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Considerações sobre a biodiversidade de abelhas brasileiras: Vícios de coleta, distribuições potenciais e fragmentação

Orientador: Prof. Dr. Paulo De Marco Jr.

Candidato: Daniel de Paiva Silva

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Considerações sobre a biodiversidade de abelhas brasileiras:

Vícios de coleta, distribuições potenciais e fragmentação

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"Só se pode alcançar um grande êxito quando nos mantemos fiéis a nós mesmos."
Friedrich Nietzche

"Se vais por um caminho que suas mãos constroem dia após dia, chegarás no lugar onde deves estar."
Máximas de Ani

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SUMÁRIO

RESUMO GERAL

O mundo vive rápidas e intensas mudanças ambientais intimamente relacionadas às atividades humanas e que, direta ou indiretamente, estão relacionadas à atual crise de biodiversidade. Assim, a existência de dados biológicos, ecológicos e distribucionais de qualidade é de extrema importância dar suporte a tomada de ações práticas de conservação. Entretanto, os déficits Linneanos (falta de dados taxonômicos) e Wallaceanos (falta de dados distribucionais) são importantes problemas que impedem a efetiva tomada de decisões conservacionistas. Neste contexto, dados provenientes de museus e coleções, após cuidadosa filtragem, são excelentes para apoiarem tais ações. Em geral, esta informação é enviesada e necessita de cuidado adequado antes de ser utilizada. Espécies de artrópodes e insetos são sub amostrados, impedindo sua utilização em propostas práticas de conservação utilizadas na Biogeografia da Conservação. Neste cenário, mesmo grupos cuja ecologia e biologia são bem conhecidas, acabam não sendo utilizados. Apesar disso, o advento de novas ferramentas computacionais aliados a boas teorias e bons dados de distribuição das espécies de insetos, é possível a contemplação do uso de vários grupos entomológicos em ações concretas de conservação. Assim, na primeira parte da presente tese, considerando abelhas do gênero *Megachile* (Capítulo 1) e da tribo Meliponini (Capítulo 2), nós analisamos os eventuais vícios de amostragem existentes nos dados de ocorrência das espécies destes gêneros, descrevendo o estado atual do conhecimento da distribuição destas abelhas e áreas para potenciais amostragens futuras. Os déficits Wallaceanos são frequentemente utilizados como justificativa para a realização de novos inventários biológicos. Deste modo, na segunda parte desta tese, nós utilizamos novas ocorrências de duas espécies de abelhas (*Agale caerulea* (Apidae: Euglossini) – Capítulo 3; e a espécie invasora *Lithurgus huberi* (Apidae: Lithurgini) – Capítulo 4) com abordagens de modelagens de distribuição

potencial para predizer suas distribuições e indicar locais ideias para novas coletas. Na terceira e última parte desta tese, considerando-se uma escala espacial mais regional, nós consideramos questões de perda de habitats e fragmentação sobre a biodiversidade de abelhas do Cerrado goiano. No capítulo 5, nós avaliamos os efeitos da quantidade de habitat e isolamento sobre duas espécies de abelhas das orquídeas do Cerrado (*Elaema nigrita* e *Eufriesea auriceps*), que, aparentemente não são afetadas pelo aumento de áreas antrópicas no bioma. Por fim, no último capítulo (Capítulo 6), nós avaliamos a resposta de toda a comunidade de abelhas coletadas em áreas de Cerrado de Goiás, bem como a resposta das espécies de grupos de abelhas solitárias e eusociais, à estrutura da paisagem dos nossos pontos de coletas, em diferentes escalas espaciais locais.

Palavras-chaves: Abelhas; fragmentação de paisagens; perda de habitat; modelos de distribuição potencial; Vícios de amostragem.

ABSTRACT

The world we live in faces fast and intense environmental changes, deeply related to human activities, which directly or indirectly are related to the current biodiversity crisis. Thus, the existence of quality biological, ecological, and distributional data is of utmost importance for the support of active conservation practices. Nonetheless, both Linnean (lack of taxonomical data) and Wallacean (lack of distributional data) shortfalls are important setbacks hindering the effectiveness of conservationist decisions. The data harbored in museums and overall collections is excellent to support conservational measures. Nonetheless, usually this data is biased and needs to be adequately filtered before being used. Insect and arthropod species are under sampled, what impedes them to be properly considered under Conservation Biogeography frameworks. In such scenario, even insect groups with relatively known biology and ecology are neglected in practical conservation actions. Despite that, with the advent of new computational tools allied with good theories and good distributional data of insect species, it is possible to contemplate those biological groups in concrete and efficient conservation actions. Therefore, in the first part of this thesis, considering bees from the *Megachile* genus (Chapter 1) and from the Meliponini tribe (Chapter 2), we evaluated potential biases affecting those data, but also evaluate potential areas for new field surveys. The Wallacean shortfalls are commonly used to justify the implementation of new field surveys. Therefore, in the second part of this thesis, we used the new occurrences of the bee species [*Aglae caerulea* (Apidae: Eulgossini) – Chapter 3; and the exotic species, *Lithurgus huberi* (Apidae: Lithurgini) – Chapter 4] allied with distribution modelling to predict these species potential distributions and indicate areas for future new samplings. On the third and last part of the thesis, we considered a regional spatial scale and habitat loss and fragmentation questions to address their effects on the bee biodiversity from

the Cerrado biome found within the Goiás state. In Chapter 5, we evaluated the effects of anthropic areas amount and their isolation on two orchid-bee species from the Cerrado (*Eulaema nigrita* and *Eufriesea auriceps*), which apparently are not affected by the increase of anthropic areas in this biome. Later, in the last chapter (Chapter 6), we evaluated the response of all bee community we sampled in Cerrado areas within state of Goiás, as well as the sub groups of eusocial and solitary species, to the landscape structure of our sampling areas, considering different local spatial scales.

Key-words: Bees; landscape fragmentation; habitat loss; species distribution modeling; sampling biases.

INTRODUÇÃO GERAL*

O mundo atual passa por rápidas mudanças ambientais, majoritariamente relacionadas às atividades humanas (Millenium Ecosystem Assessment, 2005), de modo que as taxas de extinção atuais são comparáveis àquelas já observadas em grandes eventos passados de extinção (Barnosky *et al.* 2011; Pimm *et al.* 1995). Processos direta ou indiretamente relacionados às alterações de origem antrópica, como a invasão de espécies exóticas, deposição de compostos nitrogenados no solo e corpos d'água, perda de hábitats, intensificação da agricultura e a fragmentação de paisagens constituem-se nas maiores ameaças atuais à biodiversidade (Millenium Ecosystem Assessment 2005; Tylianakis et al. 2008). Adicionalmente, a contínua e elevada emissão de gases de efeito estufa na atmosfera terrestre e as mudanças climáticas consequentes também são tidas como sérias ameaças à biodiversidade mundial (Parmesan 2006; Schweiger *et al.* 2012; Thomas *et al.* 2004; Tylianakis *et al.* 2008).

Neste sentido, bons dados relativos à biologia, ecologia, história natural e distribuição espacial das espécies são de extrema importância para auxiliar tanto biólogos da conservação como tomadores de decisão na implementação de ações práticas de conservação (Balmford *et al.* 1996; Bini *et al.* 2006; Cabeza *et al.* 2004; Margules & Pressey 2000; Pinto & Grelle 2009; Rodrigues *et al.* 2004; Sarkar *et al.* 2006; Whittaker *et al.* 2005;). A falta de tais dados constitui uma das maiores justificativas para a instauração de novos programas de coletas padronizadas de biodiversidade. Apesar disto, dados confiáveis e de qualidade relativos à (1) taxonomia, (2) distribuição dos organismos (respectivamente, os déficits Linneanos e Wallaceanos; Brown & Lomolino 1998; Whittaker *et al.* 2005), (3) abundância das espécies e suas

* Formatada segundo as normas da revista *Natureza & Conservação*.

variações no tempo e espaço, (4) sua sensitividade a alterações de hábitats (respectivamente, os déficits Prestoniano e Hutchinsoniano; Cardoso *et al.* 2011), ou mesmo (5) informações sobre suas relações filogenéticas com outras espécies do grupo (o déficit Darwiniano; Diniz-Filho *et al.* 2013) são escassas.

