in the Amazon compared to the other Brazilian biomes (Oliveira et al., 2017; Soares-Filho et al., 2010). On the other hand, *M. scutellaris* and *M. subnitida* that are distributed in the northeastern Brazil presented the smaller percentages of suitable ranges within PAs, which coincide with the lower number of PAs in that region (Oliveira et al., 2017). Although the species distributed in the north region showed the highest percentages, they do not reach 50%, which suggests that the established PAs may be ineffective to promote species conservation (Oliveira et al., 2017; Rayner et al., 2013). This is expected, considering that creation of PAs is based on political issues rather than in ecological criteria such as endemism (Oliveira et al., 2016; Oliveira et al., 2017; Rayner et al., 2013). According to Oliveira et al. (2017) about 55% of the Brazilian species and 40% of the evolutionary lineages are not found within protected areas in Brazil.

Here, we estimated the distribution range of ten species of stingless bees from Brazil and evaluated the recent changes in land use within the estimated suitable areas. Additionally, the proportion of the areas estimated as suitable protected by conservation units were estimated for each species. We demonstrated that land use changes vary

within the range of each species, and most species face a reduction in the availability of natural habitats due to agriculture intensification. Also we observed that Brazilian conservation units have little effectiveness for conservation of the studied species. Therefore, we argue that land use needs to be considered when planning strategies for conservation, especially when creating new conservation units. More importantly, our results highlight the necessity to discuss agricultural practices in order to guarantee ecosystem services provided by pollinators in the future. In summary, our study provides a strong baseline database for developing broad-scale adaptive strategies for species conservation planning.

Acknowledgments

We thank CAPES for the scholarship, GEOPAM/UFMA on behalf of Professor Dr. Murilo Drummond for occurrence data and Geomatic Lab/UFSC on behalf of Professor Dr. Alexandre ten Caten for the technological resources.

References

- Almpanidoua, V., Schofield, G., Kallimanis, A. S., Türkozan, O., Hays, G. C., & Mazaris, A. D. (2016). Using climatic suitability thresholds to identify past, present and future population viability. *Ecological Indicators*, 71, 551-556.
- Anderson, R. P., & Raza, A. (2010). The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, 37, 1378-1393.
- Araújo, E. D., Costa, M., Chaud-Netto, J., & Fowler, H. G. (2004). Body size and flight distance in stingless bees (Hymenoptera: Meliponini): Inference of flight range and possible ecological implications. *Brazilian Journal of Biology*, 64, 563-568.
- Ashraf, U., Peterson, A. T., Chaudhry, M. N., Ashraf, I., Saqib, Z., Rashid Ahmad, S., & Ali. H. (2017). Ecological niche model comparison under different climate scenarios: a case study of *Olea* spp. in Asia. *Ecosphere* 8(5):e01825. 10.1002/ecs2.1825.
- Assis, J., Araújo, N. B., & Serrão, E. A. (2017). Projected climate

changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biology*. Doi: 10.1111/gcb.13818

Balram, S., Dragicevic, S., & Meredith, T. (2004). A collaborative GIS method for integrating local and technical knowledge in establishing biodiversity conservation priorities. *Biodiversity and Conservation*, 13, 1195-1208.

Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D., & Matthews, T. J. (2011). Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *Plos One* 6, e23459. (doi:10.1371/journal.pone.0023459)

Bean, W. T., Stafford, R., & Brashers, J. S. (2011). The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. *Ecography*, 34, 1-9.

Biesmeijer, J. C., Roberts, S. P., Reemer, M., Ohlemüller, R., Edwards, 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.

Boria, R. A., Olson, L. E., Goodman, S. T., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, 275, 73-77.

Breeze, T. D., Gallai, N., Garibaldi, L. A., & Li, X. S. (2016). Economic Measures of Pollination Services: Shortcomings and Future Directions. *Trends in Ecology & Evolution*, 31, 927-939.

Cariveau, D. P., Williams, N. M., Benjamin, F. E., & Winfree, R. (2013). Response diversity to land use occurs but does not consistently stabilise ecosystem services provided by native pollinators. *Ecology Letters*, 16, 903-911.

De palma, A. et al. (2016). Predicting bee community responses to land-use changes: Effects of geographic and taxonomic biases. *Nature*, 6, 1-14.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., & Ferrier, S.

(2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330-342.

Elith, J., Phillips, S., Hastie, T., Dudík, M., Chee, Y., & Yates, C. A. (2011). Statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43-57.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38-49.

Fourcade, Y., Besnard, A. G., & Secondi, J. (2017). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, Doi 10.1111/geb.12684.

Garibaldi, L. et al. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, 351, 388-391.

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.

Giannini, T. C., Cordeiro, G. D., Freitas, B., Saraiva, A. M., & Imperatriz-Fonseca, V. L. (2015). The dependence of crops for pollinators and the economic value of pollination in Brazil. *Journal of Economic Entomology*, 108, 839-848.

Henry, M., Béguin, M., Requier, F., Rollin, O., Odoux, J. F., Aupinel, P., Aptel, J., Tchamitchian, S., Decourtye, A. (2012). A common pesticide decreases foraging success and survival in honey bees. *Science*, 336, 348-350.

Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, 29, 773-785.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Stocker, T. F., Qin, D, G. K., Tignor, M. S., Allen, K.; Boschung, J., Nauels, A., Xia, Y.; Bex, V., Midgley, P. M. Eds. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 1535.

Jha, S., & Kremen, C. (2013). Urban land use limits regional bumble bee gene flow. *Molecular Ecology*, 22, 2483-2495.

Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smith, I., Pawelzik, E., & Tscharntke, T. (2015). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society of London B*, 281: 20132440. <http://dx.doi.org/10.1098/rspb.2013.2440>.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London*, 274, 303-313.

Krishnamurthy, L. R.; Sumithra Krishnamurthy; Indumathi Rajagopal; Peralta Solares, A. (2017). Family agriculture for inclusive rural development. *Terra Latino americana*, 35, 135-147.

Kulay, L., Gripp, V. S., Nogueira, A. R., & Silva, G. A. (2016). Verifying the effectiveness of environmental performance improvement actions in the chain of production of an agrochemical produced in Brazil. *The International Journal of Life Cycle Assessment*, 22, 22, 644-655.

Lautenbach, S., Seppelt, R., liebscher, J., & Dormann, C. F. (2012). Spatial and temporal trends of global pollination benefit. *Plos one* 7, e35954.

Loiselle, B. A., Howell, C. A., Graham, C. H., Goerck, J. M., Brooks, T., Kimberly G. Smith, K. G., & Williams, P. H. (2003). Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology*, 17, 1591-1600.

Merow, C., Smith, M. J., & Silander, J. A. Jr. (2013). A practical guide

to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36, 1-12.

Morales et al. (2017). MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ* 5:e3093; Doi 10.7717/peerj.3093

Meyer, A. L. S., Pie, M. R., & Passos, F. C. (2014). Assessing the Exposure of Lion Tamarins (*Leontopithecus* spp.) to Future Climate Change. *American Journal of Primatology*, 76, 551-562.

Michell, E. A. D., Mulhauser, B., Mulo, M., Mutabazi, A., Glauser, G., Aebi, A. (2017). A worldwide survey of neonicotinoids in honey. *Science*, 358, 109-111.

Millennium Ecosystem Assessment. (2005). Ecosystems and human well-being: scenarios, vol 2. Island Press, Washington, DC.

Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems: a review. *Agronomy for Sustainable Development*, 33, 257-274.

Oliveira et al. (2017). Biodiversity conservation gaps in the Brazilian protected areas. *Nature*, 7: 9141 | doi:10.1038/s41598-017-08707-2.

Oliveira, S. N., Prasad, S., & Gomes, R. A. T. (2017). Landscape-fragmentation change due to recent agricultural expansion in the Brazilian Savanna, Western Bahia, Brazil. *Regional Environmental Change*, 17, 411-423.

Oliveira, U. et al. (2016). The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. *Diversity and Distribution*, 22, 1232-1244.

Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, 346, 1360-1362.

Osgathorpe, L. M., Park, K., Goulson, D. (2012). The use of off-farm habitats by foraging bumblebees in agricultural landscapes: implications for conservation management. *Apidologie* 43, 113-127.

Pereira, J. C., Vincenzi, M. L., Lovato, P. E. (2003). Roland Ristow: uma contribuição ao estudo da agricultura sustentável. *Eisforia*, 1, 63-97.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., et al. (2011). Ecological niches and geographic distributions. Princeton University Press, Princeton, p 314.

Phillips, S. J., & Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161-175.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231-259.

Pisa, L. W. et al. (2015). Effects of neonicotinoids and fipronil on non-target invertebrates. *Environmental Science and Pollution Research*, 22, 68-102.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220-229.

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distribution: complexity, overfitting and evaluation. *Journal of Biogeography*, 41, 629-643.

Ramalho, M. (2004). “Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a Tight Relationship”. *Acta Botânica Brasileira*, 18, 37-47.

Rayner, L., Lindenmayer, D. B., Wood, J. T., Gibbons, P., & Manning, A. D. (2013). Are protected areas maintaining bird diversity? *Ecography*, 36, 01-11.

Rutherford, M. C. (1997). Categorization of biomes. In: Cowling RM, Richardson DM, Pierce SM (eds) *Vegetation of southern Africa*. Cambridge University Press, Cambridge, 91-98.

Schaffer-Smith, D. & Swenson, J. J. (2016). Open Source Remote Sensing and (Some) GIS for Ecologists, Landscape Ecology, Doi 10.1007/s10980-016-0468-5.

Scheper, J. et al. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in the Netherlands. *Proceedings of the National Academy of Sciences*, Doi: 10.1073/pnas.1412973111.

Senapathi, D., Carvalheiro, L. G., Biesmeijer, J. C., Dodson, C., Evans, R. L., Mckerchar, M., Morton, R. D., Moss, E. D., Roberts, S. P. M., Kunin, W. E., Potts, S. G. (2017). The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society of London*, 282: 20150294.

Silva, C. I., Kátia Paula Aleixo, K. P., Nunes-Silva, B., Freitas, B. M., & Imperatriz-Fonseca, V. L. Guia Ilustrado de Abelhas Polinizadoras no Brasil. São Paulo: Instituto de Estudos Avançados da Universidade de São Paulo, (2014). Co-editor: Ministério do Meio Ambiente - Brasil ISBN: 978-85-63007-07-0.

Silva, D. P., Nogueira, D. S., De Marco Jr., P. (2017). Pollen resources used by *Melipona quadrifasciata anthidioides* Lepeletier in an urban forest in Rio de Janeiro city, Brazil. *Neotropical Entomology*, 46, 264-274.

Silva, M. (2005). The Brazilian protected areas program. *Conservation Biology*, 3, 608-611.

Slaa, E. J., Sánchez-Chaves, L. A., Malagodi-Braga, K. S., & Hofstede, F. E. (2006). Stingless bees in applied pollination: practice and perspectives. *Apidologie*, 37, 293-315.

Slater H., & Michael, E. (2012). Predicting the current and future potential distributions of lymphatic filariasis in Africa using maximum entropy ecological niche modelling. *Plos One* 7(2): e32202. doi:10.1371/journal.pone.0032202.

Soares-Filho, B., Moutinho, P., Nepstad, D., Anderson, A., Rodrigues, H., Garcia, R., Dietzsch, L., Merry, F., Bowman, M., Hissa, L., Silvestrini., Maretti, C. (2010). Role of Brazilian Amazon protected

areas in climate change mitigation. *Proceedings of the National Academy of Sciences*, 107, 10821-10826.

Soares-Filho, B., Rajão, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., Rodrigues, H., Alencar, A. (2014). Cracking Brazil's Forest Code *Science*, 344, 363-364.

Syfert, M. M., Smith, M. J., & Coomes, D. A. (2013). The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PlosOne* 8, e55158.

Uuemaa, E., Antrop, M., Roosaare, J., Marja, R., & Mander, Ü. (2009) Landscape metrics and indices: an overview of their use in landscape research. Living reviews in landscape research. doi:10.12942/lrlr-2009.

Van der Sluijs, J. P. et al. (2015). Conclusions of the Worldwide Integrated Assessment on the risks of neonicotinoids and pronil to biodiversity and ecosystem functioning. *Environmental Science and Pollution Research*, 22, 148-154.

Villas-Bôas, J. (2012). Manual Tecnológico: Mel de Abelhas sem Ferrão. Brasília-DF. Instituto Sociedade, População e Natureza (ISPN).

Warren, D. L., & Seifert, S. N. (2011). Ecological niche modelling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21, 335-342.

Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, 33, 607-611.

Warren, D. L., Wright, A. N., Seifert, S. N., & Shaffer, H. B. (2014). Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distribution*, 20, 334-343.

Warren, R., Van Der Wal, J., Price, J. J., Welbergen, J. A., Atkinson, I., Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams, S. E., & Lowe, J. (2013). Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, 3, 678-682.

- West, A. M., Kumar, S., Wakie, T., Brown, C. S., Stohlgren, T. J., Laituri, M., & Bromberg, J. (2015). Using high-resolution future climate scenarios to forecast *Bromus tectorum* invasion in rocky mountain national park. *Plos One* 10(2): e0117893.
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitat. In *The conservation of bees* (eds A Matheson, SL Buchman, C O'Toole, P Westrich, IH Williams), pp. 1 – 16. London, UK: Academic Press.
- Wisz, M., Hijmans, R., Li, J., Peterson, A., Graham, C., & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, 14, 763-773.
- Woodcock, B. A., Bullock, J. M., Shore, R. F., Heard, M. S., Pereira, M. G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Sároszpataki, M., Saure, C., Edwards, M., Genersch, E., Knabe, S., & Pywell, R. F. (2017). Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science*, 356, 1393-1395.

Chapter 2 - Impacts of climate change on the distribution of stingless bees in Brazil

Abstract

The present study aimed to understand whether climate change will affect the distribution of species of the genus *Melipona*. Further, we quantified the changes in the distribution of *Melipona* species and identified the climatically stable areas that remain suitable for the species in the different scenarios of climate change evaluated using ecological niche modeling approaches. The algorithm maximum entropy was employed to estimate the cumulative probability of maximum entropy based on species occurrence records and current and future environmental data. The developed models fitted to current climatic conditions were projected onto the future climatic conditions predicted for 2050 and 2070 using two different climate change scenarios (RCP4.5 and RCP8.5) provided by the Intergovernmental Panel on Climate Change. Our models predicted that 7 of the 10 species will face a reduction in the climatic suitable areas and 3 species will experience an increase in the suitable areas in the different climate scenarios evaluated. The species predicted to have the greatest habitat loss were *M. s. abunensis*, *M. melanoventer* and *M. flavolineata* in both RCP scenarios, while *M. fasciculata*, *M. amazonica* and *M. subnitida* were predicted to expand their suitable ranges. Most of the species evaluated will face a reduction of the climatically suitable areas available to them. Given the key role that stingless bees play as pollinators in natural and agroecosystems, this may have serious consequences for the food production and conservation of native plant species.

KEYWORDS: Bee conservation, Climate shifts, Conservation biogeography, Species distribution modeling.

Introduction

Successful conservation strategies for biological resources rely on a straightforward understanding of the distribution of the target species (Guo et al., 2017). Climate change is one of the most important factors affecting species distribution and causing biodiversity loss (Ashraf et al., 2017; Boria et al., 2014; Peterson et al., 2015, Warren et al., 2013). This strong relationship between species distribution and climate explains the changes in the patterns of distribution of species observed in the past years (Ashraf et al., 2017; Inoue; Berg, 2017). In this context, strategies such as the delimitation of priority areas for species conservation should consider the risks related to the loss of suitable areas in a scenario of climate change.

The Intergovernmental Panel on Climate Change (IPCC) under the auspices of the United Nations (UN) estimates that if the Earth average temperature increases of 2 to 3 °C, about 20 to 30% of all terrestrial biodiversity would be at high risk of extinction by the end of the century (IPCC, 2007). In the last century, global temperature rose by 0.85 °C and it is estimated an increase between 0.3 °C and 4.8 °C by 2100 without mitigating measures to reduce greenhouse gas emissions (IPCC, 2013). In this scenario, both cosmopolitan and endemic species will suffer irreparable consequences with regarding to their distribution range and abundance (Warren et al., 2013).

Species are affected by climate in different ways such as range shifts, relative abundance changes and subtle changes in the time of activity and microhabitat use (Bates et al., 2014). The redistribution of species as one of the consequences of climate change can result in discordant species range shifts, which may affect biotic interactions generating impacts at the community level (Sorte et al. 2010, Cahil et al. 2013). Because the production of goods and services depends on the ecosystem health, the climate-driven effects on biodiversity may have several impacts on economic development, ecosystems health and, as a consequence, on human well-being (Pecl et al., 2017). An example that illustrates this is the pollination services provided by animals, particularly insects, which operate in the maintenance of forests and contribute to food production.