Na direção contrária a estes problemas, o uso de informações provenientes em museus e coleções podem contribuir diretamente para a conservação da biodiversidade, indicando os locais onde os recursos financeiros garantirão uma maior proteção às espécies (Funk & Richardson 2002; Graham *et al.* 2004). Entretanto, estes dados sempre necessitam ser utilizados com cuidado, uma vez que possuem muitos vícios intrínsecos (Graham *et al.* 2004; Newbold 2010; Pyke & Ehrlich 2010; Reddy & Davalos 2003). Usualmente, as informações sobre as ocorrências de biodiversidade não são aleatoriamente distribuídas no espaço geográfico (Sastre & Lobo 2009) e ocorrem frequentemente mais próximos a estradas e a margens de rios e riachos, ou mesmo próximo às zonas de atuação de pesquisadores e suas instituições de pesquisa, cidades ou dentro de limites geopolíticos (estados ou países), que não possuem real significado biológico (Farber & Kadmon 2003; Graham *et al.* 2004; Newbold 2010; Pyke & Ehrlich 2010; Reddy & Davalos 2003; Whittaker *et al.* 2005).

Adicionalmente, estes dados também são viciados em direção a determinados grupos de organismos, em geral aqueles carismáticos, espécies guarda-chuva e/ou espécies-chave, em detrimento a grupos biológicos menos carismáticos (Cardoso *et al.* 2011; Diniz-Filho *et al.* 2010; Newbold 2010). Por fim, estes dados podem não ser os mais atuais ou precisos, havendo importantes problemas relacionados à sua identificação taxonômica que afetam sua qualidade (De Giovanni *et al.* 2012; Graham *et al.* 2004). Apesar destes problemas, quando devidamente controlados e aliados a abordagens teóricas (e.g. nicho Grinelliano, conservação de nicho, abordagem de táxons

superiores, medidas alternativas [*surrogates*] da biodiversidade, modelos de distribuição potencial de espécies), estes dados são de valor incalculável e podem oferecer grandes auxílios à futuras ações relacionadas à priorização espacial voltada à conservação de espécies (Margules & Pressey 2000; Graham *et al.* 2004).

Os insetos (e invertebrados, em geral), apesar de seu importantíssimo papel ecológico, sendo responsáveis pela manutenção de diversas funções e processos ecológicos (Losey & Vaughan 2006; Wilson 1987), são usualmente um dos grupos biológicos mais negligenciados em programas relacionados à biogeografia da conservação (Cardoso *et al.* 2011; Diniz-Filho *et al.* 2010; Zamin *et al.* 2010). Mesmo grupos com uma maior disponibilidade de conhecimentos relativos à sua biologia e ecologia (formigas, borboletas, abelhas) possuem sérias restrições quanto à quantidade de dados disponíveis para a implementação de ações práticas de conversação (Diniz-Filho *et al.* 2010). Tomando-se como exemplo as abelhas brasileiras, atualmente são conhecidas e devidamente validadas taxonomicamente em torno de 1.500-1.700 espécies (de um total estimado de aproximadamente 3.000; Silveira *et al.* 2002). Entretanto, após criteriosa avaliação por especialistas, somente três deles, cujos dados ecológicos possibilitavam tal análise, foram inclusas na Lista de Espécies da Fauna Brasileira Ameaçadas de Extinção (MMA 2003). O que sugere que nossas informações sobre as espécies ainda são muito escassas, impedindo que reflitam o real nível de ameaça que o grupo biológico sofre.

Abelhas e outros organismos polinizadores são responsáveis por aproximadamente 35% da produção mundial de alimentos (Klein *et al.* 2007) e também são responsáveis pela manutenção das populações de várias espécies de plantas nativas (Kearns *et al.* 1998). Dentre estes organismos, as abelhas são os que possuem maior importância ecológica (Losey & Vaughan 2006), tanto pela diversidade de espécies

quanto pelas variadas estratégias de história de vida (Michener 2007). Estes insetos são responsáveis diretos por expressivos incrementos na produção de determinadas culturas agrícolas como o café (De Marco Jr & Coelho 2004; Klein *et al.* 2003; Ricketts *et al.* 2004), girassol (Greenleaf & Kremen 2006a), tomate (Greenleaf & Kremen 2006b) e muitas outras culturas agrícolas em todo mundo (Klein *et al.* 2007). Apesar disso, ultimamente sua conservação tem atraído grande atenção, uma vez que impactos antrópicos, como a perda de hábitat e a fragmentação de paisagens (Bartomeus *et al.* 2013; Burkle *et al.* 2013; Cameron *et al.* 2011; Kennedy *et al.* 2013; Kevan & Phillips 2001; Winfree *et al.* 2009), a intensificação da agricultura (Brittain *et al.* 2010) e o aumento do uso de pesticidas (Stokstad 2013) são tidos como grandes causadores da atual perda de abelhas e suposta da crise de polinização (Biesmeijer *et al.* 2006; Ghazoul 2005; Kearns *et al.* 1998). Este cenário torna-se ainda mais preocupante devido à maior demanda da população humana por alimentos polinizados por agentes biológicos, que não tem sido acompanhada na mesma intensidade pelo aumento no estoque mundial de colônias comerciais de abelhas (em especial *Apis mellifera*) não tem aumentado na mesma intensidade (Aizen & Harder 2009).

Considerando-se a importância ecológica das abelhas, no ***Capítulo 1*** avaliamos os potenciais vícios de coleta em uma escala espacial ampla relacionados ao gênero *Megachile*, que compõe um dos maiores grupos taxonômicos existentes em Apoidea. Entretanto, as abelhas deste gênero usualmente são muito difíceis de identificar e, de forma geral, o grupo todo necessita de uma urgente revisão taxonômica (Silveira *et al.* 2002). Apesar destas limitações e da pequena quantidade de dados de distribuição disponíveis, nós descrevemos alguns dos vícios existentes no banco de dados obtido e usando técnicas de modelagem de distribuição potencial de espécies, indicamos áreas adequadas, mas sub amostradas que deveriam ser foco de futuras coletas destas abelhas.

No ***Capítulo* 2**, ainda considerando-se macro escalas, nós utilizamos o grupo de abelhas sem-ferrão da tribo Meliponini, com diferentes características ecológicas e biológicas e gêneros melhor revisados taxonomicamente, para descrever os potenciais vícios existentes nos dados de distribuição disponíveis para estas abelhas. Nestes dois primeiros capítulos, à parte das questões empíricas e lacunas de conhecimento distribucionais, nossas hipóteses abordam questões relacionadas a substitutos de biodiversidade. Assumindo-se que as espécies relacionadas (taxonomicamente, filogeneticamente) co-ocorrentes em determinada área requerem recursos de forma semelhante por um possuírem um nicho ecológico conservado (Wiens & Graham, 2005), espera-se que a riqueza de espécies de grupos taxonomicamente superiores (p.ex. gêneros) podem ser substitutos da riqueza de espécies dos grupos taxonomicos inferiores (p.ex. espécies; Balmford *et al.*, 1996a; 1996b; 2000).