Bees are the main pollinators of wild plants and agricultural crops (Breeze et al., 2016; Garibaldi et al., 2016; Potts et al., 2016;

Ollerton et al., 2011). Historical data shows that the decline of pollinators has been intensified by climate change (Dupont et al., 2011), which might have serious environmental and social consequences, considering that one-third of agricultural production is dependent on pollination services (Potts et al., 2016; Novais et al., 2016). Also, the sharp decline of pollinators will directly affect the production of some crops on a global scale, thereby compromising the population nutrition (Gallai et al., 2009). In this context, the knowledge on the vulnerability of pollinators to climate change is fundamental for the adoption of conservation policies in order to maintain a higher pollination dynamics (Garibaldi et al., 2016; Novais et al., 2016).

The stingless bees of the genus *Melipona* Illiger, 1806 (Meliponini tribe) are eusocial species and have an exclusive distribution in the Neotropical region (Yurrita et al., 2017). They are economically and culturally relevant as their honey, pollen and wax are frequently used for medicines, food supplementation and religion practices (Ayala et al., 2013). Apart from their ecological role as pollinators, many species of *Melipona* can also be used in meliponiculture, a sustainable activity that contributes to the conservation of ecosystems and production of income for smallholders (Pereira, 2003).

Ecological niche models (ENMs) are the most widely tool used to assess the impacts of climate change on the distribution of species (Ashraf et al., 2017, Franklin, 2009, Guisan, Thuiller, 2005, Guisan and Zimmermann, 2000). These models associate known occurrence records of species with environmental data to estimate the current climatic conditions tolerated by the species (Peterson et al., 2015; Nabout et al. 2012). Once the model is developed, it can be projected onto future climatic conditions to identify the suitable areas for the species under different scenarios of climate change. This information provides important subsidies for the development of conservation strategies (Guisan; Thuiller, 2005). In this study, we applied ENMs approaches aiming to understand whether climate change will affect the distribution of species of the genus *Melipona*. We also compared the changes in the distribution of *Melipona* species and estimated the climatically stable areas that remain suitable for the species in different scenarios of climate change.

Materials and methods

Species occurrence data

The effects of climate change on the distribution of ten species of *Melipona* in Brazil were evaluated: *Melipona scutellaris* Latreille, 1811, *Melipona quadrifasciata anthidioides* Lepeletier, 1836, *Melipona quadrifasciata quadrifasciata* Lepeletier, 1836, *Melipona melanoventer* Schwarz, 1932, *Melipona seminigra abunensis* Cockerell, 1912, *Melipona flavolineata* Friese, 1900, *Melipona fasciculata* Smith, 1854, *Melipona amazonica* Schulz, 1905, *Melipona subnitida* Ducke, 1910 and *Melipona paraensis* Ducke, 1916. The occurrence data were obtained from the literature and online database such as Global Biodiversity Information Facility (<http://www.gbif.org>) and SpeciesLink (<http://splink.cria.org.br>). In addition, for those locations not georeferenced we obtained the geographic coordinates using Google Earth. Occurrence records that extrapolate the known distribution range of the species obtained in the Moure's Catalog webpage (<http://moure.cria.org.br>) were removed.

Environmental data

Altitude data and 19 bioclimatic variables were obtained from the Worldclim version 1.4. (<http://worldclim.org>) in the resolution of 5 arc-min. These bioclimatic variables are widely used in ecological niche modeling because they capture annual variations and well-defined limits of temperature and precipitation that constraint species distribution range (Slater & Michael 2012). Data from the bioclimatic variables were also obtained for 2050 and 2070 based on two different scenarios of greenhouse gas emissions named Representative Concentration Pathways (RCP 4.5 and RCP 8.5). The RCP 4.5 scenario predicts that temperature will rise from 1.1 °C to 2.6 °C, while the RCP 8.5 scenario is based on the assumption that emissions will continue to rise throughout this century resulting in an increase ranging from 2.6 °C to 4.8 °C in Earth mean temperature by 2070. The climate projections were performed according to the fifth IPCC assessment report (AR5).

Species distribution models and projections of future climate change

Current species distribution models were built using the

software MaxEnt v. 3.3.3k (Phillips et al., 2006), which uses an algorithm that estimates the cumulative probability of maximum entropy based on occurrence records and environmental variables (Elith, et al., 2011; Phillips et al., 2006; Phillips; Dudík, 2008). In order to build more parsimonious models we followed the literature recommendation, including spatial filtering the occurrence data, reduction of the number of environmental predictors by means of an *a priori* selection of uncorrelated variables based on Pearsons' correlation test, delimitation of the study area, and tested different combinations of feature classes and regulation multiplier values. The evaluation of the models was performed using the area under the curve (AUC) of the receiver-operating characteristic (Fielding & Bell, 1997, Peterson et al., 2011) (see Chapter 1 for more details).

The final model selected for each species was projected onto future climatic conditions expected for 2050 and 2070, according to the two different scenarios of greenhouse gases emission (RCP 4.5 and RCP 8.5). To quantify the changes within the climatically suitable areas for each species, we created binary maps (suitable and unsuitable areas) using the *Maximum training sensitivity plus specificity logistics threshold*, which maximizes the sensitivity and specificity of the model. This threshold is indicated to determine areas for conservation because it reduces false-positives (Loiselle et al., 2003). In order to diminish the uncertainties of future projections, we projected the models to future climate scenarios using five different general circulation models (GCMs): BCC-CSM1-1, CCSM4, HadGEM2-ES, MIROC5 and MIROC5. We constructed consensus maps considering suitable areas those predicted as suitable by at least three GCMs (Araújo; New, 2007). These changes were quantified using SDMtoolbox (Brown, 2014), depicting the percentage of areas gained, contracted and/or maintained stabled over the periods and future climate scenarios evaluated. We executed the centroid analysis by calculating the distributional changes between two binary SDMs (current and future). This analysis reduces the distribution of each species to a single central point (centroid) and automatically creates a vector file that shows the magnitude and direction of the change over the time. This analysis was carried out using the toolkit SDMtoolbox (Brown, 2014). To depict the areas of habitat contraction and expansion for all *Melipona* species, we calculated the species richness by summing the binary maps obtained for 2050 and 2070 in the different scenarios of climate change, and then calculate the percentage of species loss for each pixel. The percentage of

species gain was not calculated because it is not possible when pixels have zero values in the richness maps for current climatic conditions. This procedure was performed using the “raster calculator” tool in the software ArcGIS 10.3.

Results

All models performed better than random showing AUC values varying from 0.76 to 0.97, which can be considered accurate (See supplementary material for detail). The changes in the distribution of the stingless bees studied varied according to the year and the future climate scenarios evaluated (Table 1). Considering the worst-case scenario (RCP 8.5 in 2070), our models showed that seven species are predicted to experience a reduction in the suitable areas. In this scenario and year, five species evaluated will have a reduction of their current distribution range greater than 70% and twenty percent will lose at least 50% of their current distribution by 2070. These species include *M. scutellaris*, distributed mainly in northeastern region, *M. q. anthidioides* and *M. q. quadrifasciata*, found in southern and southeastern regions and *M. melanoventer*, *M. s. abunensis* and *M. flavolineata*, found in northern region (Figure 1 and 2, Table 1). The worst loss in the suitable areas was predicted for *M. flavolineata*, *M. s. abunensis* and *M. melanoventer*, and the latter two species may lose all climatically suitable areas in Brazil (Table 1). The results show that *M. melanoventer* will not have suitable habitats in Brazil based on predictions for the scenario RCP 8.5 in 2070, and *M. s. abunensis* will not have climatically suitable areas for 2050 in the scenario RCP 4.5 (Table 1).

On the other hand, the areas predicted as suitable for *M. fasciculata*, *M. amazonica* and *M. subnitida* increased in the different years and scenarios of climate change (Table 1, Figs 1 and 2). The species *M. paraensis* and *M. amazonica* will experience a significant increase in their suitable ranges in 2050 and 2070 in the scenario RCP 4.5 and in 2050 in the scenario RCP 8.5 (Figure 1, Table 1). However, in the future projections for 2070 based on the scenario RCP 8.5 the model predicted that both species will have only a subtle increase of 2.00% and 1.87% in the suitable ranges, respectively (Table 1). Interestingly, *M. paraensis* showed a different pattern with a predicted increase in the suitable ranges of 48.16% and 6.04% for 2050 and 2070 in the scenario RCP 4.5 and a decrease of 12.87% and 42.47% in the suitable ranges for 2050 and 2070 in the scenario RCP 8.5, respectively (Table 1).

The figure 3 representing the percentage of predicted habitat contraction and expansion based on the distribution of the ten species evaluated demonstrates different magnitudes of contraction and expansion according to the region, year and future climate scenarios evaluated. For instance, higher percentage of area loss was registered in the western region of the Atlantic forest biome, while in the Cerrado biome the losses were predicted to occur mainly in the state of Tocantins. In the Amazon region, the area loss was more intense in the southern region of the biome. In general, area loss increased according to the years and was more intense in the scenario RCP 8.5 for most species. According to the models, most of the areas predicted to increase the number of stingless bees species are in the northern and isolated areas in central Brazil (Fig. 3).

The centroid analysis for each species in 2070 based on the scenario RCP 8.5 demonstrates that both magnitude and direction of the distribution shifts varied according to the species. The species *M. q. anthidioides*, *M. q. quadrifasciata* and *M. scutellaris* shifted the core of their distribution to the southeastern direction, while the species distributed in western Amazon (*M. amazonica* and *M. paraensis*) shifted to the western direction. The exception was *M. flavolineata*, *M. fasciculata* and *M. subnitida* whose distribution distributions shifted to northeastern, northwestern and southwestern directions, respectively (Fig. 3).

Table 1. Predicted habitat suitability of *Melipona* species under two different climate change scenarios in Brazil.

| Species | RCP 4.5* | | RCP 8.5* | |
|-----------------------------|----------|---------|----------|---------|
| | 2050 | 2070 | 2050 | 2070 |
| <i>M. scutellaris</i> | -7.96% | -14.86% | -14.92% | -24.27% |
| <i>M. q. anthidioides</i> | -46.58% | -58.05% | -56.90% | -77.41% |
| <i>M. q. quadrifasciata</i> | -37.74% | -46.55% | -46.07% | -72.60% |
| <i>M. melanoventer</i> | -90.98% | -94.61% | -98.45% | -100% |
| <i>M. s. abunensis</i> | -97.22% | -99.82% | -100% | -100% |
| <i>M. flavolineata</i> | -83.82% | -87.08% | -89.07% | -94.57% |
| <i>M. fasciculata</i> | 87.77% | 73.97% | 62.41% | 2.00% |
| <i>M. amazonica</i> | 213.33% | 224.89% | 215.15% | 1.87% |
| <i>M. subnitida</i> | 14.53% | 18.36% | 23.53% | 31.24% |
| <i>M. paraensis</i> | 48.16% | 6.04% | -12.87% | -42.47% |

* Negative values refer to a decrease in potential areas.

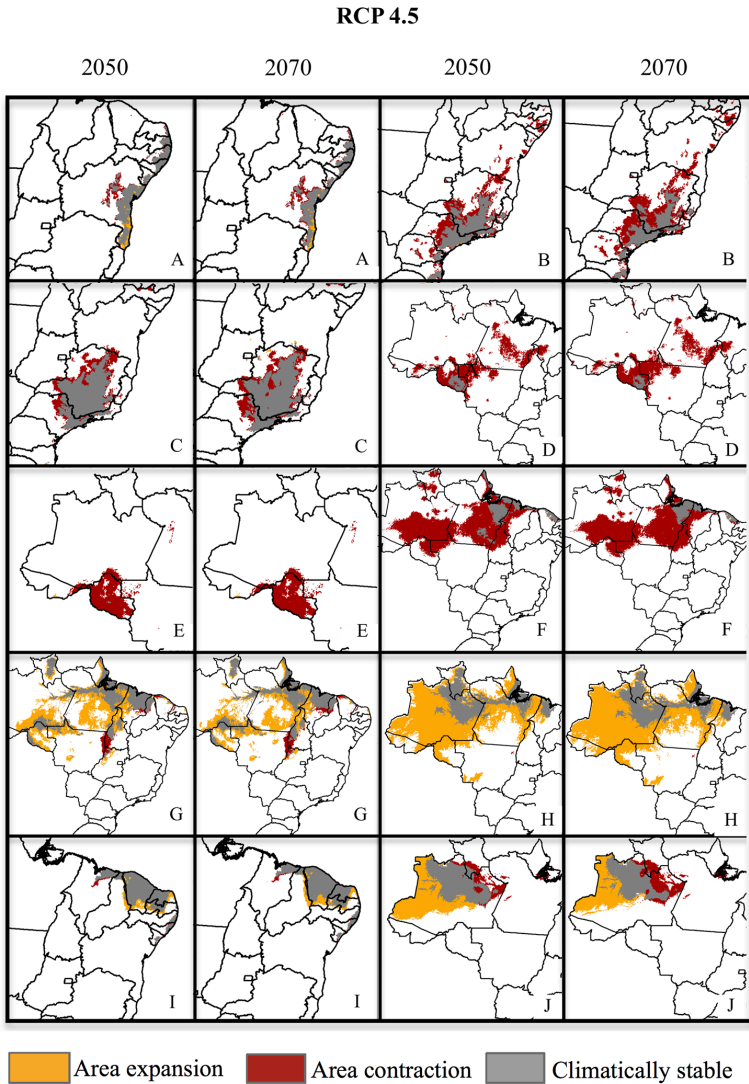


Figure 1. Predicted future habitat for *Melipona* species with RCP 4.5 projection for 2050 and 2070 in Brazil. **A.** *M. scutellaris*, **B.** *M. q. anthidioides*, **C.** *M. q. quadrifasciata*, **D.** *M. melanoventer*, **E.** *M. s. abunensis*, **F.** *M. flavolineata*, **G.** *M. fasciculata*, **H.** *M. amazonica*, **I.** *M. subnitida* and **J.** *M. paraensis*. Binary

maps were constructed using the maximum training sensitivity plus specificity logistic threshold.

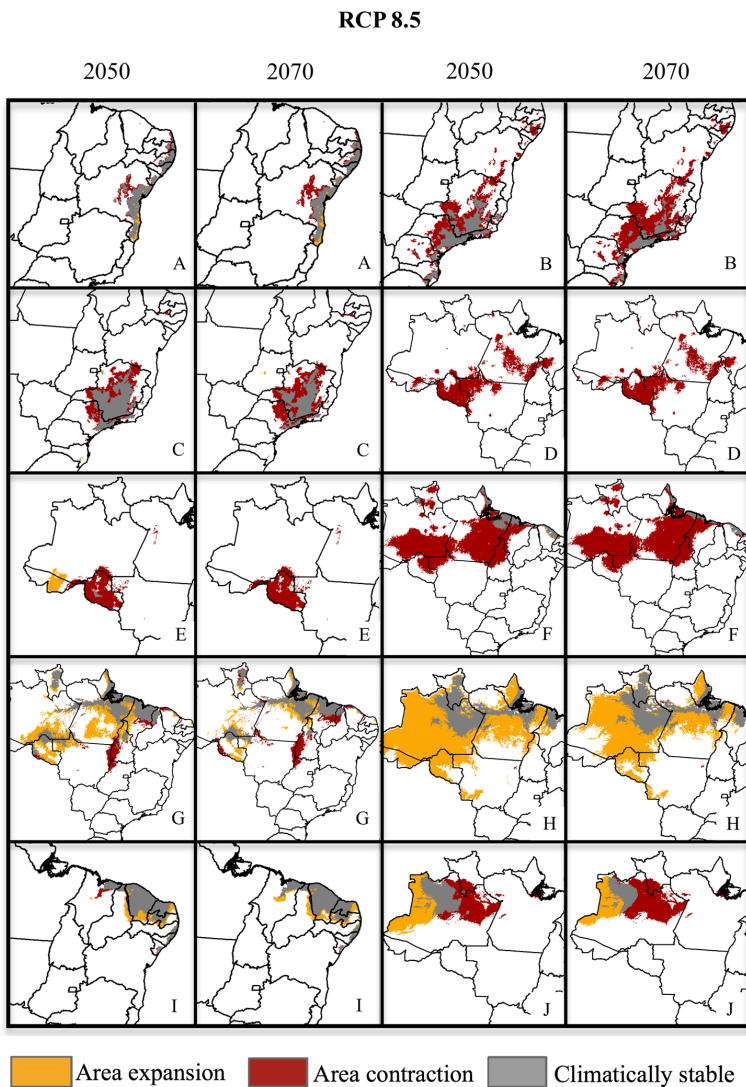


Figure 2. Predicted future habitat for *Melipona* species with RCP 8.5 projection for 2050 and 2070 in Brazil. A. *M. scutellaris*, B. *M. q. anthidioides*, C. *M. q.*

quadrifasciata, *D. M. melanoventer*, *E. M. s. abunensis*, *F. M. flavolineata*, *G. M. fasciculata*, *H. M. amazonica*, *I. M. subnitida* and *J. M. paraensis*. Binary maps were constructed using the maximum training sensitivity plus specificity logistic threshold.

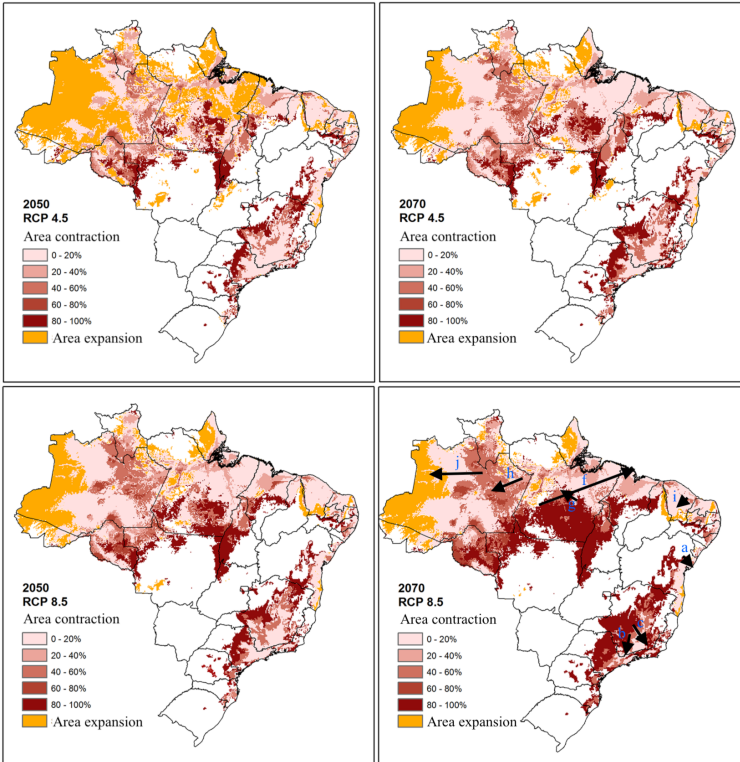


Figure 3. Predicted shifts in *Melipona* species richness for each pixel (grid). Different shades of red indicates the percentage of species loss for each pixel in the evaluated scenarios of climate changes. Yellow pixels represent species gain because it is not possible to calculate percentage of species gain from pixels when richness maps for current climatic conditions have zero values. Spatial vectors show the magnitude and direction of the distribution shifts for **a.** *M. scutellaris*, **b.** *M. q. anthidioides*, **c.** *M. q. quadrifasciata*, **f.** *M. flavolineata*, **g.** *M. fasciculata*, **h.** *M. amazonica*, **i.** *M. subnitida* and **j.** *M. paraensis*.

Discussion

Observed and projected climate changes for the 21st century are comparable in magnitude to the largest global changes in the past 65 million years (Diffenbaugh & Field, 2013). Current changes in Earth's climate condition already are resulting in global-scale biological response (Pecl et al. 2017), and drastic changes in the distribution of species are predicted for the future (Warren et al. 2013). Regarding to future distribution of the ten *Melipona* species evaluated in this study, the models predicted that the response to climate change might vary according to the species. While some species will face an increase in the climatically suitable areas, such as *M. fasciculata*, *M. amazonica* and *M. subnitida*, others will have a drastic reduction in the climatically suitable habitats: *M. scutellaris*, *M. q. anthidioides*, *M. q. quadrifasciata*, *M. melanoventer*, *M. s. abunensis*, *M. flavolineata* and *M. paraensis*. The extension of the area losses may have important consequences for species conservation. Species such as *M. s. abunensis*, *M. melanoventer* and *M. flavolineata* are predicted to lose more than 80% of their suitable ranges in all climate scenarios. In fact, depending on the year and future climate scenario, both *M. s. abunensis* and *M. melanoventer* may no longer have climatically suitable areas in Brazil.

Studies have been pointing out climate change as one of the causes of the world decline of pollinating bees (Biesmeijer et al., 2006; Dupont et al., 2011, Giannini et al., 2012). Our study suggests that this decline of pollinators may intensify in the next years once that seven of the ten species studied here are predicted to lose suitable habitats in different future climate scenarios. Despite the importance of studies like these, there are few attempts to consider the impact of future climate change on Brazilian bees. Giannini et al. (2012, 2015) evaluated the impact of climate change on species and subspecies of the genus *Melipona* and *Centris* and found a potential reduction in their suitable ranges varying from less than 5% to 35% in two climate change scenarios. Furthermore, similarly to our study, Giannini et al. (2017) estimated the impact of climate change on the distribution of *M. subnitida* finding a subtle increase in the suitable ranges for the species as a consequence of climate change (1.4%).

In addition to climatic changes, habitat fragmentation is indicated as one of the main factors that increase vulnerability to the studied species (Chapter I). The species *M. scutellaris*, *M. q.*

anthidioides and *M. q. quadrifasciata* occurred predominantly in agricultural mosaics and forest remnants, indicating that changes in land use, especially with regard to the conversion of natural vegetation to urban and agricultural areas, are often cited as drive for bee population declines (Ollerton et al., 2004; De Palma et al. , 2016). Furthermore, the Conservation Units of Brazil demonstrated low effectiveness varying from 6.54% to 31.54% for protecting the studied species (Chapter I).

Although ecological niche models can be used to estimate the climatically suitable ranges in the future, some species may adapt to future conditions through changes in their physiology leading to an increase in the tolerance to temperature and humidity conditions that currently constrain its distribution. This adaptation is more likely in species showing short life–cycles, and high speciation rates combined with low natural levels of extinction, such as insects (Alamgir et al., 2015; Feeley et al., 2012; Loucks et al., 2010; Ramirez-Villegas et al., 2014; Harsch et al., 2017). In this context, for some species the area predicted to be lost might be smaller than the estimated by the models due to evolutionary mechanisms.

Although studies have shown reduction of suitable areas for several species as a result of climate change, other species may expand their range (Giannini et al., 2017; Khanum et al., 2013, Qin et al., 2017). Although our study demonstrates an increase in the suitable areas for *M. fasciculata*, *M. amazonica* and *M. subnitida*, there is no guarantee of its range expansion, because other factors related to the difficulties of species to disperse to the predicted suitable areas and changes in land use may constraint species dispersal (Harsch et al., 2017, Bates et al., 2011; Cariveau et al., 2013; Jha & Kremen, 2013). In this context, the delimitation of areas for conservation based on the regions showing climatic stability over the years and the establishment of ecological corridors to connect protected areas with climatically suitable conditions may be used as conservation strategy for these species aiming to mitigate biodiversity loss.

Although studies have evaluated the impact of climate change on pollinating bees of some agricultural crops such as coffee (Giannini et al., 2015), passion fruit (Giannini et al., 2013), cashew, acerola, guava, avocado (Giannini et al., 2012), pepper and annatto (Giannini et al., 2017), the knowledge on this subject is still scarce. Among the

studied species and their respective agricultural crops, we can highlight: *M. fasciculata* cited as pollinator of açai palm (*Euterpe oleracea*), eggplant (*Solanum melongena*), cashew (*Anacardium occidentale*), tomato (*Lycopersicon esculentum*) and annatto (*Bixa orellana*); *M. q. quadrifasciata* and *M. q. anthidioides* as an important pollinator of pumpkin (*Cucurbita moschata*), sweet and chili peppers (*Capsicum annum*), chili pepper (*Capsicum frutescens*) and tomato (*L. esculentum*); *M. flavolineata* as pollinator of açai palm (*E. oleracea*), sunflower (*Helianthus annuus*) and annatto (*B. orellana*); *Melipona scutellaris* pollinating avocado (*Persea americana*), sweet and chili peppers (*Capsicum annum*) and pitanga (*Eugenia uniflora*) and *M. s. abunensis* as an important pollinator of cashew (*A. occidentale*), guarana (*Paullinia cupana*) and annatto (*B. orellana*). All these crops and its production may be affected by the reduction in the distribution range of the stingless bees (Silva et al., 2014). This may have severe social and economic consequences because smallholders use the majority of the agricultural crops mentioned as the main source of income. For instance, our results showed that *M. s. abunensis*, a pollinator of annatto, is predicted to lose all suitable areas by 2050. Considering that the state of Rondonia is one of the leading producers of annatto in Brazil, the absence of its main pollinator may significantly affect crop production (Moreira et al., 2015).

Stingless beekeeping is an activity of great importance since it can ensure a growing agricultural demand and increase smallholder income (mean of US\$ 1.300 annually) (Giannini et al., 2017; Jaffé et al, 2015). Our study provides two main insights for beekeepers. First, the information about current and future climate stability for each species can be used to identify priority areas for the production of stingless bees. Second, the knowledge on the areas predicted to lose species can be used to identify the regions where the beekeeping may be under risk, anticipating future socioeconomic problems and, consequently, allowing the adoption economic measures for local communities.

Here, we evaluated the effect of climate changes on ten species of native bees distributed in Brazil. The results showed that climate changes may negatively affect the distribution range of 70% of the species evaluated, which may have direct consequences for production of food and reproduction of native plant species, since these bees are essential for the pollination of agricultural and natural ecosystems. Our study provides an important contribution to knowledge of stingless bees

vulnerability to climate change and it can be used for conservation purposes by decision-makers.

Acknowledgments

We thank CAPES for the scholarship, GEOPAM/UFMA on behalf of Professor Dr. Murilo Drummond for occurrence data and Geomatic Lab/UFSC on behalf of Professor Dr. Alexandre ten Caten for the technological resources.

References

- Ashraf, U., Peterson, A. T., Chaudhry, M. N., Ashraf, I., Saqib, Z., Rashid Ahmad, S., & Ali, H. (2017). Ecological niche model comparison under different climate scenarios: a case study of *Olea* spp. in Asia. *Ecosphere* 8(5):e01825. 10.1002/ecs2.1825.
- Ayala, R., Gonzalez, V. H., & Engel, M. S. (2013). Mexican stingless bees (Hymenoptera: Apidae): diversity, distribution and indigenous knowledge. In: Vit, P., Pedro, S. R. M., Roubik, D.W. (eds.) *Pot-Honey a Legacy of Stingless Bee*, pp. 135-152. Springer, New York.
- Bates, A. E. et al. (2014). Defining and observing stages of climate-mediated range shifts in marine systems. *Global Environmental Change*, 26, 27-38.
- Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D., & Matthews, T. J. (2011). Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *Plos One* 6, e23459. (Doi:10.1371/journal.pone.0023459)
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, 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.
- Boria, R. A., Olson, L. E., Goodman, S. T., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, 275, 73-77.

- Breeze, T. D., Gallai, N., Garibaldi, L. A., & Li, X. S. (2016). Economic Measures of Pollination Services: Shortcomings and Future Directions. *Trends in Ecology & Evolution*, 31, 927-939.
- BROWN, J. L. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution*, 5, 694-7000.
- Cariveau, D. P., Williams, N. M., Benjamin, F. E., & Winfree, R. (2013). Response diversity to land use occurs but does not consistently stabilise ecosystem services provided by native pollinators. *Ecology Letters*, 16, 903-911.
- Diffenbaugh, N. S. & Field, C. B. (2013). Changes in Ecologically Critical Terrestrial Climate Conditions. *Science*, 341, 486-492.
- Dupont, Y. L., Damgaard, C., & Simonsen, V. (2011). Quantitative historical change in bumblebee (*Bombus* spp.) assemblages of red clover fields. *PlosOne* 6, e25172.
- Dupont, Y. L., Damgaard, C., Simonsen, V. (2011). Quantitative historical change in bumblebee (*Bombus* spp.) assemblages of red clover fields. *PlosOne* 6, e25172.
- Elith, J., Phillips, S., Hastie, T., Dudík, M., Chee, Y., & Yates, C. A. (2011). Statistical Explanation of MaxEnt for Ecologists. *Diversity and Distributions*, 17, 43-57.
- Feeley, K. J., Malhi, Y., Zelazowski, P., & Silman, M. R. (2012). The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species. *Global Change Biology*, 18, 2636e2647.
- Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38-49.
- Franklin, J. (2009). Mapping Species Distribution. Spatial Inference and Prediction. Cambridge University Press, New York.

Gallai, N., Salles, J. M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, 68, 810-821.

Garibaldi, L. et al. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, 351, 388-391.

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.

Giannini, T. C., Maia-Silva, C., Acosta, A. L., Jaffé, R., Carvalho, A. T., Martins, C. F., Zanella, F. C. V., Carvalho, C. A. L., Hrncir, M., Saraiva, A. M., Siqueira, J. O. S., Imperatriz-Fonseca, V. L. (2017). Protecting a managed bee pollinator against climate change: strategies for an area with extreme climatic conditions and socioeconomic vulnerability. *Apidologie*, doi: 10.1007/s13592-017-0523-5.

Giannini, T. C., Tambosi, L. R., Acosta, A. L., Jaffé, R., Saraiva, A. M., Imperatriz-Fonseca, V. L., Metzger, J. P. (2015). Safeguarding Ecosystem Services: A Methodological Framework to Buffer the Joint Effect of Habitat Configuration and Climate Change. *PlosOne*, doi:10.1371/journal.pone.0129225.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993-1009.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147-186.

Guo, Y. et al. 2017. Prediction of the potential geographic distribution of the ectomycorrhizal mushroom *Tricholoma matsutake* under multiple climate change scenarios. *Nature*, doi: 10.1038/srep46221.

Harsch, M. A., Phillips, A., Zhou, Y., Leung, M. R., Rinnan, D. S., & Kot, M. (2017). Moving forward: insights and applications of moving-habitat models for climate change ecology. *Journal of Ecology*, doi: 10.1111/1365-2745.12724.

Inoue, K., & Berg, D. J. (2017). Predicting the effects of climate change on population connectivity and genetic diversity of an imperiled freshwater mussel, *Cumberlandia monodonta* (Bivalvia: Margaritiferidae), in riverine systems. *Global Change Biology*, 23, 94-107.

IPCC, 2007: Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Parry, M. L.; Canziani, O. F.; Palutikof, J. P.; Van Der Linden, P. J.; Hanson, C. E. Eds. Cambridge University Press, Cambridge, United Kingdom, p. 976.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Stocker, T. F., Qin, D, G. K., Tignor, M. S., Allen, K.; Boschung, J., Nauels, A., Xia, Y.; Bex, V., Midgley, P. M. Eds. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 1535.

Jaffé, R., Pope, N., Carvalho, A. T., Maia, U. M., Blochtein, B., de Carvalho, C. A. L., et al. (2015). Bees for Development: Brazilian Survey Reveals How to Optimize Stingless Beekeeping. *PLoS ONE* 10(3): e0121157. <https://doi.org/10.1371/journal.pone.0121157>

Jha, S., & Kremen, C. (2013). Urban land use limits regional bumble bee gene flow. *Molecular Ecology*, 22, 2483-2495.

Khanum, R., Mumtaz, A. S., & Kumar, S. (2013). Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modeling. *Acta Oecologica*, 49, 23-31.

Loucks, C., Barber-Meyer, S., Hossain, M. A. A., Barlow, A., & Chowdhury, R. M. (2010). Sea level rise and tigers: predicted impacts to Bangladesh's sundarbans mangroves, a letter. *Climatic Change*, 98, 291e298.

Mohammed Alamgir , Sharif Ahmed Mukul, Stephen M. Turton. (2016). Modelling spatial distribution of critically endangered Asian elephant and Hoolock gibbon in Bangladesh forest ecosystems under a changing climate. *Applied Geography*, 60, 10-19.

Moreira, P. A., Lins, J., Dequigiovanni, G., Veasey, E., & Clement, C. R. (2015). The Domestication of Annatto (*Bixa orellana*) from *Bixa urucurana* in Amazonia. *Economic botany*, 10, 1-9.

Nabout, J. C., Carvalho, P., Prado, M. U., Borges, P. P., Machado, K. B., Haddad, K. B., Michelant, S., Cunha, H. F., & Soares, T. N. (2012). Trends and biases in global climate change literature. *Brazilian Journal for Nature Conservation*, 10, 45-51.

Novais, S. M. A., Nunes, C. A., Santos, N. B., D'amico, A. R., Fernandes, G. W., Quesada, M., Braga, R. F., & Neves, A. C. O. (2016). Effects of a possible pollinator crisis on food crop production in Brazil. *PlosOne*, 11, 1-12.

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, 120, 321-326.

Pecl, G. T. et al. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, 1389.

Pereira, J. C., Vincenzi, M. L., Lovato, P. E. (2003). Roland Ristow: uma contribuição ao estudo da agricultura sustentável. *Eisforia*, 1, 63-97.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., et al. (2011). Ecological niches and geographic distributions. Princeton University Press, Princeton, p 314.

Peterson, A. T., Monica Papes, M., Soberon, J. (2015). Mechanistic and Correlative Models of Ecological Niches. *European Journal of Ecology*, 1(2):28-38, doi: 10.1515/eje-2015-0014.

Phillips, S. J., & Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161-175.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231-259.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220-229.