Apesar de tantos obstáculos ao uso de dados entomológicos em abordagens relacionadas à biogeografia da conservação, Diniz-Filho *et al.* (2010) e Cardoso *et al.* (2011) possuem visões muito otimistas de como utilizar a enorme quantidade de informações entomológicas, existente em museus, coleções, e bancos de dados digitais em abordagens macroecológicas. Assim, utilizando-se dos seus argumentos, provocações e incentivos, nos ***Capítulos 3*** e ***Capítulo 4***, utilizamos novas informações relativas à distribuição de abelhas que coletamos no Cerrado goiano [respectivamente, *Aglae caerulea* (Apidae: Euglossinae) e *Lithurgus huberi* (Apidae: Megachilinae)] para descrever suas distribuições potenciais e áreas para potenciais coletas futuras de dados. Nestes capítulos, consideramos o nicho das espécies amodeladas em um senso Grinnelliano (Grinnell 1924; Soberón 2007). Segundo esta teoria, apesar da distribuição de uma dada espécie em determinada área em parte depender de interações biológicas e a disponibilidade de recursos, segundo o nicho Grinnelliano e na escala espacial

considerada (Hortal *et al.* 2010), variáveis climáticas abióticas seriam as mais importantes na determinação das distribuições geográficas, juntamente com limitações históricas à dispersão (Soberón & Peterson, 2005; Soberón 2007). Especialmente no ***Capítulo 4***, nós tentamos incorporar a porção biótica do nicho ecológico de *L. huberi* nas modelagens de distribuição potencial, considerando-se algumas espécies vegetais que esta abelha utiliza como fonte de pólen, para melhorar as predições de sua distribuição potencial na América do Sul.

Considerando-se a temática de fragmentação de hábitats, a matrix é extremamente importante para determinar os fluxos biológicos em uma dada paisagem e determinar da presença e abundância de espécies, juntamente com a quantidade de habitat existente (Fischer & Lindenmayer 2007; Kupfer *et al.* 2006; Ricketts 2001). Assim, a maneira como os mosaicos de habitat nas paisagens estão organizadas, também conhecido como estrutura de paisagem, é um importante determinante da biodiversidade existente em paisagens fragmentadas. Entretanto, considerando-se a perspectiva das espécies, nem sempre em uma mesma paisagem as espécies responderão à estrutura das paisagens da mesma maneira, uma vez que diferentes traços ecológicos podem determinar maior ou menor sensibilidade a alterações na estrutura da paisagem (Davies *et al.* 2004; Henle *et al.* 2004). Adicionalmente, diferentes processos podem afetar as espécies de uma mesma paisagem de maneiras diferentes, uma vez que eles podem variam de acordo com a escala espacial considerada, o que também pode afetar a maneira como as espécies se relacionam com as paisagens. Numa escala geográfica mais regional, voltada a questões de perda de hábitat e fragmentação de paisagens e seus efeitos sobre populações locais e metacomunidades, nos ***Capítulo 5*** e ***Capítulo 6***, mensuramos as escalas espaciais locais mais relevantes para abelhas, dada a estrutura das paisagens amostradas em diferentes escalas. Especificamente, no ***Capítulo 5***, nós

avaliamos o efeito da estrutura das paisagens em diferentes escalas espaciais locais para avaliar seus efeitos sobre a probabilidade de ocorrência e as abundâncias das abelhas *Eulaema nigrita* e *Eufriesea auriceps* (Apidae: Euglossini) coletadas no Cerrado em Goiás. Já no ***Capítulo 6***, utilizando-se da mesma lógica do capítulo anterior, nós medimos os efeitos da estrutura da paisagem em diferentes escalas espaciais locais sobre toda a assembleia de abelhas e, separadamente, também para os grupos de abelhas eussociais e solitárias do Cerrado goiano, utilizando-se abordagens relacionadas à teoria de metacomunidades.

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CAPÍTULO I – Modeling distributions for the Brazilian leaf-cutter bees, *Megachile* (Apoidea: Megachilinae), using fragmentary occurrence data: biases, sampling effort, and future surveys[†]

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ABSTRACT

Conservation actions usually depend on distributional data, especially when they are based on species distribution modeling (SDM) and/or higher-taxon approach (HTA). Nonetheless, data adequacy and reliability are rarely assessed. In this study, we: 1) estimated intrinsic biases in specimen records for *Megachile* bees from Brazil, 2) investigated if *Megachile* subgenera may be used as surrogates for *Megachile* species diversity, and 3) created maps based on SDMs that could inform future surveys. We evaluated the effects of human- and environment-related variables on our *Megachile* occurrence dataset and calculated spatial Spearman's correlations between subgenera and species richness to test the HTA. We also suggest areas for future *Megachile* surveys with the resulting suitability maps for subgenera/species obtained from the SDM and data on human-density. Both subgenera and species data were spatially correlated, and we found conspicuous biases in our data. Our analyses suggested several areas as priority for future surveys. Despite the observed biases, future surveys in unknown regions with standardized sampling procedures and subsequent taxonomic work may reveal an unknown diversity of *Megachile* and facilitate meaningful quantitative comparisons with better known faunas. Standardized sampling for *Megachile* informed by modeled distributions, combined with efforts to elucidate phylogenetic relationships, distribution, life history, taxonomy, and identification are required to overcome intrinsic problems that have impeded further studies of these pollinators at broad spatial scales.

Keywords: *Megachile*; sampling biases; survey priorities; conservation biogeography, species distribution modeling

1.1 INTRODUCTION

High-quality ecological, life history, and distributional data are essential building-blocks used by conservationists and stakeholders to implement practical conservation plans (Whittaker *et al.*, 2005; Bini *et al.*, 2006). Nevertheless, compilation of and access to these data requires prior species description and classification, development of reliable and accessible diagnostic tools, documentation of their distribution in time and space, compilation of biodiversity information (e.g. ecological, phylogenetic), and results dissemination (Ebach et al. 2011; Wheeler et al. 2012). As only 1.2 of the 9 million species estimated to live on Earth's have been taxonomically validated (Mora et al. 2011), much of the planet's biodiversity still remains unknown and potentially threatened (Fontaine et al. 2012). The general lack of comprehensive taxonomic (the Linnean shortfall) and distributional information (the Wallacean shortfall) are the major setbacks to practical conservation decisions (Diniz-Filho et al. 2010; Whittaker et al. 2005), since basic analyses rely on reliable species' identification and distributions (Diniz-Filho et al. 2010). Therefore, the increase of species description rates and standardized biological surveys are required to overcome these shortfalls (Cardoso et al. 2011).

Otherwise, even the available fragmentary information, available from museum and private collections, print publications, or other sources may be useful if it helps researchers to overcome such obstacles (Newbold 2010). However, these data need to be handled with care, given their intrinsic biases. Among those are 1) misidentifications; 2) uncertain delimitation and diagnosis of species; 3) biases in samples selected to be identified, curated, and digitized; and 4) sampling biases towards "easy-to-study" biological groups, easily accessible areas or those which provide species-rich samples (e.g., near roads, rivers, research institutions or cities), and 5)

putatively most favorable seasons (Ebach et al. 2011; Newbold 2010; Pyke and Ehrlich 2010; Reddy and Davalos 2003; Sastre and Lobo 2009). In particular, small-sized and/or inconspicuous organisms, and those inhabiting remote or sparsely populated areas (e.g. deserts, tropical forests) have been poorly sampled as compared to flagship species or those inhabiting temperate regions (Newbold 2010). After properly controlling for these biases, these biological information may effectively help practical conservation actions to transcend both the Linnean and Wallacean shortfalls, especially when theoretical approaches are concomitantly considered (e.g. Grinnellian niche, niche conservatism, higher-taxon approach (HTA), species distribution modeling (SDM); Diniz-Filho et al. 2010; Newbold 2010).