Qin, A., Liu, B., Guo, Q., Bussmann, R. W., Ma, F., Jian, Z., Xu, G., Peie, S. (2017). Maxent modeling for predicting impacts of climate change on the potential distribution of *Thuja sutchuenensis* Franch., an extremely endangered conifer from southwestern China. *Global Ecology and Conservation*, 10, 139-146.

Ramirez-Villegas, J., Cuesta, F., Devenish, C., Peralvo, M., Jarvis, A., & Arnillas, C. A. (2014). Using species distributions models for designing conservation strategies of Tropical Andean biodiversity under climate change. *Journal for Nature Conservation*, 22, 391e404.

Silva, C. I., Kátia Paula Aleixo, K. P., Nunes-Silva, B., Freitas, B. M., & Imperatriz-Fonseca, V. L. Guia Ilustrado de Abelhas Polinizadoras no Brasil. São Paulo: Instituto de Estudos Avançados da Universidade de São Paulo, (2014). Co-editor: Ministério do Meio Ambiente - Brasil ISBN: 978-85-63007-07-0.

Slater H., & Michael, E. (2012). Predicting the current and future potential distributions of lymphatic filariasis in Africa using maximum entropy ecological niche modelling. *Plos One* 7(2): e32202. doi:10.1371/journal.pone.0032202.

Warren, R., Van Der Wal, J., Price1, J. J., Welbergen, J. A., Atkinson, I.; Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams, S. E., & Lowe, J. (2013). Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, 3, 678-682.

Yurrita, C. L., Ortega-Huerta, A., & Ayla, R. (2017). Distributional analysis of *Melipona* stingless bees (Apidae: Meliponini) in Central America and Mexico: setting baseline information for their conservation. *Apidologie*, 48, 247-258.

Final considerations

In short, we predicted that the suitable areas for *Melipona* species are distributed in different regions and biomes of Brazil. The species *M. melanoventer* Schwarz, 1932, *M. s. abunensis*, *M. flavolineata*, *M. fasciculata*, *M. amazonica*, *M. subnitida* and *M. paraensis* are mostly distributed in areas with natural vegetation, while *M. scutellaris*, *M. q. anthidioides* and *M. q. quadrifasciata* occurs predominantly in areas with mosaic of agriculture and forest remnants. The species *M. melanoventer*, *M. s. abunensis*, *M. flavolineata*, *M. fasciculata*, *M. amazonica*, *M. subnitida* and *M. paraensis* are mostly distributed in natural areas while the species *M. scutellaris*, *M. q. anthidioides* and *M. q. quadrifasciata* occur predominantly in areas with mosaic between agriculture and forest remnants. The species *M. paraensis* presented 31.54%, the highest percentage of their suitable range covered by PAs and *M. scutellaris* the lowest (6.54%). Brazilian protected areas presented poor effectiveness for the conservation of the studied species. Our future models predicted that seven of the ten species will face a reduction in their suitable areas and three species will find an increase in the available suitable areas in the different climate change scenarios evaluated.

In accordance with the information provided in this study, we conclude that some species are under higher threat than others. The species *M. scutellaris*, *M. q. anthidioides*, *M. q. quadrifasciata*, *M. melanoventer*, *M. s. abunensis*, *M. flavolineata* and *M. paraensis* are threatened by land use and climate change. The species *M. melanoventer* and *M. s. abunensis* are the most threatened species by climate change since they will not find suitable areas for future conditions. In addition, *M. scutellaris*, *M. q. anthidioides* and *M. q. quadrifasciata* have their suitable ranges within mosaics of agriculture and forest remnants, thus conferring a greater threat by exposure to large quantities of pesticides used in agricultural areas. Among these, the species *M. scutellaris* may have greater vulnerability when compared to the others, for presenting a restricted geographic distribution, predominantly in the region of Chapada Diamantina and east coast from Bahia and for having the least amount of its suitable areas protected by conservation units (6.54%).

Based on the risk from climate change and land use here provided, we strongly recommend the following priority areas for the conservation of these meliponines: Southern of Pará; Western of

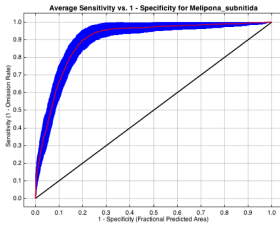
Tocantins; Northwestern of Mato Grosso; the central region of Rondonia; Southern and eastern of Maranhão; Chapada Diamantina in Bahia; Southeastern of Bahia and Northern of Minas Gerais; Southern region of Minas Gerais; Central part of Bauru, Ribeirão Preto e São Paulo Capital regionsa; Central region, general fields and Northern of Paraná; Northern, Valley, Eastern and Southern regions of Santa Catarina.

Therefore, we argue that land use and climate change need to be considered when planning strategies for conservation, especially when creating new Protected Areas. We highlight the necessity to discuss agricultural practices in order to guarantee ecosystem services provided by pollinators in the future and we suggest that biodiversity-friendly strategies such as meliponiculture should be considered in order to ensure ecosystem services as well as increase the economic income and well-being of local populations. Although our study provides an important contribution to knowledge of stingless bees distribution and their vulnerability to climate change, other important drivers of pollination decline were not considered here. In other words, the threats for the conservation of the stingless bees species studied here may be even higher than the discussed in our study. Further studies should consider the other drivers in order to clearly understand the risks of biodiversity loss of these important pollinators, as well as the consequences for natural vegetation maintenance and food production.

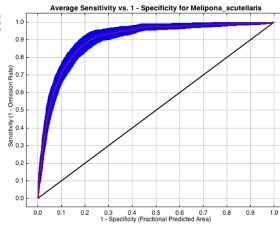
Supplementary material

1. AUC (Area Under Curve of receiver operating graph) values of each final model

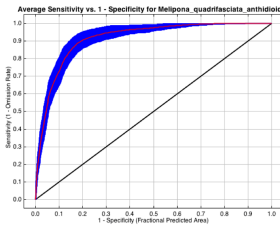
Melipona subnitida



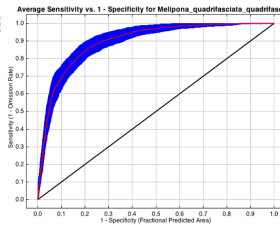
Melipona scutellaris



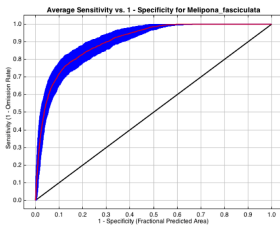
Melipona quadrifasciata anthidioides



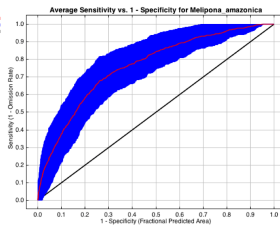
Melipona quadrifasciata quadrifasciata

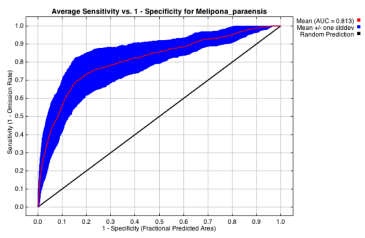
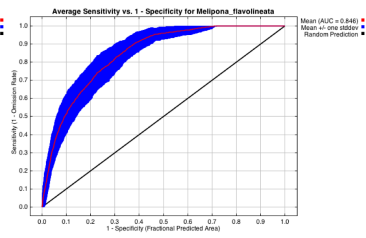
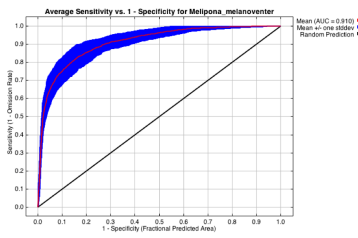
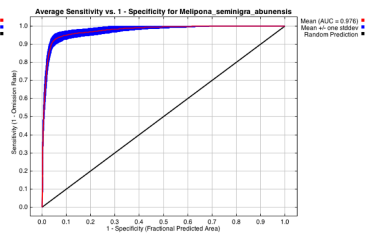


Melipona fasciculata



Melipona amazonica



Melipona paraensis*Melipona flavolineata**Melipona melanoventer**Melipona seminigra abunensis*

2. Number of occurrence records regarding distribution of *Melipona* species in Brazil.

| Species | Number of records | Number of records after filtering |
|---|-------------------|-----------------------------------|
| <i>Melipona scutellaris</i> | 118 | 117 |
| <i>Melipona quadrifasciata anthidioides</i> | 63 | 63 |
| <i>Melipona quadrifasciata quadrifasciata</i> | 71 | 70 |
| <i>Melipona melanoventer</i> | 68 | 61 |
| <i>Melipona seminigra abunensis</i> | 123 | 116 |
| <i>Melipona flavolineata</i> | 62 | 40 |
| <i>Melipona fasciculata</i> | 174 | 75 |
| <i>Melipona amazonica</i> | 25 | 18 |
| <i>Melipona subnitida</i> | 55 | 48 |
| <i>Melipona paraensis</i> | 35 | 31 |
| Total | 794 | 639 |

3. Relative contribution of the bioclimatic variables used in the final model.

| Species | Description | Contribution (%) |
|-----------------------------|--------------------------------------|-------------------------|
| <i>M. scutellaris</i> | Precipitation Seasonality | 44.5 |
| | Annual Precipitation | 21 |
| | Temperature Annual Range | 13.7 |
| | Precipitation of Driest Month | 12.6 |
| | Annual Mean Temperature | 2.4 |
| | Precipitation of Wettest Month | 2.4 |
| | Temperature Seasonality | 1.8 |
| | Altitude | 1.6 |
| <i>M. q. anthidioides</i> | Annual Mean Temperature | 53.9 |
| | Precipitation of Wettest Month | 18.7 |
| | Precipitation Seasonality | 7.9 |
| | Temperature Annual Range | 7.7 |
| | Temperature Seasonality | 6.2 |
| | Annual Precipitation | 3.4 |
| | Altitude | 2.1 |
| <i>M. q. quadrifasciata</i> | Precipitation of Wettest Month | 30.6 |
| | Temperature Seasonality | 25.6 |
| | Precipitation Seasonality | 22.9 |
| | Altitude | 8.7 |
| | Maximum Temperature of Warmest Month | 6.3 |
| | Annual Mean Temperature | 5 |
| | Temperature Annual Range | 0.8 |
| <i>M. melanoventer</i> | Altitude | 27.5 |
| | Precipitation of Driest Month | 17.9 |
| | Annual Mean Temperature | 15.3 |
| | Temperature Annual Range | 15.1 |
| | Annual Precipitation | 12.7 |
| | Precipitation Seasonality | 7.7 |

| | | |
|------------------------|--------------------------------------|------|
| | Maximum Temperature of Warmest Month | 2.6 |
| | Precipitation of Wettest Month | 1.2 |
| <i>M. s. abunensis</i> | Temperature Seasonality | 30.2 |
| | Precipitation Seasonality | 16.3 |
| | Temperature Annual Range | 16.2 |
| | Maximum Temperature of Warmest Month | 13.2 |
| | Annual Mean Temperature | 10.5 |
| | Altitude | 5.5 |
| | Precipitation of Wettest Month | 5.4 |
| | Annual Precipitation | 2.7 |
| <i>M. flavolineata</i> | Temperature Seasonality | 67.6 |
| | Precipitation of Driest Month | 14.6 |
| | Altitude | 14 |
| | Precipitation of Wettest Month | 2.1 |
| | Temperature Annual Range | 0.6 |
| | Precipitation Seasonality | 0.5 |
| | Maximum Temperature of Warmest Month | 0.5 |
| | Annual Precipitation | 0.1 |
| <i>M. fasciculata</i> | Annual Mean Temperature | 0.1 |
| | Altitude | 27.3 |
| | Annual Mean Temperature | 23.3 |
| | Precipitation Seasonality | 17.4 |
| | Maximum Temperature of Warmest Month | 11.1 |
| | Precipitation of Driest Month | 8.3 |
| | Temperature Seasonality | 5.4 |
| | Annual Precipitation | 4 |
| <i>M. amazonica</i> | Precipitation of Wettest Month | 2.6 |
| | Temperature Annual Range | 0.6 |
| | Annual Mean Temperature | 36 |
| | Altitude | 30.3 |
| | Temperature Seasonality | 9 |
| | Temperature Annual Range | 7.2 |
| | Max Temperature of Warmest | 5.5 |

| | | |
|---------------------|--------------------------------|------|
| | Month | |
| | Precipitation of Wettest Month | 5.2 |
| | Annual Precipitation | 4 |
| | Precipitation Seasonality | 2.8 |
| | Temperature Annual Range | 64.4 |
| | Precipitation Seasonality | 23.4 |
| | Altitude | 3.5 |
| <i>M. subnitida</i> | Annual Mean Temperature | 3.5 |
| | Temperature Seasonality | 2.5 |
| | Precipitation of Driest Month | 1.7 |
| | Annual Precipitation | 1 |
| | Precipitation Seasonality | 31.2 |
| | Altitude | 22.5 |
| | Annual Mean Temperature | 19.8 |
| <i>M. paraensis</i> | Temperature Annual Range | 15.8 |
| | Temperature Seasonality | 10.1 |
| | Precipitation of Wettest Month | 0.5 |
| | Annual Precipitation | 0.1 |

4. Statistics of selected models for *Melipona* species in Brazil. Selected models are highlighted in bold.

| Species | Feature classes | Regularization | AICc* | AUC | Δ AICc |
|-----------------------------|-----------------|----------------|----------------|-------------|---------------|
| <i>M. scutellaris</i> | LQ | 1 | 1706.73 | 0.9 | 0 |
| | LQ | 5 | 1746.23 | 0.88 | 0.03 |
| | LQ | 3 | 1740.49 | 0.89 | 0.95 |
| | LQHPT | 3 | 1726.65 | 0.9 | 1.06 |
| | L | 1 | 1747.93 | 0.88 | 1.7 |
| | LQHPT | 5 | 1751.83 | 0.89 | 1.93 |
| | L | 3 | 1749.9 | 0.88 | 1.97 |
| | L | 5 | 1755.88 | 0.88 | 4.05 |
| | LQHPT | 1 | 1830.33 | 0.93 | 4.72 |
| | H | 3 | 1746.2 | 0.89 | 5.71 |
| | H | 5 | 1764.17 | 0.88 | 8.29 |
| | LQH | 5 | 1739.54 | 0.89 | 12.89 |
| | LQH | 3 | 1725.59 | 0.9 | 18.86 |
| | LQH | 1 | 1825.61 | 0.92 | 61.44 |
| H | 1 | 1903.88 | 0.92 | 73.55 | |
| <i>M. q. anthidioides</i> | LQ | 1 | 1049.79 | 0.86 | 0 |
| | H | 1 | 1143.31 | 0.88 | 0.08 |
| | L | 3 | 1066.56 | 0.82 | 0.46 |
| | LQH | 3 | 1066.1 | 0.86 | 0.56 |
| | L | 1 | 1068.91 | 0.82 | 0.56 |
| | H | 3 | 1071.86 | 0.86 | 1.36 |
| | L | 5 | 1070.5 | 0.82 | 1.59 |
| | LQ | 5 | 1068.35 | 0.82 | 1.79 |
| | LQHPT | 3 | 1081.54 | 0.86 | 1.81 |
| | H | 5 | 1083.79 | 0.85 | 2.25 |
| | LQH | 5 | 1065.54 | 0.84 | 2.47 |
| | LQHPT | 5 | 1079.73 | 0.85 | 7.87 |
| | LQHPT | 1 | 1143.23 | 0.88 | 9.71 |
| | LQ | 3 | 1063.07 | 0.83 | 13.28 |
| LQH | 1 | 1133.52 | 0.88 | 49.73 | |
| <i>M. q. quadrifasciata</i> | LQ | 1 | 1329.18 | 0.83 | 0 |
| | LQHPT | 1 | 1335.12 | 0.9 | 0.1 |
| | LQH | 3 | 1335.02 | 0.84 | 0.16 |
| | L | 3 | 1337.19 | 0.82 | 0.39 |

| | | | | | |
|--|--------------|----------|----------------|-------------|----------|
| | LQ | 5 | 1341.99 | 0.82 | 0.51 |
| | LQ | 3 | 1336.8 | 0.82 | 1.68 |
| | LQHPT | 5 | 1349.58 | 0.83 | 2 |
| | L | 5 | 1341.48 | 0.81 | 4.29 |
| | LQHPT | 3 | 1347.58 | 0.84 | 5.59 |
| | L | 1 | 1334.86 | 0.82 | 5.68 |
| | H | 5 | 1379.03 | 0.84 | 7.45 |
| | H | 3 | 1386.59 | 0.86 | 7.56 |
| | LQH | 5 | 1404.71 | 0.84 | 9.01 |
| | H | 1 | 1395.7 | 0.88 | 9.11 |
| | LQH | 1 | 1371.58 | 0.88 | 22 |
| | LQ | 1 | 1163.65 | 0.9 | 0 |
| | LQH | 3 | 1195.61 | 0.9 | 0.7 |
| | LQHPT | 1 | 1197.44 | 0.95 | 1.83 |
| | LQ | 5 | 1200.55 | 0.88 | 3.11 |
| | L | 3 | 1204.05 | 0.87 | 3.5 |
| | L | 1 | 1194.91 | 0.87 | 7.31 |
| | L | 5 | 1212.69 | 0.87 | 8.64 |
| | LQHPT | 3 | 1231.76 | 0.91 | 19.07 |
| | LQ | 3 | 1187.6 | 0.88 | 23.95 |
| | H | 5 | 1259.04 | 0.89 | 27.28 |
| | LQH | 5 | 1483.79 | 0.88 | 42.7 |
| | H | 3 | 1538.31 | 0.9 | 54.52 |
| | LQH | 1 | 1341.09 | 0.93 | 82.05 |
| | LQHPT | 5 | 1441.09 | 0.91 | 100 |
| | H | 1 | 1961.83 | 0.93 | 423.52 |
| | LQHPT | 1 | 519.18 | 0.93 | 0 |
| | LQ | 5 | 522.18 | 0.77 | 0.06 |
| | L | 3 | 524.45 | 0.76 | 0.18 |
| | H | 5 | 524.73 | 0.76 | 0.28 |
| | L | 5 | 525.58 | 0.74 | 0.85 |
| | LQHPT | 3 | 526.78 | 0.85 | 1.2 |
| | LQ | 3 | 528.62 | 0.78 | 1.84 |
| | LQH | 3 | 524.27 | 0.85 | 2.09 |
| | L | 1 | 522.12 | 0.78 | 2.94 |
| | LQ | 1 | 558.14 | 0.8 | 29.52 |
| | H | 3 | 589.15 | 0.83 | 31.01 |
| | H | 1 | x | 0.91 | x |
| | LQH | 1 | x | 0.91 | x |

*M.
melanoventer*

*M. s.
abunensis*

| | | | | | |
|------------------------|-----------------------|--------------|---------------|----------------|-------------|
| | LQH | 5 | x | 0.77 | x |
| | LQHPT | 5 | x | 0.77 | x |
| <i>M. flavolineata</i> | L | 3 | 833.3 | 0.84 | 0 |
| | LQ | 3 | 837.72 | 0.83 | 0 |
| | L | 5 | 833.82 | 0.83 | 0.24 |
| | L | 1 | 833.58 | 0.84 | 0.28 |
| | H | 3 | 837.72 | 0.86 | 0.29 |
| | LQH | 3 | 837.43 | 0.86 | 0.82 |
| | LQHPT | 3 | 839.57 | 0.88 | 1.85 |
| | LQ | 5 | 836.61 | 0.83 | 2.79 |
| | LQ | 1 | 842.55 | 0.84 | 2.98 |
| | H | 5 | 845.97 | 0.84 | 3.42 |
| | LQHPT | 1 | 854.04 | 0.89 | 8.07 |
| | LQH | 5 | 2175.49 | 0.84 | 1321.45 |
| | H | 1 | x | 0.89 | x |
| | LQH | 1 | x | 0.89 | x |
| | LQHPT | 5 | x | 0.83 | x |
| | <i>M. fasciculata</i> | LQHPT | 1 | 1487.07 | 0.92 |
| LQHPT | | 5 | 1914.93 | 0.88 | 0 |
| LQ | | 5 | 1541.98 | 0.85 | 0.93 |
| LQH | | 3 | 1523.17 | 0.87 | 1.17 |
| H | | 5 | 1527.71 | 0.86 | 1.39 |
| LQ | | 3 | 1534.27 | 0.85 | 1.5 |
| L | | 3 | 1541.05 | 0.84 | 1.88 |
| LQH | | 5 | 1522 | 0.86 | 2.4 |
| LQHPT | | 3 | 1526.32 | 0.88 | 3.15 |
| L | | 5 | 1539.17 | 0.84 | 4.9 |
| L | | 1 | 1532.77 | 0.85 | 5.06 |
| LQ | | 1 | 1519.6 | 0.86 | 13.25 |
| H | | 3 | 1506.35 | 0.88 | 19.28 |
| LQH | | 1 | 1621.19 | 0.9 | 79.21 |
| H | | 1 | 1914.93 | 0.9 | 293.74 |
| | L | 1 | 523.17 | 0.75 | 0 |
| | H | 3 | 528.1 | 0.77 | 0.05 |
| | LQ | 1 | 528.05 | 0.75 | 0.16 |
| | H | 5 | 533.41 | 0.76 | 0.33 |
| | L | 5 | 533.79 | 0.75 | 0.38 |
| | LQ | 5 | 528.93 | 0.75 | 0.83 |
| | LQH | 3 | 525 | 0.76 | 0.91 |

| | | | | | |
|---------------------|-----------|----------|---------------|-------------|----------|
| <i>M. amazonica</i> | LQ | 3 | 524.09 | 0.75 | 0.92 |
| | LQHPT | 3 | 527.89 | 0.77 | 1.39 |
| | L | 3 | 526.5 | 0.75 | 1.5 |
| | LQHPT | 5 | 533.08 | 0.77 | 1.97 |
| | LQH | 5 | 531.11 | 0.75 | 2.18 |
| | LQHPT | 1 | 587.84 | 0.86 | 54.05 |
| | LQH | 1 | 643.7 | 0.83 | 55.86 |
| | H | 1 | 743.72 | 0.83 | 100.02 |
| <i>M. subnitida</i> | LQ | 1 | 838.35 | 0.88 | 0 |
| | LQ | 5 | 846.74 | 0.87 | 0.1 |
| | LQ | 3 | 849.1 | 0.87 | 0.21 |
| | H | 5 | 852.73 | 0.88 | 0.34 |
| | L | 1 | 838.74 | 0.87 | 0.39 |
| | LQHPT | 5 | 849.87 | 0.88 | 0.77 |
| | L | 5 | 850.89 | 0.86 | 1.02 |
| | LQH | 5 | 846.64 | 0.87 | 1.06 |
| | LQH | 1 | 881.02 | 0.91 | 1.34 |
| | LQHPT | 3 | 852.39 | 0.88 | 1.5 |
| | LQH | 3 | 848.89 | 0.87 | 2.15 |
| | L | 3 | 845.58 | 0.87 | 6.84 |
| | H | 3 | 862.85 | 0.88 | 10.12 |
| | LQHPT | 1 | 879.68 | 0.91 | 16.83 |
| | H | 1 | 1614.45 | 0.9 | 733.43 |
| <i>M. paraensis</i> | L | 3 | 617.47 | 0.8 | 0 |
| | LQHPT | 5 | 635.31 | 0.81 | 0 |
| | L | 5 | 620.43 | 0.8 | 0.25 |
| | LQ | 1 | 622.34 | 0.81 | 0.91 |
| | L | 1 | 621.43 | 0.81 | 1 |
| | H | 3 | 628 | 0.82 | 1.3 |
| | LQHPT | 1 | 637.32 | 0.9 | 2.01 |
| | LQH | 3 | 630.22 | 0.81 | 2.22 |
| | LQ | 3 | 620.18 | 0.8 | 2.71 |
| | LQ | 5 | 626.7 | 0.8 | 4.36 |
| | LQHPT | 3 | 635.31 | 0.82 | 5.09 |
| | H | 5 | 643.36 | 0.8 | 6.04 |
| | H | 1 | 1368.76 | 0.9 | 291.43 |
| | LQH | 5 | 1077.33 | 0.81 | 433.97 |
| LQH | 1 | x | 0.89 | x | |

*The values of "x" indicate that the models have more parameters than occurrence data, thus violating the assumptions of the AICc. In this case, the metrics for these models were not calculated.

5. Occurrence data used for modeling the stingless bees in Brazil.

| Species | Longitude | Latitude |
|-----------------------------|------------------|-----------------|
| <i>Melipona scutellaris</i> | -36.1756 | -10.1256 |
| <i>Melipona scutellaris</i> | -36.17631 | -10.12651 |
| <i>Melipona scutellaris</i> | -36.204361 | -10.076149 |
| <i>Melipona scutellaris</i> | -38.4192 | -12.1356 |
| <i>Melipona scutellaris</i> | -39.147642 | -13.734371 |
| <i>Melipona scutellaris</i> | -39.15 | -13.73333 |
| <i>Melipona scutellaris</i> | -41.39 | -12.563056 |
| <i>Melipona scutellaris</i> | -38.678611 | -12.888333 |
| <i>Melipona scutellaris</i> | -41.772778 | -13.151389 |
| <i>Melipona scutellaris</i> | -38.378889 | -12.353056 |
| <i>Melipona scutellaris</i> | -38.383333 | -12.883333 |
| <i>Melipona scutellaris</i> | -38.962 | -12.2555 |
| <i>Melipona scutellaris</i> | -39.04 | -12.678 |
| <i>Melipona scutellaris</i> | -39.659 | -13.084 |
| <i>Melipona scutellaris</i> | -38.042 | -12.263 |
| <i>Melipona scutellaris</i> | -38.015 | -12.581 |
| <i>Melipona scutellaris</i> | -39.462 | -12.462 |
| <i>Melipona scutellaris</i> | -39.224 | -12.211 |
| <i>Melipona scutellaris</i> | -38.193 | -12.415 |
| <i>Melipona scutellaris</i> | -38.328 | -12.431 |
| <i>Melipona scutellaris</i> | -38.379 | -12.353 |
| <i>Melipona scutellaris</i> | -39.199 | -12.809 |
| <i>Melipona scutellaris</i> | -41.328 | -12.798 |

| | | |
|-----------------------------|------------|------------|
| <i>Melipona scutellaris</i> | -41.313 | -12.852 |
| <i>Melipona scutellaris</i> | -41.092 | -11.33 |
| <i>Melipona scutellaris</i> | -41.294 | -12.594 |
| <i>Melipona scutellaris</i> | -40.495 | -12.289 |
| <i>Melipona scutellaris</i> | -41.094 | -12.082 |
| <i>Melipona scutellaris</i> | -40.495 | -12.051 |
| <i>Melipona scutellaris</i> | -40.321 | -10.508 |
| <i>Melipona scutellaris</i> | -40.435 | -11.091 |
| <i>Melipona scutellaris</i> | -41.156 | -11.55 |
| <i>Melipona scutellaris</i> | -39.036 | -12.682 |
| <i>Melipona scutellaris</i> | -39.619 | -13.001 |
| <i>Melipona scutellaris</i> | -40.125 | -13.392 |
| <i>Melipona scutellaris</i> | -40.431 | -13.441 |
| <i>Melipona scutellaris</i> | -40.302 | -13.426 |
| <i>Melipona scutellaris</i> | -40.111876 | -10.463084 |
| <i>Melipona scutellaris</i> | -38.428061 | -12.933042 |
| <i>Melipona scutellaris</i> | -39.16534 | -14.019323 |
| <i>Melipona scutellaris</i> | -41.174962 | -13.556415 |
| <i>Melipona scutellaris</i> | -39.370667 | -12.096823 |
| <i>Melipona scutellaris</i> | -39.743499 | -12.160767 |
| <i>Melipona scutellaris</i> | -40.163915 | -11.936255 |
| <i>Melipona scutellaris</i> | -40.366478 | -10.699814 |
| <i>Melipona scutellaris</i> | -40.43468 | -10.894397 |
| <i>Melipona scutellaris</i> | -40.441637 | -11.838357 |
| <i>Melipona scutellaris</i> | -37.604298 | -11.603897 |
| <i>Melipona scutellaris</i> | -39.424974 | -12.760159 |
| <i>Melipona scutellaris</i> | -40.734814 | -11.928274 |
| <i>Melipona scutellaris</i> | -36.578 | -7.068 |
| <i>Melipona scutellaris</i> | -35.910838 | -7.224781 |
| <i>Melipona scutellaris</i> | -35.58 | -6.80306 |
| <i>Melipona scutellaris</i> | -35.12583 | -6.83833 |

| | | |
|-----------------------------|-----------|----------|
| <i>Melipona scutellaris</i> | -35.69167 | -6.96306 |
| <i>Melipona scutellaris</i> | -34.833 | -7.413 |
| <i>Melipona scutellaris</i> | -34.911 | -7.399 |
| <i>Melipona scutellaris</i> | -34.902 | -7.413 |
| <i>Melipona scutellaris</i> | -34.886 | -7.318 |
| <i>Melipona scutellaris</i> | -34.895 | -7.31 |
| <i>Melipona scutellaris</i> | -35.692 | -6.967 |
| <i>Melipona scutellaris</i> | -35.615 | -6.7 |
| <i>Melipona scutellaris</i> | -34.816 | -7.195 |
| <i>Melipona scutellaris</i> | -35.091 | -6.69 |
| <i>Melipona scutellaris</i> | -35.097 | -6.681 |
| <i>Melipona scutellaris</i> | -35.087 | -6.657 |
| <i>Melipona scutellaris</i> | -35.799 | -7.104 |
| <i>Melipona scutellaris</i> | -35.756 | -7.134 |
| <i>Melipona scutellaris</i> | -35.755 | -7.101 |
| <i>Melipona scutellaris</i> | -35.766 | -7.106 |
| <i>Melipona scutellaris</i> | -35.76 | -7.108 |
| <i>Melipona scutellaris</i> | -35.76 | -7.109 |
| <i>Melipona scutellaris</i> | -35.772 | -7.093 |
| <i>Melipona scutellaris</i> | -35.773 | -7.094 |
| <i>Melipona scutellaris</i> | -35.585 | -6.759 |
| <i>Melipona scutellaris</i> | -35.585 | -6.761 |
| <i>Melipona scutellaris</i> | -35.571 | -6.75 |
| <i>Melipona scutellaris</i> | -35.573 | -6.734 |
| <i>Melipona scutellaris</i> | -35.57 | -6.735 |
| <i>Melipona scutellaris</i> | -35.581 | -6.744 |
| <i>Melipona scutellaris</i> | -35.591 | -6.743 |
| <i>Melipona scutellaris</i> | -35.617 | -6.726 |
| <i>Melipona scutellaris</i> | -35.586 | -6.713 |
| <i>Melipona scutellaris</i> | -34.9064 | -7.8342 |
| <i>Melipona scutellaris</i> | -34.8731 | -7.9408 |

| | | |
|-----------------------------|------------|-----------|
| <i>Melipona scutellaris</i> | -35.96 | -8.28 |
| <i>Melipona scutellaris</i> | -34.9 | -8.05 |
| <i>Melipona scutellaris</i> | -39.5511 | -7.63083 |
| <i>Melipona scutellaris</i> | -34.834902 | -7.759797 |
| <i>Melipona scutellaris</i> | -35 | -8 |
| <i>Melipona scutellaris</i> | -35.035 | -8.28667 |
| <i>Melipona scutellaris</i> | -35.4525 | -8.383056 |
| <i>Melipona scutellaris</i> | -34.8811 | -8.05389 |
| <i>Melipona scutellaris</i> | -34.95333 | -7.8125 |
| <i>Melipona scutellaris</i> | -35.01833 | -7.7675 |
| <i>Melipona scutellaris</i> | -35.0025 | -7.69139 |
| <i>Melipona scutellaris</i> | -34.86306 | -7.115 |
| <i>Melipona scutellaris</i> | -35.47028 | -8.18861 |
| <i>Melipona scutellaris</i> | -34.99139 | -7.97361 |
| <i>Melipona scutellaris</i> | -34.88083 | -8.05389 |
| <i>Melipona scutellaris</i> | -34.98389 | -7.74722 |
| <i>Melipona scutellaris</i> | -35.02389 | -7.79111 |
| <i>Melipona scutellaris</i> | -35.697 | -8.285 |
| <i>Melipona scutellaris</i> | -35.687 | -8.288 |
| <i>Melipona scutellaris</i> | -34.905 | -7.835 |
| <i>Melipona scutellaris</i> | -35.591 | -7.8 |
| <i>Melipona scutellaris</i> | -35.154 | -8.73 |
| <i>Melipona scutellaris</i> | -36.7744 | -6.5844 |
| <i>Melipona scutellaris</i> | -35.21229 | -6.478571 |
| <i>Melipona scutellaris</i> | -35.21067 | -5.80021 |
| <i>Melipona scutellaris</i> | -36.84028 | -10.21083 |
| <i>Melipona scutellaris</i> | -36.96 | -10.582 |
| <i>Melipona scutellaris</i> | -37.202 | -11.021 |
| <i>Melipona scutellaris</i> | -37.224 | -10.382 |
| <i>Melipona scutellaris</i> | -36.841 | -10.619 |
| <i>Melipona scutellaris</i> | -34.90667 | -7.83444 |