Based on the target species' known occurrences and the environmental variables available for those areas, SDMs estimate niche parameters and project the target species' potential distribution in environmentally similar areas onto the geographic space. Therefore, SDMs are promising tools and may help on the discovery of unknown or rare species (Raxworthy et al. 2003; De Siqueira et al. 2009), guide and optimize future biological surveys (Sousa-Baena et al. 2013a), and indicate priority areas for future conservation actions (e.g. Nóbrega and De Marco 2011; Sousa-Baena et al. 2013b). The HTA relies on the close relationship between an indicator group and the overall species richness, within a given spatial unit. Once closely-related species are expected to use similar resources, higher taxa richness is expected to be correlated to the richness of their lower taxa (Balmford *et al.*, 1996a, 1996b, 2000). Despite criticisms about the application of these methods to insects (Rosser and Eggleton 2012), major problems related to alpha taxonomy may be reduced under HTA, since subgeneric, generic, familial or any other taxonomic information may serve as biodiversity

surrogates of a taxonomically flawed species richness (Diniz-Filho et al. 2010; Vianna and De Marco Jr 2012).

Although insects compose one of the most diverse groups on Earth (Gullan and Cranston 2005), responsible essential ecosystem functioning (Losey and Vaughan 2006), they are often neglected in practical conservation plans (Cardoso et al. 2011; Diniz-Filho et al. 2010). Even better known groups (e.g. bees, ants, butterflies) usually lack comprehensive and accessible taxonomic, ecological, and distributional data. Therefore, here we assembled the distributional data for the Brazilian *Megachile*, the leaf-cutter bees, to evaluate some of the potential biases hindering their use on practical conservation biogeography frameworks. Additionally, based on HTA and SDM, we suggest approaches to transcend the group's Linnean and Wallacean shortfalls, with the intention of guide and direct future data acquisition and field surveys for these bees. Specifically our goals were: 1) to evaluate some of the biases affecting *Megachile* distributional data, providing a map for sampling gaps in available specimen data; 2) to test whether *Megachile* subgeneric richness may be used as a surrogate for *Megachile* species richness under HTA; and 3) based on potential distributions obtained from SDMs, to generate priority maps for optimized *Megachile* surveys.

1.2 MATERIAL AND METHODS

1.2.1 Megachile, *the leaf-cutter bees*

Megachile (sensu lato, i.e. Michener 2007) is the largest genus in Megachilinae, with more than 56 subgenera and 1,561 described species (Ascher and Pickering 2013; Michener 2007), 161 them occurring in Brazil (Moure et al. 2007; Silveira et al. 2002). *Megachile* includes the well-known leaf-cutter bees, some of

which are important and even commercially significant pollinators, notably the Alfalfa Leaf-cutter Bee *M. rotundata*, but also resin and dauber bees.

Megachile species are known for their diversified nest placements (stone/tree bark crevices, empty termite nests), construction materials for brood cells, cell partitions, and nest closures (mud, resins and wood fibers, and petal and leaf pieces; Michener 2007). Their body size may range from 5 mm to 40 mm in *M. pluto* from Indonesia, the world's largest bee, and occur a wide variety of habitats, including tropical lowland rain forests, boreal forests, deserts, and alpine areas. Some species are habitat specialists and oligolectic, but many tolerate a broad range of environmental conditions and are polylectic, making use of pollen from diverse crops and other flowering plants. The broad ecological and morphological variability of *Megachile* and their realized or potential utility as pollinators are primary reasons why this genus should be prioritized for taxonomic revisions (Silveira et al. 2002), as well as distributional and biogeographic analyses.

1.2.2 Megachile *occurrence dataset*

We compiled records for Brazilian *Megachile* from 1) online databases [GBIF (http://www.gbif.org); CRIA Species Link (http://www.splink.cria.org.br)]; 2) published literature studies and reports (Supplementary Materials); and 3) digitized occurrences from the Division of Invertebrate Zoology database of the American Museum of Natural History (Schuh et al. 2010) captured using the Arthropod Easy Capture Software (Available at: http://sourceforge.net/p/arthropodeasy, v. 1.34, 2013, last accessed 06/26/13). Data from other research institutions consulted were not digitized, not publicly accessible, or otherwise unavailable. We used city hall coordinates as a proxy information for sampling sites for records lacking the exact

sampling site information, obtained with Google Earth (Google Inc. 2013). Records lacking reliable geographic information, or georeferenced at sea, or containing only general information on the specimen's occurrence were excluded. We checked the quality of all occurrences by classified them as "City" (coordinates distant with less than 4 km from the nearest city hall coordinates) or "GPS" (coordinates distant farther than 4 km from the nearest city hall coordinates) records. We followed Moure's Bee Catalogue (Moure et al. 2007) to assess taxonomic nomenclature and also minimize outdated or erroneous identifications.

1.2.3 Sampling effort, HTA, and bias analyses

We built a grid with 709 1º cells (~ 110 km in the tropics) covering Brazil, within which we derived our predictor variables and assessed the effects of potential geographic, spatial, and additional human-related biases in our *Megachile* bees occurrence dataset. We obtained data from Brazilian government agencies (Table S1), for the predictor variables within each grid cell for the following known sources of biases in biological collections (Newbold 2010; Pyke and Ehrlich 2010; Reddy and Davalos 2003): 1) human demographic density (HDD), 2) gross regional product (GRP), 3) human development index (HDI), 4) road density (RDD), and 5) river density (RVD). Additionally, for all grid cell containing *Megachile* sampling events, we measured the distance (DIST) from the cell's centroid to the nearest research institution involved with any aspects of melittological research (taxonomy, ecology, and/or life history aspects; Table S2 and Figure S1) and considered the estimated number of bee specimens within their entomological collections. As some socio-economic variables were collinear (Table S3), the final variables set included only HDD, GRP, RVD, and DIST.

Different sampling methods (e.g. active vs. passive) and other biases (e.g. related to identification and databasing processes) may introduce artifacts to the final observed species richness of a given area, affecting data's reliability (Gotelli and Colwell 2001). Therefore, we used sample-based rarefaction curves to standardize the observed *Megachile* data, and derived six biological variables within each grid cell: 1) rarefied subgeneric richness; 2) rarefied species richness; 3) observed subgeneric richness; 4) observed species richness; 5) observed subgeneric occurrences, and 6) observed species occurrences. Given the overall lack of *Megachile* data (see below), we only calculated these variables in grid cells with 10, 15, and 20 records. We log-transformed (log+1) all response variables to assure their normality and variance homogeneity. We also assessed the congruency of higher (subgenera) and lower (species) *Megachile* taxa, under the HTA assumptions, through pair-wise spatial Spearman's correlations between each taxonomic level's biological variable. We used Simultaneous Autoregressive models (SAR) to assess the effects of all predictors on the response variables, assessed the effects of spatial autocorrelation (SAC) through autocorrelograms with Moran's *I*, in SAM v4.0 (Rangel et al. 2010).

We also tested our *Megachile* data for spatial bias related to the distance of each sampling event to the nearest institution/city through randomization tests. We did not used "City" records because they were already georeferenced by city hall coordinates. At first, we summed up the observed distances of each "GPS" sampling event to the nearest institution/city to obtain observed summed distance values. Later, we randomly placed the same amount of occurrences onto the geographic space 999 times to obtain randomized distributions of summed distances values to the nearest research institution/city. Thus, we could calculate the probability of randomly obtaining

the spatial pattern we observed in our dataset. In all these analyses, multiple records of the same taxon in the same geographic coordinates were considered as a single one.