| | | |
|---|------------------|-----------------|
| <i>Melipona scutellaris</i> | -34.99944 | -7.83556 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona quadrifasciata anthidioides</i> | -49.403 | -25.586 |
| <i>Melipona quadrifasciata anthidioides</i> | -49.2731 | -25.4278 |
| <i>Melipona quadrifasciata anthidioides</i> | -49.25 | -25.41667 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.33442 | -23.96155 |
| <i>Melipona quadrifasciata anthidioides</i> | -45.409722 | -23.776667 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.9192 | -23.6039 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.63642 | -23.54855 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.69189 | -23.53377 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.6167 | -23.5333 |
| <i>Melipona quadrifasciata anthidioides</i> | -45.8464 | -23.5322 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.74142 | -23.36455 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.8667 | -23.1833 |
| <i>Melipona quadrifasciata anthidioides</i> | -44.9597 | -23.0744 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.27721 | -22.95831 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.21198 | -22.95413 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.0833 | -22.9 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.2333 | -22.9 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.30904 | -22.78604 |
| <i>Melipona quadrifasciata anthidioides</i> | -45.591389 | -22.739444 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.9167 | -22.7167 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.1961 | -22.6458 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.1844 | -22.5108 |
| <i>Melipona quadrifasciata anthidioides</i> | -44.5633 | -22.4961 |
| <i>Melipona quadrifasciata anthidioides</i> | -42.96639 | -22.41256 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.55 | -22.4 |
| <i>Melipona quadrifasciata anthidioides</i> | -44.96308 | -22.38857 |
| <i>Melipona quadrifasciata anthidioides</i> | -42.170278 | -22.320833 |
| <i>Melipona quadrifasciata anthidioides</i> | -51.170833 | -22.145833 |

| | | |
|---|------------|------------|
| <i>Melipona quadrifasciata anthidioides</i> | -46.56666 | -22.06666 |
| <i>Melipona quadrifasciata anthidioides</i> | -46 | -22 |
| <i>Melipona quadrifasciata anthidioides</i> | -43 | -22 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.5614 | -21.7878 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.4781 | -21.7103 |
| <i>Melipona quadrifasciata anthidioides</i> | -45.43465 | -21.55975 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.7044 | -21.555 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.169722 | -21.282778 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.3 | -21.27 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.81 | -21.17 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.633333 | -21.166667 |
| <i>Melipona quadrifasciata anthidioides</i> | -48.221667 | -21.009444 |
| <i>Melipona quadrifasciata anthidioides</i> | -43 | -21 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.59014 | -20.89218 |
| <i>Melipona quadrifasciata anthidioides</i> | -40.645556 | -20.805833 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.483333 | -20.433333 |
| <i>Melipona quadrifasciata anthidioides</i> | -42.9086 | -20.4164 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.50361 | -20.38528 |
| <i>Melipona quadrifasciata anthidioides</i> | -43.5081 | -20.2875 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.476667 | -20.255556 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.416667 | -20.25 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.9406 | -19.5933 |
| <i>Melipona quadrifasciata anthidioides</i> | -46.91666 | -19.58333 |
| <i>Melipona quadrifasciata anthidioides</i> | -48.277222 | -18.918611 |
| <i>Melipona quadrifasciata anthidioides</i> | -42.716667 | -16.95 |
| <i>Melipona quadrifasciata anthidioides</i> | -48.608056 | -16.658889 |
| <i>Melipona quadrifasciata anthidioides</i> | -47.9503 | -16.2525 |
| <i>Melipona quadrifasciata anthidioides</i> | -44.391389 | -15.606667 |
| <i>Melipona quadrifasciata anthidioides</i> | -44.416667 | -15.3 |
| <i>Melipona quadrifasciata anthidioides</i> | -41.772778 | -13.151389 |
| <i>Melipona quadrifasciata anthidioides</i> | -38.4192 | -12.1356 |

| | | |
|---|------------------|-----------------|
| <i>Melipona quadrifasciata anthidioides</i> | -36.6964 | -8.35778 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona quadrifasciata quadrifasciata</i> | -42.518716 | -20.668661 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.939463 | -19.576421 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.772979 | -21.219616 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.826878 | -17.111985 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -45.988024 | -16.568221 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.137358 | -22.751765 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.486355 | -20.099824 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.9232 | -20.58429 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.406108 | -20.073323 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.219158 | -21.67787 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.807312 | -20.824524 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.613113 | -18.227267 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.234989 | -17.312926 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -45.855674 | -22.656643 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -41.936085 | -18.891676 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.543372 | -19.507072 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -47.137603 | -20.46507 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.305744 | -17.063623 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -42.868825 | -17.858416 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.3175 | -21.762584 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.881538 | -19.662088 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -45.341579 | -21.974036 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.989683 | -21.245826 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.792256 | -21.842237 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -42.390363 | -18.800668 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -42.584963 | -17.221853 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.86054 | -19.994469 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.422078 | -21.124516 |

| | | |
|---|------------|------------|
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.828187 | -20.699674 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.50085 | -20.40891 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.620367 | -20.733137 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.517528 | -18.593603 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -47.292871 | -19.352112 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.299192 | -20.684196 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.560519 | -21.790654 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -42.895427 | -20.409586 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.231783 | -20.922492 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.757328 | -21.059119 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -47.441258 | -19.872685 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.37774 | -18.00977 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.248958 | -21.128688 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.340501 | -20.256077 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.385898 | -18.602601 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.821648 | -19.924736 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -47.931671 | -19.759012 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -48.241013 | -18.919765 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -45.43397 | -21.562333 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -42.880935 | -20.761664 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.414178 | -15.297227 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.305749 | -15.817017 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.365107 | -15.485426 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.249674 | -15.729156 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.395324 | -15.603638 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.855304 | -15.956929 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -45.738845 | -16.121182 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -51.23 | -30.0331 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -49 | -28 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -52.424167 | -27.163611 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -49.008333 | -26.610556 |

| | | |
|---|------------------|-----------------|
| <i>Melipona quadrifasciata quadrifasciata</i> | -49.2731 | -25.4278 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -49.25 | -25.41667 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -47.8833 | -24.7167 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.9192 | -23.6039 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -46.6361 | -23.5475 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -47.4 | -20.53 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -45.966667 | -16.566667 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -43.7106 | -16.3244 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.391389 | -15.606667 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -44.416667 | -15.3 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -38.9667 | -11.3333 |
| <i>Melipona quadrifasciata quadrifasciata</i> | -37.7011 | -10.3608 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona melanoventer</i> | -56.0967 | -15.5961 |
| <i>Melipona melanoventer</i> | -59.8 | -12.75 |
| <i>Melipona melanoventer</i> | -55.711389 | -12.545278 |
| <i>Melipona melanoventer</i> | -64.333889 | -12.434722 |
| <i>Melipona melanoventer</i> | -64.05 | -12.283333 |
| <i>Melipona melanoventer</i> | -62 | -12.116667 |
| <i>Melipona melanoventer</i> | -64.366667 | -12.05 |
| <i>Melipona melanoventer</i> | -64.316667 | -12 |
| <i>Melipona melanoventer</i> | -62.716667 | -11.933333 |
| <i>Melipona melanoventer</i> | -55.50445 | -11.86449 |
| <i>Melipona melanoventer</i> | -62.6 | -11.85 |
| <i>Melipona melanoventer</i> | -62.833333 | -11.816667 |
| <i>Melipona melanoventer</i> | -62.733333 | -11.716667 |
| <i>Melipona melanoventer</i> | -61.7 | -11.65 |
| <i>Melipona melanoventer</i> | -61.916667 | -11.6 |
| <i>Melipona melanoventer</i> | -62.844444 | -11.190556 |
| <i>Melipona melanoventer</i> | -62.765556 | -11.166944 |

| | | |
|------------------------------|-------------|-------------|
| <i>Melipona melanoventer</i> | -62.85 | -11.166667 |
| <i>Melipona melanoventer</i> | -62.740556 | -11.16 |
| <i>Melipona melanoventer</i> | -62.811667 | -11.072222 |
| <i>Melipona melanoventer</i> | -62.665278 | -11.065278 |
| <i>Melipona melanoventer</i> | -62.931667 | -11.051944 |
| <i>Melipona melanoventer</i> | -62.7 | -11.05 |
| <i>Melipona melanoventer</i> | -62.866667 | -11.016667 |
| <i>Melipona melanoventer</i> | -62.558889 | -11.014444 |
| <i>Melipona melanoventer</i> | -62.818056 | -11.001111 |
| <i>Melipona melanoventer</i> | -62.788333 | -11.001111 |
| <i>Melipona melanoventer</i> | -62.75 | -11 |
| <i>Melipona melanoventer</i> | -60.5 | -11 |
| <i>Melipona melanoventer</i> | -62.7 | -10.933333 |
| <i>Melipona melanoventer</i> | -62.485556 | -10.871667 |
| <i>Melipona melanoventer</i> | -62.583333 | -10.866667 |
| <i>Melipona melanoventer</i> | -62.45 | -10.866667 |
| <i>Melipona melanoventer</i> | -62.6109 | -10.8504333 |
| <i>Melipona melanoventer</i> | -62.571667 | -10.848889 |
| <i>Melipona melanoventer</i> | -62.4646389 | -10.8435556 |
| <i>Melipona melanoventer</i> | -64.916667 | -10.833333 |
| <i>Melipona melanoventer</i> | -62.55 | -10.8 |
| <i>Melipona melanoventer</i> | -64.683333 | -10.75 |
| <i>Melipona melanoventer</i> | -62.390833 | -10.687778 |
| <i>Melipona melanoventer</i> | -62.470833 | -10.677778 |
| <i>Melipona melanoventer</i> | -68.504444 | -10.651667 |
| <i>Melipona melanoventer</i> | -64.756389 | -10.573889 |
| <i>Melipona melanoventer</i> | -63.864444 | -10.451667 |
| <i>Melipona melanoventer</i> | -64.55 | -10.316667 |
| <i>Melipona melanoventer</i> | -66.663333 | -9.786111 |
| <i>Melipona melanoventer</i> | -66.628056 | -9.779722 |
| <i>Melipona melanoventer</i> | -66.449444 | -9.748889 |

| | | |
|-------------------------------------|------------------|-----------------|
| <i>Melipona melanoventer</i> | -65.031667 | -9.663333 |
| <i>Melipona melanoventer</i> | -61.816667 | -9.383333 |
| <i>Melipona melanoventer</i> | -63.9 | -8.76667 |
| <i>Melipona melanoventer</i> | -51 | -8 |
| <i>Melipona melanoventer</i> | -52.7028 | -6.2071 |
| <i>Melipona melanoventer</i> | -54.9372 | -2.6364 |
| <i>Melipona melanoventer</i> | -54.7 | -2.4333 |
| <i>Melipona melanoventer</i> | -45.504444 | -1.455833 |
| <i>Melipona melanoventer</i> | -48.5044 | -1.45583 |
| <i>Melipona melanoventer</i> | -48.48333 | -1.45 |
| <i>Melipona melanoventer</i> | -48.47061 | -1.43728 |
| <i>Melipona melanoventer</i> | -47.92204 | -1.2953 |
| <i>Melipona melanoventer</i> | -50.78555 | -0.51911 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona seminigra abunensis</i> | -56.0967 | -15.5961 |
| <i>Melipona seminigra abunensis</i> | -59.8 | -12.75 |
| <i>Melipona seminigra abunensis</i> | -60.1458 | -12.7406 |
| <i>Melipona seminigra abunensis</i> | -61.4 | -12.6 |
| <i>Melipona seminigra abunensis</i> | -61.216667 | -12.55 |
| <i>Melipona seminigra abunensis</i> | -61.166667 | -12.533333 |
| <i>Melipona seminigra abunensis</i> | -64.333889 | -12.434722 |
| <i>Melipona seminigra abunensis</i> | -64.233333 | -12.316667 |
| <i>Melipona seminigra abunensis</i> | -64.016667 | -12.283333 |
| <i>Melipona seminigra abunensis</i> | -64.366667 | -12.05 |
| <i>Melipona seminigra abunensis</i> | -64.316667 | -12 |
| <i>Melipona seminigra abunensis</i> | -61.983333 | -11.966667 |
| <i>Melipona seminigra abunensis</i> | -62.716667 | -11.933333 |
| <i>Melipona seminigra abunensis</i> | -64.2 | -11.9 |
| <i>Melipona seminigra abunensis</i> | -62.833333 | -11.883333 |
| <i>Melipona seminigra abunensis</i> | -62.464444 | -11.843333 |

| | | |
|-------------------------------------|------------|-------------|
| <i>Melipona seminigra abunensis</i> | -62.733333 | -11.716667 |
| <i>Melipona seminigra abunensis</i> | -62.716667 | -11.666667 |
| <i>Melipona seminigra abunensis</i> | -61.7 | -11.65 |
| <i>Melipona seminigra abunensis</i> | -61.916667 | -11.6 |
| <i>Melipona seminigra abunensis</i> | -62.844444 | -11.190556 |
| <i>Melipona seminigra abunensis</i> | -62.782778 | -11.176667 |
| <i>Melipona seminigra abunensis</i> | -62.666667 | -11.171389 |
| <i>Melipona seminigra abunensis</i> | -62.818056 | -11.168056 |
| <i>Melipona seminigra abunensis</i> | -62.765556 | -11.166944 |
| <i>Melipona seminigra abunensis</i> | -62.748889 | -11.152778 |
| <i>Melipona seminigra abunensis</i> | -62.889167 | -11.133611 |
| <i>Melipona seminigra abunensis</i> | -62.7 | -11.133333 |
| <i>Melipona seminigra abunensis</i> | -62.8 | -11.116667 |
| <i>Melipona seminigra abunensis</i> | -62.824444 | -11.112778 |
| <i>Melipona seminigra abunensis</i> | -62.840833 | -11.088611 |
| <i>Melipona seminigra abunensis</i> | -62.741944 | -11.087222 |
| <i>Melipona seminigra abunensis</i> | -62.606667 | -11.083611 |
| <i>Melipona seminigra abunensis</i> | -62.72395 | -11.0746833 |
| <i>Melipona seminigra abunensis</i> | -62.9 | -11.066667 |
| <i>Melipona seminigra abunensis</i> | -62.931667 | -11.051944 |
| <i>Melipona seminigra abunensis</i> | -62.866667 | -11.05 |
| <i>Melipona seminigra abunensis</i> | -62.7 | -11.05 |
| <i>Melipona seminigra abunensis</i> | -62.833333 | -11.033333 |
| <i>Melipona seminigra abunensis</i> | -62.866667 | -11.016667 |
| <i>Melipona seminigra abunensis</i> | -62.8 | -11.016667 |
| <i>Melipona seminigra abunensis</i> | -62.818056 | -11.001111 |
| <i>Melipona seminigra abunensis</i> | -62.788333 | -11.001111 |
| <i>Melipona seminigra abunensis</i> | -60.5 | -11 |
| <i>Melipona seminigra abunensis</i> | -62.571667 | -10.989722 |
| <i>Melipona seminigra abunensis</i> | -62.833333 | -10.983333 |
| <i>Melipona seminigra abunensis</i> | -62.666667 | -10.983333 |

| | | |
|-------------------------------------|------------|-------------|
| <i>Melipona seminigra abunensis</i> | -62.702778 | -10.969444 |
| <i>Melipona seminigra abunensis</i> | -62.681111 | -10.943611 |
| <i>Melipona seminigra abunensis</i> | -62.7 | -10.933333 |
| <i>Melipona seminigra abunensis</i> | -62.481944 | -10.930278 |
| <i>Melipona seminigra abunensis</i> | -62.634444 | -10.889167 |
| <i>Melipona seminigra abunensis</i> | -62.736944 | -10.876389 |
| <i>Melipona seminigra abunensis</i> | -62.583333 | -10.866667 |
| <i>Melipona seminigra abunensis</i> | -62.5 | -10.866667 |
| <i>Melipona seminigra abunensis</i> | -62.45 | -10.866667 |
| <i>Melipona seminigra abunensis</i> | -62.6109 | -10.8504333 |
| <i>Melipona seminigra abunensis</i> | -64.966667 | -10.85 |
| <i>Melipona seminigra abunensis</i> | -62.571667 | -10.848889 |
| <i>Melipona seminigra abunensis</i> | -62.667222 | -10.848611 |
| <i>Melipona seminigra abunensis</i> | -64.95 | -10.833333 |
| <i>Melipona seminigra abunensis</i> | -62.539444 | -10.831667 |
| <i>Melipona seminigra abunensis</i> | -62.434722 | -10.83 |
| <i>Melipona seminigra abunensis</i> | -62.290278 | -10.826944 |
| <i>Melipona seminigra abunensis</i> | -62.355556 | -10.818056 |
| <i>Melipona seminigra abunensis</i> | -64.8 | -10.8 |
| <i>Melipona seminigra abunensis</i> | -62.416389 | -10.795278 |
| <i>Melipona seminigra abunensis</i> | -62.316667 | -10.783333 |
| <i>Melipona seminigra abunensis</i> | -65.3394 | -10.7828 |
| <i>Melipona seminigra abunensis</i> | -62.433333 | -10.766667 |
| <i>Melipona seminigra abunensis</i> | -64.7 | -10.75 |
| <i>Melipona seminigra abunensis</i> | -62.3 | -10.733333 |
| <i>Melipona seminigra abunensis</i> | -62.3325 | -10.730556 |
| <i>Melipona seminigra abunensis</i> | -62.313333 | -10.716944 |
| <i>Melipona seminigra abunensis</i> | -62.415556 | -10.702778 |
| <i>Melipona seminigra abunensis</i> | -62.366667 | -10.7 |
| <i>Melipona seminigra abunensis</i> | -62.316667 | -10.683333 |
| <i>Melipona seminigra abunensis</i> | -62.470833 | -10.677778 |

| | | |
|-------------------------------------|-------------|------------|
| <i>Melipona seminigra abunensis</i> | -62.399167 | -10.656944 |
| <i>Melipona seminigra abunensis</i> | -62.370278 | -10.636389 |
| <i>Melipona seminigra abunensis</i> | -64.756389 | -10.573889 |
| <i>Melipona seminigra abunensis</i> | -67.675556 | -10.572778 |
| <i>Melipona seminigra abunensis</i> | -64.75 | -10.55 |
| <i>Melipona seminigra abunensis</i> | -64.126667 | -10.436944 |
| <i>Melipona seminigra abunensis</i> | -65.166667 | -10.366667 |
| <i>Melipona seminigra abunensis</i> | -64.166667 | -10.366667 |
| <i>Melipona seminigra abunensis</i> | -67.2 | -10.333333 |
| <i>Melipona seminigra abunensis</i> | -64.766667 | -10.316667 |
| <i>Melipona seminigra abunensis</i> | -64.55 | -10.316667 |
| <i>Melipona seminigra abunensis</i> | -62.86666 | -10.3 |
| <i>Melipona seminigra abunensis</i> | -62.767778 | -10.139444 |
| <i>Melipona seminigra abunensis</i> | -67.81 | -9.97472 |
| <i>Melipona seminigra abunensis</i> | -63.0408 | -9.91333 |
| <i>Melipona seminigra abunensis</i> | -66.602778 | -9.798889 |
| <i>Melipona seminigra abunensis</i> | -66.663333 | -9.786111 |
| <i>Melipona seminigra abunensis</i> | -65.031667 | -9.663333 |
| <i>Melipona seminigra abunensis</i> | -62.55 | -9.4 |
| <i>Melipona seminigra abunensis</i> | -62.566667 | -9.383333 |
| <i>Melipona seminigra abunensis</i> | -61.816667 | -9.383333 |
| <i>Melipona seminigra abunensis</i> | -62.6 | -9.333333 |
| <i>Melipona seminigra abunensis</i> | -62.566667 | -9.333333 |
| <i>Melipona seminigra abunensis</i> | -61.8666667 | -9.2333333 |
| <i>Melipona seminigra abunensis</i> | -64.1675 | -9.144167 |
| <i>Melipona seminigra abunensis</i> | -62.05 | -9.05 |
| <i>Melipona seminigra abunensis</i> | -54.9 | -8.95 |
| <i>Melipona seminigra abunensis</i> | -63.9 | -8.76667 |
| <i>Melipona seminigra abunensis</i> | -63.533611 | -8.392778 |
| <i>Melipona seminigra abunensis</i> | -63.539444 | -8.37 |
| <i>Melipona seminigra abunensis</i> | -63.629167 | -8.362222 |

| | | |
|-------------------------------------|------------------|-----------------|
| <i>Melipona seminigra abunensis</i> | -63.524722 | -8.333333 |
| <i>Melipona seminigra abunensis</i> | -63.372778 | -8.182222 |
| <i>Melipona seminigra abunensis</i> | -63.416667 | -6.083333 |
| <i>Melipona seminigra abunensis</i> | -63.416667 | -6 |
| <i>Melipona seminigra abunensis</i> | -63.683333 | -5.716667 |
| <i>Melipona seminigra abunensis</i> | -64.416667 | -5.666667 |
| <i>Melipona seminigra abunensis</i> | -62.133333 | -4.733333 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona flavolineata</i> | -45.2433 | -5.5056 |
| <i>Melipona flavolineata</i> | -47.4694 | -7.3328 |
| <i>Melipona flavolineata</i> | -44.302778 | -2.529722 |
| <i>Melipona flavolineata</i> | -45.38 | -3.666944 |
| <i>Melipona flavolineata</i> | -46 | -3 |
| <i>Melipona flavolineata</i> | -54.9372 | -2.6364 |
| <i>Melipona flavolineata</i> | -49.3553 | -6.1042 |
| <i>Melipona flavolineata</i> | -54.73655 | -1.94196 |
| <i>Melipona flavolineata</i> | -52.7028 | -6.2071 |
| <i>Melipona flavolineata</i> | -47.62181 | -1.1282 |
| <i>Melipona flavolineata</i> | -50.78555 | -0.51911 |
| <i>Melipona flavolineata</i> | -49 | -1 |
| <i>Melipona flavolineata</i> | -45.504444 | -1.455833 |
| <i>Melipona flavolineata</i> | -51.116667 | -7.8 |
| <i>Melipona flavolineata</i> | -51 | -8 |
| <i>Melipona flavolineata</i> | -47.261077 | -0.762454 |
| <i>Melipona flavolineata</i> | -48.47061 | -1.43728 |
| <i>Melipona flavolineata</i> | -49.514963 | -8.110276 |
| <i>Melipona flavolineata</i> | -49.58333 | -2.55 |
| <i>Melipona flavolineata</i> | -48.5044 | -1.45583 |
| <i>Melipona flavolineata</i> | -51.90361 | -7.73222 |
| <i>Melipona flavolineata</i> | -50.47472 | -7.44972 |

| | | |
|------------------------------|------------------|-----------------|
| <i>Melipona flavolineata</i> | -51.94028 | -6.61 |
| <i>Melipona flavolineata</i> | -50.44833 | -7.29889 |
| <i>Melipona flavolineata</i> | -50.7875 | -6.16361 |
| <i>Melipona flavolineata</i> | -50.53944 | -7.41639 |
| <i>Melipona flavolineata</i> | -51.86167 | -7.54111 |
| <i>Melipona flavolineata</i> | -52.6273 | -9.7192 |
| <i>Melipona flavolineata</i> | -68.5044 | -10.6517 |
| <i>Melipona flavolineata</i> | -56.798056 | -3.651667 |
| <i>Melipona flavolineata</i> | -56.936944 | -3.400556 |
| <i>Melipona flavolineata</i> | -48.48333 | -1.45 |
| <i>Melipona flavolineata</i> | -51.06642 | 0.03857 |
| <i>Melipona flavolineata</i> | -59.86526 | 3.330791 |
| <i>Melipona flavolineata</i> | -61.872656 | -3.461709 |
| <i>Melipona flavolineata</i> | -65.451058 | -3.767182 |
| <i>Melipona flavolineata</i> | -64.098248 | -4.814519 |
| <i>Melipona flavolineata</i> | -59.821621 | -10.007566 |
| <i>Melipona flavolineata</i> | -61.829017 | -9.527536 |
| <i>Melipona flavolineata</i> | -63.312745 | -9.702092 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona fasciculata</i> | -43.21666 | -5.15 |
| <i>Melipona fasciculata</i> | -47.461449 | -5.525943 |
| <i>Melipona fasciculata</i> | -43.4036 | -3.2078 |
| <i>Melipona fasciculata</i> | -44.3028 | -2.5297 |
| <i>Melipona fasciculata</i> | -47.469167 | -7.332778 |
| <i>Melipona fasciculata</i> | -45 | -3 |
| <i>Melipona fasciculata</i> | -44.763333 | -3.453611 |
| <i>Melipona fasciculata</i> | -45.243333 | -5.505556 |
| <i>Melipona fasciculata</i> | -45.481111 | -7.021667 |
| <i>Melipona fasciculata</i> | -43.885556 | -4.455278 |
| <i>Melipona fasciculata</i> | -44.829291 | -2.698267 |

| | | |
|-----------------------------|------------|------------|
| <i>Melipona fasciculata</i> | -55.5 | -1.276666 |
| <i>Melipona fasciculata</i> | -52.476978 | -10.030804 |
| <i>Melipona fasciculata</i> | -54.7 | -2.4333 |
| <i>Melipona fasciculata</i> | -51.2333 | -0.51666 |
| <i>Melipona fasciculata</i> | -55.51729 | -1.90486 |
| <i>Melipona fasciculata</i> | -54.9 | -8.95 |
| <i>Melipona fasciculata</i> | -48.47061 | -1.43728 |
| <i>Melipona fasciculata</i> | -49.46832 | -8.09532 |
| <i>Melipona fasciculata</i> | -57.553701 | -7.166773 |
| <i>Melipona fasciculata</i> | -48 | -1 |
| <i>Melipona fasciculata</i> | -51.116667 | -7.8 |
| <i>Melipona fasciculata</i> | -55.966667 | -4.21667 |
| <i>Melipona fasciculata</i> | -55.116667 | -3.083333 |
| <i>Melipona fasciculata</i> | -51 | -8 |
| <i>Melipona fasciculata</i> | -47.366667 | -8.483333 |
| <i>Melipona fasciculata</i> | -47.266667 | -9.533333 |
| <i>Melipona fasciculata</i> | -50.664773 | -11.576884 |
| <i>Melipona fasciculata</i> | -51.42469 | -0.74489 |
| <i>Melipona fasciculata</i> | -56.40458 | -3.4844 |
| <i>Melipona fasciculata</i> | -56.13417 | -1.50139 |
| <i>Melipona fasciculata</i> | -43.06802 | -3.39856 |
| <i>Melipona fasciculata</i> | -43.02983 | -3.41148 |
| <i>Melipona fasciculata</i> | -43.01623 | -3.42353 |
| <i>Melipona fasciculata</i> | -43.01967 | -3.11397 |
| <i>Melipona fasciculata</i> | -43.0105 | -3.34829 |
| <i>Melipona fasciculata</i> | -43.01473 | -3.32214 |
| <i>Melipona fasciculata</i> | -43.03873 | -3.30921 |
| <i>Melipona fasciculata</i> | -43.08707 | -3.35422 |
| <i>Melipona fasciculata</i> | -43.11134 | -3.34346 |
| <i>Melipona fasciculata</i> | -43.13724 | -3.36871 |
| <i>Melipona fasciculata</i> | -43.18536 | -3.34839 |

| | | |
|-----------------------------|------------|------------|
| <i>Melipona fasciculata</i> | -43.16751 | -3.37337 |
| <i>Melipona fasciculata</i> | -43.17064 | -3.43923 |
| <i>Melipona fasciculata</i> | -43.16276 | -3.46211 |
| <i>Melipona fasciculata</i> | -43.18087 | -3.28284 |
| <i>Melipona fasciculata</i> | -43.16853 | -3.29832 |
| <i>Melipona fasciculata</i> | -43.16574 | -3.32129 |
| <i>Melipona fasciculata</i> | -43.14644 | -3.33286 |
| <i>Melipona fasciculata</i> | -43.15867 | -3.34903 |
| <i>Melipona fasciculata</i> | -43.1734 | -3.47665 |
| <i>Melipona fasciculata</i> | -43.16761 | -3.49447 |
| <i>Melipona fasciculata</i> | -43.18955 | -3.46553 |
| <i>Melipona fasciculata</i> | -43.21839 | -3.43727 |
| <i>Melipona fasciculata</i> | -43.34309 | -3.41478 |
| <i>Melipona fasciculata</i> | -43.10724 | -3.39253 |
| <i>Melipona fasciculata</i> | -43.28658 | -3.34879 |
| <i>Melipona fasciculata</i> | -43.31901 | -3.47478 |
| <i>Melipona fasciculata</i> | -43.32764 | -3.37629 |
| <i>Melipona fasciculata</i> | -43.20204 | -3.36474 |
| <i>Melipona fasciculata</i> | -43.05471 | -3.33011 |
| <i>Melipona fasciculata</i> | -43.3747 | -3.37081 |
| <i>Melipona fasciculata</i> | -43.36606 | -3.34674 |
| <i>Melipona fasciculata</i> | -43.19709 | -3.05021 |
| <i>Melipona fasciculata</i> | -43.21693 | -3.06954 |
| <i>Melipona fasciculata</i> | -55.98333 | -14.8333 |
| <i>Melipona fasciculata</i> | -49.6575 | -14.257778 |
| <i>Melipona fasciculata</i> | -55.5 | -12.76666 |
| <i>Melipona fasciculata</i> | -55.45624 | -11.85928 |
| <i>Melipona fasciculata</i> | -57.966667 | -2.55 |
| <i>Melipona fasciculata</i> | -55.86389 | -1.76528 |
| <i>Melipona fasciculata</i> | -48.5044 | -1.45583 |
| <i>Melipona fasciculata</i> | -48.48333 | -1.45 |

| | | |
|-----------------------------|------------------|-----------------|
| <i>Melipona fasciculata</i> | -51.83333 | 3.83333 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona amazonica</i> | -67.8 | -9.97 |
| <i>Melipona amazonica</i> | -62.93333 | -7.31667 |
| <i>Melipona amazonica</i> | -52.7028 | -6.2071 |
| <i>Melipona amazonica</i> | -55.5189 | -1.9083 |
| <i>Melipona amazonica</i> | -60.025 | -3.10194 |
| <i>Melipona amazonica</i> | -49.3553 | -6.1042 |
| <i>Melipona amazonica</i> | -56.85 | -1.416667 |
| <i>Melipona amazonica</i> | -51 | -8 |
| <i>Melipona amazonica</i> | -63.903333 | -8.762222 |
| <i>Melipona amazonica</i> | -58.4442 | -3.14306 |
| <i>Melipona amazonica</i> | -58.833333 | -3.033333 |
| <i>Melipona amazonica</i> | -56.7131 | -2.18611 |
| <i>Melipona amazonica</i> | -67.929944 | -1.955667 |
| <i>Melipona amazonica</i> | -62.983333 | -1.616667 |
| <i>Melipona amazonica</i> | -60.344181 | -2.44097 |
| <i>Melipona amazonica</i> | -63.779132 | -10.479584 |
| <i>Melipona amazonica</i> | -49.641285 | -3.866865 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona subnitida</i> | -35.7353 | -9.66583 |
| <i>Melipona subnitida</i> | -38.214722 | -9.406111 |
| <i>Melipona subnitida</i> | -38.5431 | -3.7172 |
| <i>Melipona subnitida</i> | -38.852639 | -6.398923 |
| <i>Melipona subnitida</i> | -38.683866 | -3.902595 |
| <i>Melipona subnitida</i> | -41.025389 | -3.953524 |
| <i>Melipona subnitida</i> | -40.382856 | -6.615561 |
| <i>Melipona subnitida</i> | -39.268889 | -3.277778 |
| <i>Melipona subnitida</i> | -37.825368 | -4.718338 |