1.2.4 Megachile *distribution modeling and target survey areas*

Since many *Megachile* records were classified as "City" (Table S4), the spatial resolution we used in our SDM procedures was 0.2º cells. Given an overall lack of species occurrences (see below) and following HTA, we used occurrences in two different ways: considering the whole *Megachile* genus as a single taxonomic unit, but we also considering each different subgenus with at least 15 unique occurrences separately. We used the following environmental data, obtained form the WorldClim database (http://www.worldclim.org/current, Hijmans et al., 2005), as environmental variables: 1) annual mean temperature, 2) temperature seasonality, 3) annual precipitation, 4) precipitation seasonality, 5) mean temperature of driest quarter, and 6) precipitation of the warmest quarter.

We divided the unique occurrences of the whole *Megachile* genus and of each *Megachile* subgenus into ten 70% training – 30% testing subsets. We used all training subsets in MaxEnt (Phillips et al. 2006; Phillips and Dudik 2008) to produce the potential distributions and the testing subsets to evaluate the resulting distributions. MaxEnt is a presence/pseudo-absence method robust to spatial errors that is able to produce potential distributions even with datasets with relatively few and/or biased records (Hernandez et al. 2006; Pearson et al. 2007), as our *Megachile* distributional data. We used MaxEnt only with the *linear* and *quadratric covariate* features activated, instead of default MaxEnt's parameterization (Elith et al. 2011; Merow et al. 2013). Additionally, we also enabled *random seed* and used 1,000 iterations.

We used the ROC-curve threshold, which balances omission and commission errors, to determine both generic and subgeneric potential distributions. We evaluated models' performance using True Skill Statistics (TSS; Allouche et al. 2006). This statistics is a threshold-dependent and prevalence insensitive measure, which varies from -1 to +1. Values near zero or negative represent distributions no better than random, while those equal to +1 represent a perfect agreement between the observed and the predicted distribution (Allouche et al. 2006). Acceptable distributions reach minimally values equal to 0.5.

By considering the generic or subgeneric summed suitability maps generated by MaxEnt and a *Megachile* Sampling Density (MSD) map, we created two maps with 1º grid cells to guide and direct future *Megachile* in Brazil, according to the equations 1 and 2:

$$FS_{gen} = \left(Suit_{gen}\right) * \frac{1}{MSD} \quad \text{(eq. 1)}$$

$$FS_{subgen} = \left(\frac{\sum_{i=1}^{j} Suit_{subgen}}{\sum_{i=1}^{j} subgen}\right) * \frac{1}{MSD} \quad \text{(eq. 2)}$$

where FS is the future survey value for each grid cell, calculated for both the *Megachile* genus (FS_{gen}), as well as for each single *Megachile* subgenus (FS_{subgen}); $Suit_{gen}$ is the mean modeled generic suitability for a given grid cell; $Suit_{subgen}$ is the mean suitability for each grid cell, considering each *Megachile* subgenus mean suitability values; and MSD is the *Megachile* sampling density map. We scaled the FS values to 1-5, where 1 are the areas with less importance to future surveys and 5 are the most important. By using this method, areas with high suitability values, but low sampling density would be assigned with high FS values, while those with high sampling densities, but with low suitability would be assigned with low FS values.

1.3 RESULTS

1.3.1 Sampling effort, HTA, and bias analyses

Considering the spatial scale of the 1º grid cells, the *Megachile* genus as a whole occupied 105 grid cells. The *Megachile* subgenera occurring in more grid cells was *Pseudocentron* (n=52), followed by *Leptorachis* (n=42), *Austromegachile* (n=33), and *Chrysosarus* (n=32). Otherwise, four subgenera only occurred in three grid cells or less (*Grafella*, *Pseudomegachile*, *Cressoniella*, and *Zonomegachile*). The *Megachile* species that occupied the highest amount of grid cells was *M. paulistana* (n=31), followed by *M. zaptlana* (n=24), and *M. susurrans* (n=19). Generally, 39 species occupied fewer than three grid cells (Table S4). While the *Megachile* subgenera occupied an average of 5.18 grid cells, the *Megachile* species had an average of 5.21 occupied grid cells.

Nearly 89.3% of the grid cells (n=635) had no occurrence data for any of the *Megachile* species, while 76 (~10.7) had at least one record (Figure 1A). Of these, almost half (n=37 cells) had a sampled observed richness of only 1-2 species. Conversely, the grid cells containing renowned research institutions in Southeastern and Southern Brazil, such as Ribeirão Preto in São Paulo state (23 species), Curitiba in Paraná (21 species), and Porto Alegre in Rio Grande do Sul (20 species), were the richest ones. When we consider the *Megachile* observed subgeneric richness, 88.3% of the grid cells (n=628) had none information at all, whereas 83 cells (~11.7%) had at least one *Megachile* record (Figure 1B). Of those, 38 showed a sampled richness of only 1-2 subgenera. The richest grid cells for the *Megachile* species were also the richest for the *Megachile* subgenera.

If we assume 15 samples within a grid cell to classify it as minimally surveyed, less than 0.01% (n=8) of them would be considered well surveyed. In general, the

majority of *Megachile* occurrences were recorded in southern, southeastern, and northeastern Brazil, and few grid cells with *Megachile* occurrences were observed in Central Brazil and Amazonia, a consistent pattern for both the species and for the subgenera information (Figure 1C and 1D, respectively). In general, 29% of all *Megachile* records were classified as "City" records (Table S4). The deficiency of *Megachile* data was also detected in the rarefied subgeneric and species richness, as only a couple of grid cells had more than 30 records (Table 1).

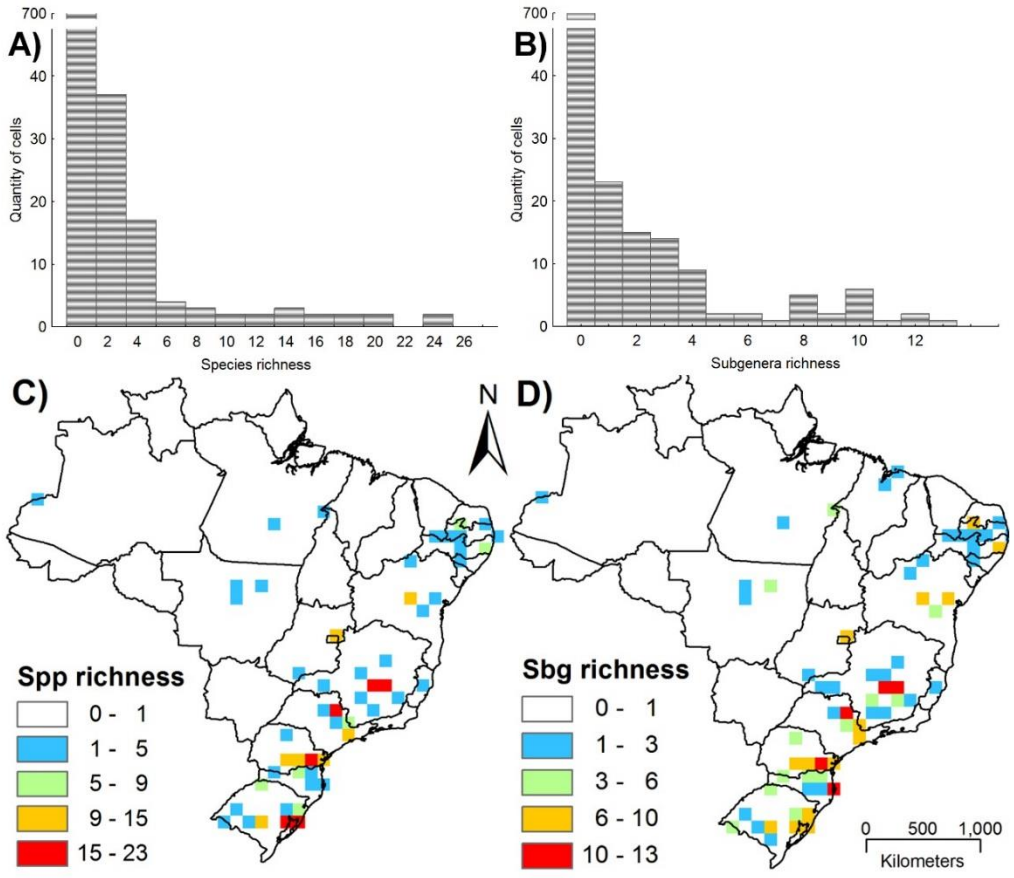

Figure 1 – Data quality and spatial distribution of sampling effort for *Megachile* bees in Brazil. (A) Histogram of the species richness in all grid cells containing *Megachile* data. (B) Histogram of the subgenera richness in all grid cells containing *Megachile* data. (C) Spatial distribution of observed *Megachile* species richness. (D) Spatial distribution of the observed *Megachile* occurrences.