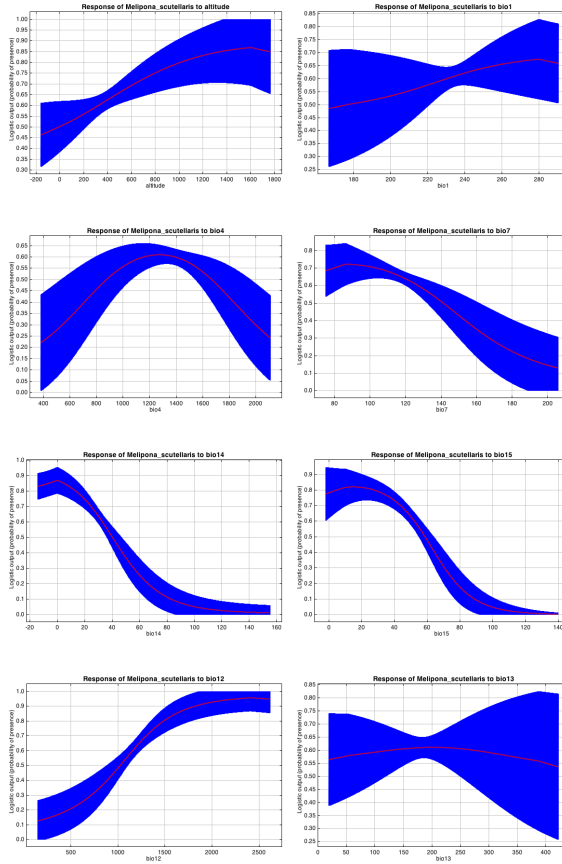
| | | |
|---------------------------|------------|-----------|
| <i>Melipona subnitida</i> | -40.342341 | -3.524108 |
| <i>Melipona subnitida</i> | -38.129371 | -5.245467 |
| <i>Melipona subnitida</i> | -39.437037 | -5.538987 |
| <i>Melipona subnitida</i> | -40.500857 | -3.209658 |
| <i>Melipona subnitida</i> | -37.847284 | -5.09967 |
| <i>Melipona subnitida</i> | -39.267231 | -3.79075 |
| <i>Melipona subnitida</i> | -40.612613 | -4.114576 |
| <i>Melipona subnitida</i> | -38.371226 | -5.737431 |
| <i>Melipona subnitida</i> | -38.760806 | -5.479112 |
| <i>Melipona subnitida</i> | -38.968973 | -3.609325 |
| <i>Melipona subnitida</i> | -40.671296 | -6.264451 |
| <i>Melipona subnitida</i> | -40.786527 | -5.587156 |
| <i>Melipona subnitida</i> | -38.931402 | -4.262719 |
| <i>Melipona subnitida</i> | -38.130556 | -4.179722 |
| <i>Melipona subnitida</i> | -39.350153 | -6.482583 |
| <i>Melipona subnitida</i> | -41.092054 | -3.56495 |
| <i>Melipona subnitida</i> | -40.383056 | -3.913333 |
| <i>Melipona subnitida</i> | -39.093961 | -4.190375 |
| <i>Melipona subnitida</i> | -38.460093 | -6.044188 |
| <i>Melipona subnitida</i> | -40.319162 | -3.660625 |
| <i>Melipona subnitida</i> | -39.524007 | -6.078198 |
| <i>Melipona subnitida</i> | -38.728324 | -4.222967 |
| <i>Melipona subnitida</i> | -40.293546 | -6.004026 |
| <i>Melipona subnitida</i> | -38.881324 | -4.332603 |
| <i>Melipona subnitida</i> | -39.297665 | -5.193745 |
| <i>Melipona subnitida</i> | -38.604995 | -3.932446 |
| <i>Melipona subnitida</i> | -36.9186 | -6.87222 |
| <i>Melipona subnitida</i> | -36.578 | -7.068 |
| <i>Melipona subnitida</i> | -37.28 | -7.02444 |
| <i>Melipona subnitida</i> | -34.9064 | -7.8342 |
| <i>Melipona subnitida</i> | -36.7744 | -6.5844 |

| | | |
|---------------------------|------------------|-----------------|
| <i>Melipona subnitida</i> | -37.1369 | -4.9561 |
| <i>Melipona subnitida</i> | -37.34389 | -5.18778 |
| <i>Melipona subnitida</i> | -37.344167 | -5.1875 |
| <i>Melipona subnitida</i> | -35.21067 | -5.80021 |
| <i>Melipona subnitida</i> | -37.97417 | -9.3425 |
| <i>Melipona subnitida</i> | -34.86306 | -7.115 |
| <i>Melipona subnitida</i> | -34.99139 | -7.97361 |
| <i>Melipona subnitida</i> | -35.12583 | -6.83833 |
| | | |
| Species | Longitude | Latitude |
| <i>Melipona paraensis</i> | -66.9 | -0.133333 |
| <i>Melipona paraensis</i> | -66.816667 | -0.216667 |
| <i>Melipona paraensis</i> | -66.433333 | -0.433333 |
| <i>Melipona paraensis</i> | -66.283333 | -0.366667 |
| <i>Melipona paraensis</i> | -65.583333 | -1.883333 |
| <i>Melipona paraensis</i> | -65.0192 | -0.413889 |
| <i>Melipona paraensis</i> | -64.083056 | -0.316667 |
| <i>Melipona paraensis</i> | -62.883333 | -0.4 |
| <i>Melipona paraensis</i> | -62.716667 | -1.116667 |
| <i>Melipona paraensis</i> | -62.204444 | -1.305833 |
| <i>Melipona paraensis</i> | -62.183889 | -1.316389 |
| <i>Melipona paraensis</i> | -61.883333 | -4.416667 |
| <i>Melipona paraensis</i> | -61.373056 | -3.898333 |
| <i>Melipona paraensis</i> | -61.241667 | 1.45 |
| <i>Melipona paraensis</i> | -61.219444 | -2.1075 |
| <i>Melipona paraensis</i> | -60.533333 | -3.033333 |
| <i>Melipona paraensis</i> | -60.025 | -3.101944 |
| <i>Melipona paraensis</i> | -58.35 | -8.55 |
| <i>Melipona paraensis</i> | -57.033333 | -1.066667 |
| <i>Melipona paraensis</i> | -56.85 | -1.416667 |
| <i>Melipona paraensis</i> | -55.966667 | -4.216667 |

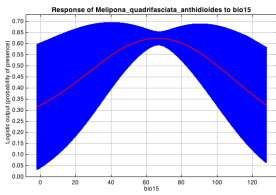
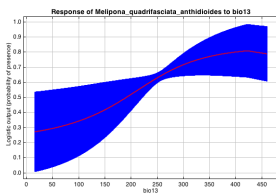
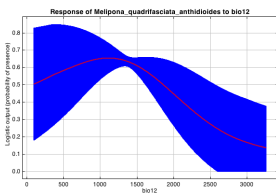
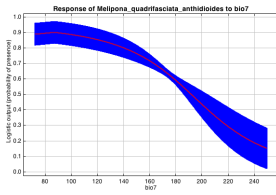
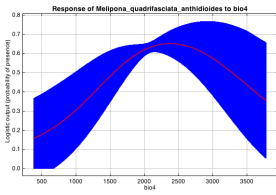
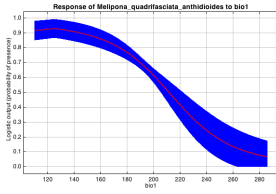
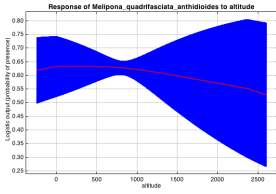
| | | |
|---------------------------|------------|-----------|
| <i>Melipona paraensis</i> | -52.7028 | -6.2071 |
| <i>Melipona paraensis</i> | -52 | -1.12 |
| <i>Melipona paraensis</i> | -51.90361 | -7.73222 |
| <i>Melipona paraensis</i> | -51.836 | 3.8322 |
| <i>Melipona paraensis</i> | -50.47472 | -7.44972 |
| <i>Melipona paraensis</i> | -47.616667 | -1.116667 |
| <i>Melipona paraensis</i> | -66.148028 | -0.283119 |
| <i>Melipona paraensis</i> | -63.99014 | -8.501975 |
| <i>Melipona paraensis</i> | -66.408211 | -0.422025 |
| <i>Melipona paraensis</i> | -61.7846 | -0.509015 |

6. Response curves from final models

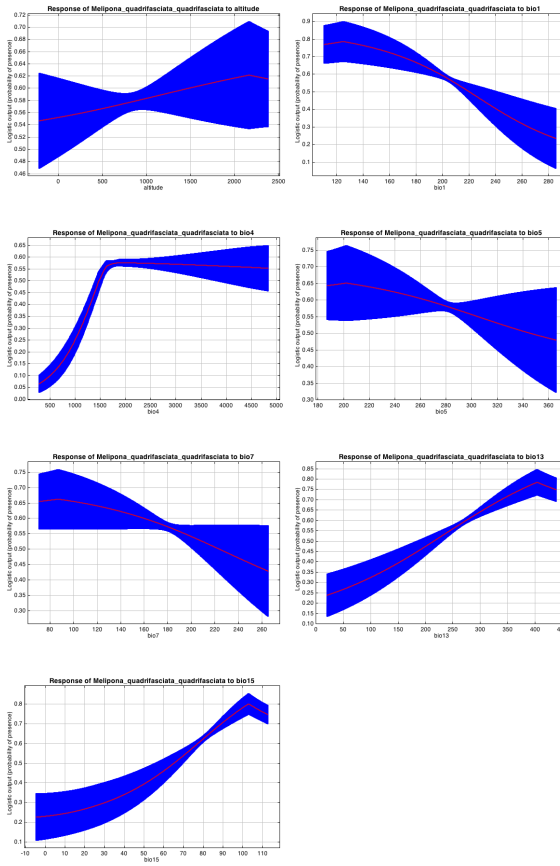
M. scutellaris



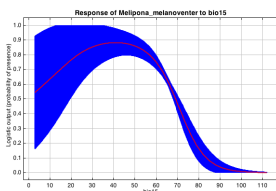
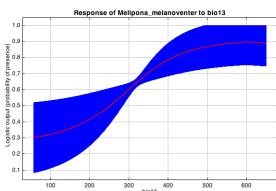
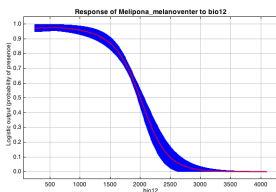
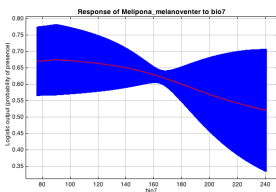
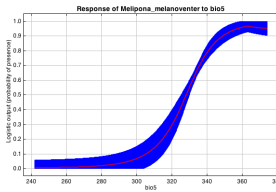
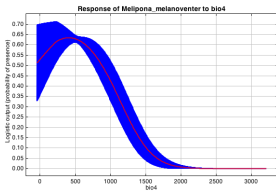
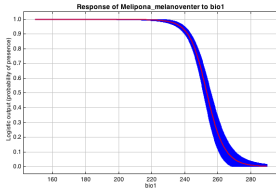
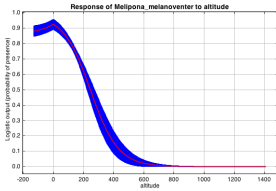
M. q. anthidioides

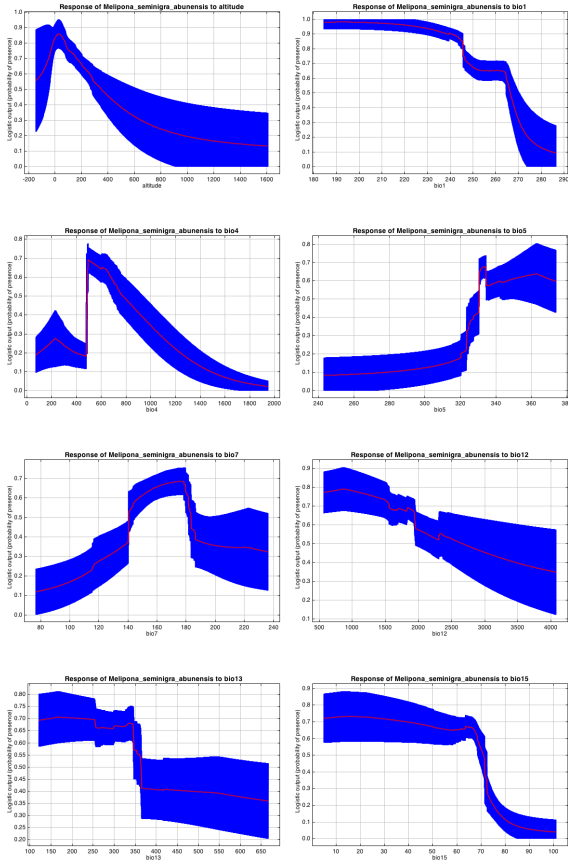


M. q. quadrifasciata

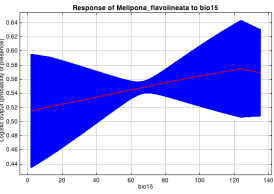
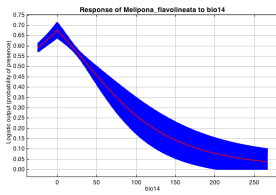
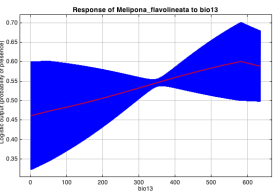
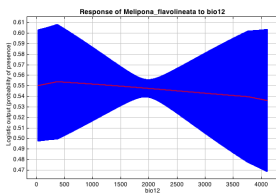
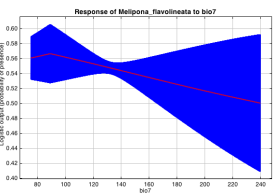
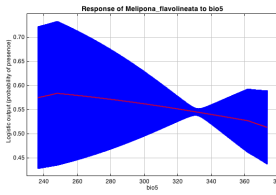
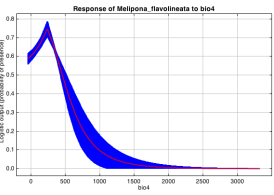
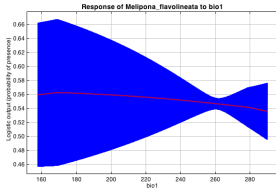
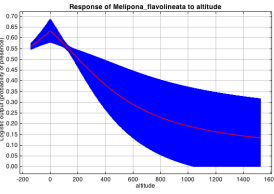


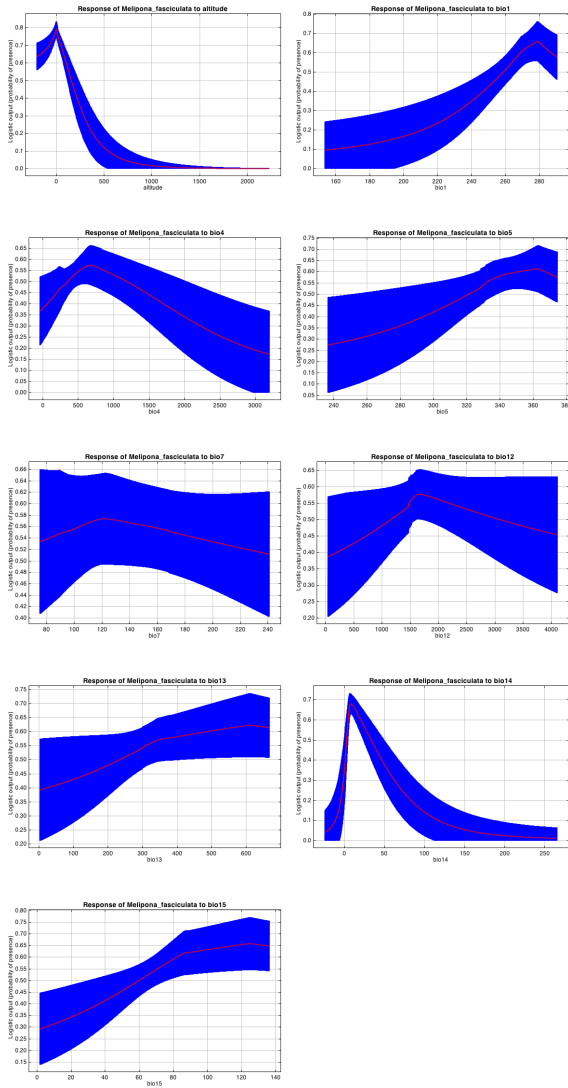
M. melanoventer



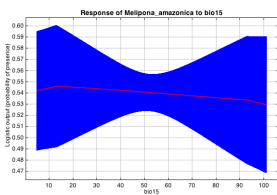
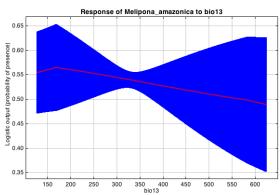
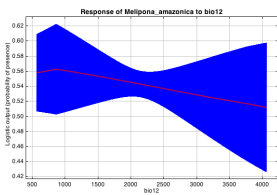
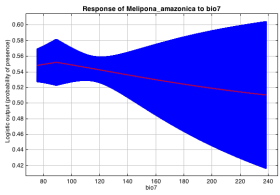
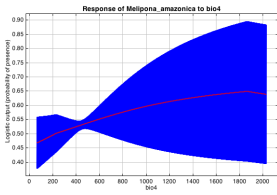
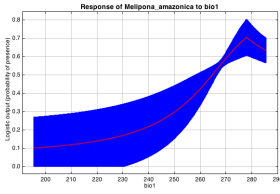
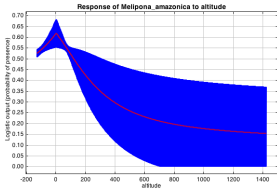
M. s. abunensis

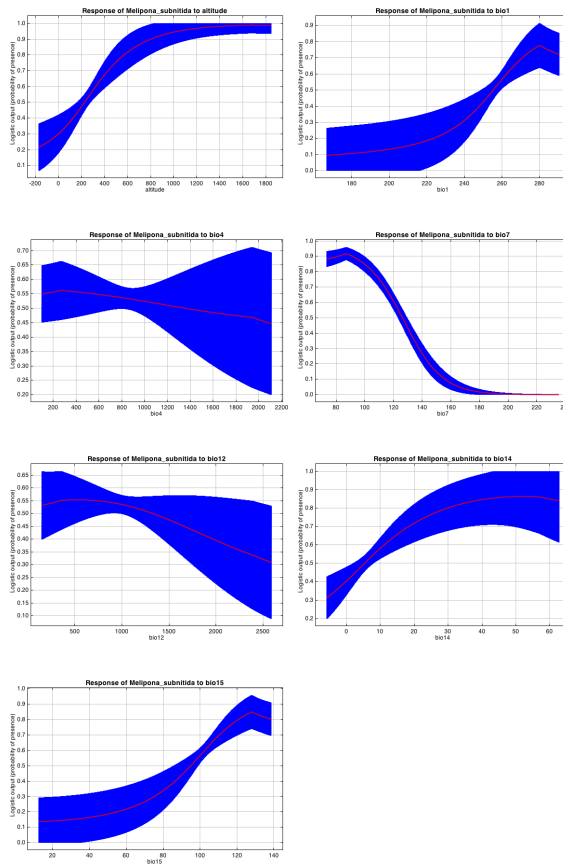
M. flavolineata



M. fasciculata

M. amazonica



M. subnitida

M. paraensis