Table 1 – Number of grid cells after rarefying the observed subgenera and species richness according to the number of records in each cell.

Rarefaction factor	Amount of remaining cells (rarefied subgeneric richness)	Amount of remaining cells (rarefied species richness)
5 records	27	25
10 records	17	16
15 records	17	13
20 records	4	6
25 records	2	3
30 records	2	2

The Brazilian *Megachile* sampling events took place near cities and research institutions more regularly than expected by chance, when compared to random distribution of sampling events. (Figure 2A and 2B, respectively). None of the spatial pair-wise Sperman's correlations of rarefied subgeneric and rarefied species richness were significant (Table 2), but their observed richness and observed occurrences were positively correlated.

Given the few grid cells with 20 samples or more (Table 1 and 2), we only considered the cells with 10 and 15-samples in the bias analyzes. The amount of variation explained by the SAR models varied according to the response variable considered, ranging from 0.304 to 0.712 for the variables related to the *Megachile* species, and 0.356 to 0.816 for the variables related to the *Megachile* subgenera (Table 3; Figure S2). The distance from sampling events to nearest research centers (DIST) had a negative effect on some of our response variables: the farther away from the research institutions, the lower were the rarefied species richness in cells with 10-samples and the observed subgeneric occurrences (Table 3). River density (RVD) also had a positive

effect on the rarefied subgeneric richness in grid cells with 15-samples: the higher the river density, the higher the richness.

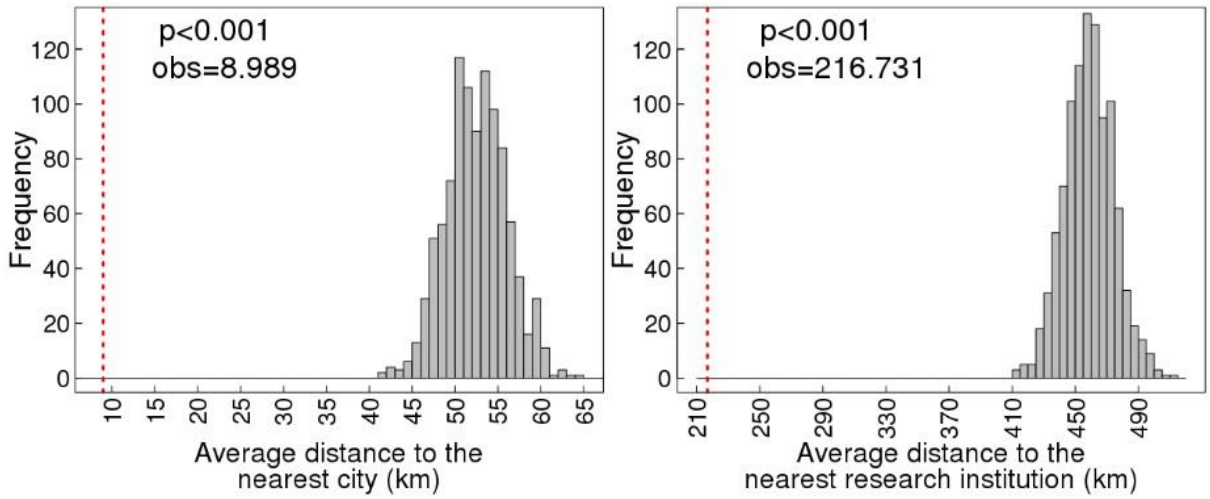

Figure 2 – Histograms of the randomization tests to evaluate whether the *Megachile* sampling events are spatially biased. A) Randomized summed distances distribution from the sampling events to the nearest city. B) Randomized summed distances distribution from the sampling events to the nearest research institution involved with bee research. The red bars represent the observed values for each randomization test (8.98 Km in A and 216.73 Km in B). In both randomization tests, *p*-value<0.001.

1.3.2 Megachile *distribution modeling and target survey areas*

Along with the whole genus, the modeled subgenera were: *Pseudocentron* (n=73; unique occurrences considering a 0.2º grid cell), *Leptorachis* (n=64), *Moureapis* (n=50), *Austromegachile* (n=42), *Chrysosarus* (n=40), *Sayapis* (n=35), *Acentron* (n=24), *Tylomegachile* (n=18), *Neochelynia* (n=17), and *Leptorachina* (n=16). We did not model the distribution of the subgenera *Cressoniella*, *Dasymegachile*, *Grafella*, *Melanosarus*, *Pseudomegachile*, *Ptilosaroides*, *Ptilosarus*, *Rhyssomegachile*,

Schrottkyapis, *Thrichurochile*, and *Zonomegachile*, once those had less than 15 unique occurrences.

Table 2 – Spearman's pair-wise correlations between *Megachile* subgenera/species occurrences, subgeneric/species observed richness and subgeneric/species rarefied richness given different rarefaction factors under the HTA. n refers to the grid cells with *Megachile* samplings according to each rarefaction factor. *means *p*-values<0.001.

	Variable	n	r
	Occurrences abundance	91	0.810**
	Observed richness	91	0.774**
Rarefaction Factor	10 records	20	-0.063
	15 records	18	-0.282
	20 records	7	0.688

The performance of the modeled distributions for the whole genus and its subgenera were acceptable, reaching values higher than 0.5 (Table S5). Generic suitability was higher along the Brazilian Atlantic coast than that observed in interior regions, such as the Amazon (Figure 3A). We observed the same pattern for subgeneric summed distribution (Figure 3B). We identified ecotone areas with good suitability and poor sampling densities between the Cerrado and the Caatinga in northeastern Brazil, between the Cerrado and the Amazon in Central Brazil, Cerrado areas in southwestern Brazil as priority regions for future surveys (categories 3-5 in Figure 3C). Although some grid cells in southwestern Brazil had high suitability for both the genus and the subgenera, they attained low FS_{gen} and FS_{subgen} values because they were already sampled before, with some portions of their *Megachile* fauna already sampled. Nevertheless, much of the interior regions, including the Amazon, had low *FS* values,

reflecting low modeled suitability for the whole *Megachile* genus. Some extra cells were added when we consider the subgenera, but the whole pattern was the same (Figure 3D).

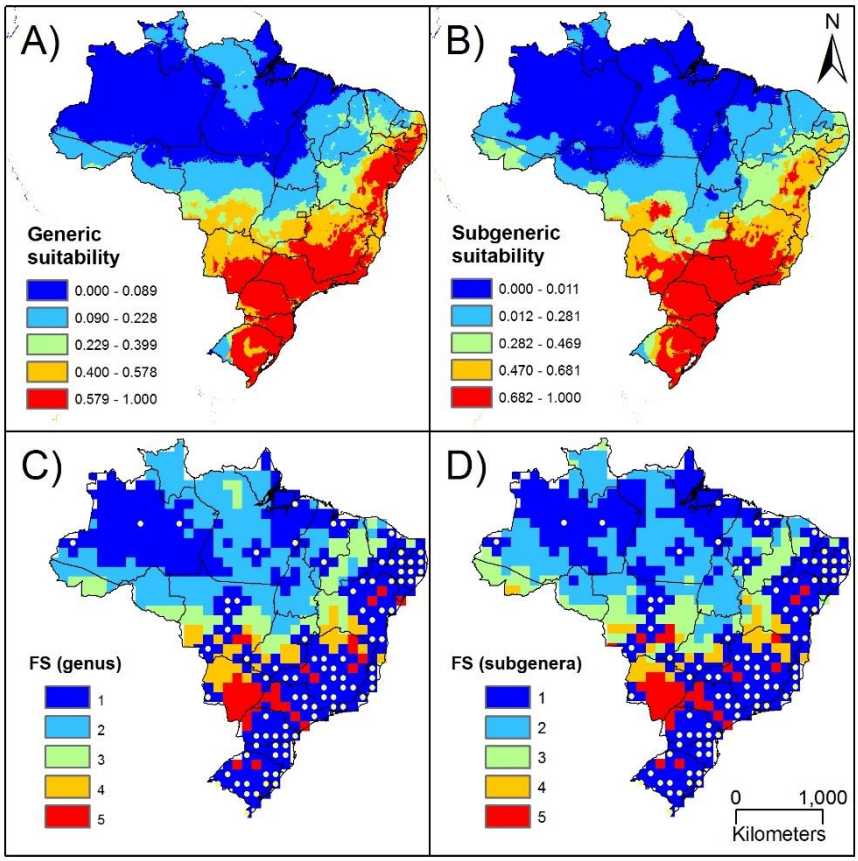

Figure 3 –*Megachile* distribution maps considering A) genus suitability, B) subgenera suitability, C) generic FS value (FS_{gen}), D) subgeneric FS value ($_{FSsubgen}$). Red colors are areas with high-modeled suitability (A and B) and higher Future Sampling values (C and D). Suitability and FS values vary from zero to 1, being zero the areas in the lowest suitability/FS value class and 1 the areas in the highest suitability/FS value. Yellow dots refer to the centroids of grid cells with *Megachile* records.

Table 3– SAR results for the species and subgenera considering observed richness, observed occurrences, and the rarified richness in 10- and 15 sample-cells. See Material and Methods for abbreviations. *p-value<0.05.

Response variable	Variable	SAR Coeff.	SE	t	p	Response variable	SAR Coeff.	SE	t	p
Obs. species richness	RVD	0.114	0.128	0.981	0.329	**Raref. species richness**	-0.128	0.115	-1.109	0.294
(n=91)	GRP	-0.002	<0.001	-0.015	0.988	**10-sample cells (n=20)**	<0.001	<0.001	1.924	0.083
R^2=0.605	HDD	0.021	0.004	0.182	0.856	**R^2=0.216**	-0.013	0.009	-1.421	0.186
	DIST	-0.201	0.389	-1.376	0.173		-0.662	0.640	-1.034	0.326
Obs. species occurrences	RVD	-0.105	0.267	-0.393	0.695	**Raref. species richness**	-0.137	0.225	-0.610	0.553
(n=91)	GRP	<0.001	<0.001	-0.665	0.508	**15-sample cells (n=18)**	<0.001	<0.001	-0.251	0.806
R^2=0.712	HDD	-0.002	0.007	-0.288	0.774	**R^2=0.401**	-0.022	0.017	-1.303	0.271
	DIST	-1.003	0.520	-1.930	0.057		-3.094	1.379	-2.244	0.044*
Obs. subgenera richness	RVD	0.048	0.080	0.597	0.552	**Raref. subgenera richness**	0.206	0.200	1.033	0.326
(n=91)	GRP	<0.001	<0.001	-0.553	0.582	**10-samples cells (n=20)**	<0.001	<0.001	1.060	0.314
R^2=0.816	HDD	<0.001	0.002	-0.274	0.785	**R^2=0.262**	0.011	0.015	0.696	0.502
	DIST	-0.389	0.242	-1.609	0.111		0.873	1.111	0.785	0.450
Obs. subgenera occurrences	RVD	<0.001	0.237	0.002	0.998	**Raref. subgenera richness**	0.219	0.095	2.298	0.040*
(n=91)	GRP	<0.001	<0.001	-0.513	0.609	**15-sample cells (n=18)**	<0.001	<0.001	1.623	0.130
R^2=0.759	HDD	-0.002	0.006	-0.393	0.695	**R^2=0.358**	-0.002	0.008	-0.257	0.802
	DIST	-0.974	0.461	-2.112	0.038*		-0.418	0.605	-0.690	0.503

1.4 DISCUSSION

1.4.1 Sampling effort, HTA, and bias analyses

The dataset of the *Megachile* leaf-cutter bees in Brazil was characterized by evident sampling and identification biases. Despite the extensive knowledge on their biological traits and ecological services performed by these bees, the low effort dedicated to their taxonomic review, the limitation regarding their taxonomic identification, and the overall low sampling effort for these bees determined the low amount of data available for us to assemble the dataset. The majority of our grid cells had no records, a deficiency already reported for other Brazilian insects (tiger moths; Ferro and Melo 2011; odonates; De Marco and Vianna 2005; Nóbrega and De Marco 2011), as well as other "well known" biological groups (mammals; Bernard et al. 2011; Patterson 1994; herpetofauna; Costa et al. 2007; birds; da Silva 1995). Such fragmentary distributional data, with overall low georeference quality, precision, and reliable identifications, is a common feature found in the Neotropical biological datasets (Kamino et al. 2011; Soberón et al. 2007), which may preclude the proper evaluation of the conservation status of those groups, as well as *Megachile*. However, we were able not only to characterize *Megachile* distribution in Brazil, but also to document biases and inform survey areas for future studies.

The leaf-cutter *Megachile* bee samplings in Brazil usually took place near cities and research institutions, reflecting the greater activity of bee collectors near more populated areas, a known bias reported in the literature (Newbold 2010; Pyke and Ehrlich 2010; Reddy and Davalos 2003). Such pattern usually arises either because researchers prefer to sample readily-accessible areas with high species richness, instead of sampling in random or systematic designs, which may describe the real species richness patterns more accurately (Dennis and Thomas 2000; Sastre and Lobo 2009)

Brazilian human occupation history, along the Atlantic coast is reflected our dataset, where occurrences are numerous as compared with interior areas. These region has always been highly populated, wealthier, and harbored more taxonomists, notably Padre J.S. Moure, D. Urban and colleagues in Curitiba (Engel et al. 2012; Urban 2003), J.M.F. Camargo (Pedro 2009), S.R.M. Pedro and colleagues in Ribeirão Preto, P. Nogueira-Neto in São Paulo, and F.A. Silveira in Belo Horizonte. The larger the overlap among species distribution, human population centers, and centers of taxonomic expertise, the higher the likelihood of sampling a given taxon (Gaston and Blackburn 1994). Inevitably, taxa with distributions not or minimally overlapping with this region were poorly represented in or absent from our dataset.

A better spatial distribution of new research institutions in interior Brazilian regions would significantly improve the quality and quantity of available distributional data for several biological groups. Brazil's current socioeconomic advances towards interior regions and governmental investments in biodiversity research should fill distributional gaps in biological datasets and reduce biases. In addition, future systematic or randomized survey designs should result in less biased and more reliable biological patterns (Sastre and Lobo 2009) , but long-term monitoring efforts, expeditions, and rapid inventory protocols designed to fill general distributional gaps should also be employed.

Rivers density exerted a positive effect on some of the rarefied subgeneric richness. Increased sampling density along rivers is a common bias found in collection-based datasets (Newbold 2010; Pyke and Ehrlich 2010; Reddy and Davalos 2003), especially in regions such as Amazonia, where major rivers have been the sole or primary human transportation corridors (e.g. De Marco and Vianna 2005).

Almost no spatial correlations between *Megachile* species and subgenera data were significant, a result that casts some doubt on use of higher taxa as a surrogate for lower ones (Rosser and Eggleton 2012). Once HTA efficiency is taxon- and scale-dependent, it may show low efficiency with broad-scale but poor datasets when compared to datasets with more available biological data (e.g. De Marco and Vianna 2005), despite the poor results we yielded with the *Megachile* bees dataset.

The overall data deficiency of *Megachile* resulting from gaps and biases in both sampling and identification are the main limitation of our results. Taxonomic uncertainties with Brazilian *Megachile* (Silveira et al. 2002), especially the difficulty to assign a specimen to a species, severely affected our dataset. Given the increasing demand for practical conservation actions, imprecise and/or unreliable identifications severely jeopardize any conservation actions (Kim and Byrne 2006). Nonetheless, *Megachile*'s life-history traits also explain the limited available occurrence data for this genus. Hidden and dispersed nests, solitary nesting and foraging habits and some specialization on particular floral hosts, contribute to its low detectability at the field, as compared with other bee groups. Otherwise, highly eusocial Meliponini bees, with their large and conspicuous nest and high recruitments rates from perennial colonies (Michener 2007), or the easily-attracted-to-bait-traps, flagship, colorful, large-bodied, Euglossini bees will certainly render bigger amounts of distributional information than *Megachile*.

Although sampling issues are the main biases sources in biological datasets, other factors also contribute to a paucity of data. A limiting factor is availability of specimen records that, along with insufficient sampling, reflects lack of resources for specimens identification and curation (Costello et al. 2013; Ebach et al. 2011; Wheeler et al. 2012). The lack of resources for capturing the label data from specimens deposited

at museums and the delivery of the captured data to biodiversity portals also constitutes major drawbacks to the limited insect distribution in the tropics (Costello et al. 2013; Ebach et al. 2011; Wheeler et al. 2012). Tropical taxa and areas underrepresented in digitized specimen records and, consequently, are those for which historical reference collections and comprehensive taxonomic keys are also lacking (Newbold 2010; Pyke and Ehrlich 2010). Thus, there is a correlation between lack of historical collections from an area and the ability of taxonomists to identify newly studied samples, reinforcing existing biases (Fontaine et al. 2012). As a result, specimen records accumulate most rapidly for already well-known species from well-sampled areas, but not for obscure species from understudied areas, which generally may remain long periods within the shelves of collections without proper taxonomical validation (Fontaine et al. 2012).

The high dependency of entomological collections on limited and *ad hoc* funding (Wheeler et al. 2012) also results in the observed fragmentary data, even in cases where taxonomic and curational expertise are available. The lack of a truly coordinated and reliably-funded effort to digitalize tropical (and global) collections, will continually result in the low coverage of determined taxa or areas (Costello et al. 2013; Wheeler et al. 2012).As a final consequence of such curation and identification biases, even though unidentified or poorly known taxa may represent an invaluable biodiversity portion, performing important ecosystem functions advised to be studies and protected, without a good taxonomic review, they are fated to be assigned as low priority for data capture, remain as unknown or poorly kwon taxa.

Finally, other potential causes of our data impediments on the *Megachile* are sociopolitical. Data that could be shared online is not due to concerns about data ownership or academic priority (Wheeler et al. 2012). We are well aware of a vast

number of relevant specimen records for Brazilian *Megachile* that exists in entomological collections that could not be included in this study for the reasons mentioned above. Through greatly expanded support for identification and digitization and much improved capacity and cooperation among data providers and aggregators (Wheeler et al. 2012), we hope to corroborate preliminary results based on a small, biased, but still demonstrably useful subset of potentially available records for the *Megachile*.

1.4.2 Megachile *distribution modeling and target survey areas*

Given the complete overall lack of distributional data on the Brazilian, any distribution estimate for these bees may provide useful and insightful areas for future field surveys, despite plausible bias caused by inherent peculiarities of the modeling algorithm used (Kramer-Schadt et al. 2013). Similar approaches to those used here have also been successfully used in similar ways with other Brazilian biological groups (Sousa-Baena et al. 2013a; 2013b). Areas within Cerrado and Caatinga biomes, with high FS values for *Megachile*, should be considered as high priorities for future surveys. Since these savanna-like/xeric subtropical areas are expected to have diverse bee faunas (Michener 2007; Michener 1979), future surveys in will certainly result in the discovery of new species, populations, life-histories traits, and increases in distribution ranges for poorly known bee taxa.

Similar model-based approaches (Nóbrega and De Marco 2011; Raxworthy et al. 2003; Silva et al. 2013; Sousa-Baena et al. 2013b) may also detect new species and new populations for rare ones, in addition to ranking knowledge gap areas for future surveys and reserve implementation. In light of the current biodiversity crisis, we

suggest that future studies should implement the approaches used here for both survey optimization and conservation actions.

1.5 CONCLUDING REMARKS

Given the current rate of species loss, a better description of Earth's biodiversity is necessary to assure the conservation of important biological and ecological features. Such process is not always possible given the paucity of distributional and taxonomical data for many groups. Nonetheless, despite the limited availability of specimen records and suboptimal quality, these data are usually the only distributional information available to inform interesting areas for new surveys and for practical conservation action. Disregarding the relatively scant data available for Brazilian leaf-cutter bees, we were able to generate the first assessment of their distributional status, some of inherent biases, but also inform areas for future surveys. Considering the conservation biogeography framework (Whittaker et al. 2005) and the importance of insect species to maintain ecosystem functioning (Losey and Vaughan 2006), similar studies are encouraged to apply the approaches used here to other taxa and areas with better available data.

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1.8 SUPPLEMENTARY MATERIALS

1.8.1 Supplementary tables

Table S1 – Internet addresses of datasets and shapefiles used in our study.

Data source	Web address
Global Biological Information Facility	http://www.gbif.org
Species Link	http://splink.cria.org.br
Brazilian Transport Ministry	http://www.transportes.gov.br/index/conteudo/id/36604
Brazilian Agency of Geography and Statistics (IBGE)	http://www.ibge.gov.br/home/download/geociencias.shtm
Natiaonal Water Agency (ANA)	http://www.ana.org.br
AMNH-IZ Database (as mapped on Discover Life)	http://www.discoverlife.org/mp/20m?kind=AMNH_BEE

Table S2 – List of renowned Brazilian collections* involved in bee research that were used in this study and their estimated number of bee specimens.

Institution Number	Institution Name	Brazilian state	Latidude	Longitude	Expected number of bee specimens
1	Univ. Federal do Acre	Acre	-9.953	-67.850	<1,000
2	Instituto de Pesquisas da Amazônia	Amazonas	-3.098	-60.016	10,000-50,000
3	Univ. Federal da Bahia	Bahia	-13.001	-38.500	10,000-50,000
4	Univ. Estadual de Feira de Santana	Bahia	-12.564	-38.750	1,000-10,000
5	Univ. Estadual de Santa Cruz	Bahia	-14.814	-39.150	<1,000
6	Univ. Federal do Maranhão	Maranhão	-2.522	-44.287	10,000-50,000
7	Univ. de Brasília	Distrito Federal	-15.736	-47.866	<1,000
8	Univ. Federal de Minas Gerais	Minas Gerais	-19.871	-43.950	10,000-50,000
9	Univ. Federal de Viçosa	Minas Gerais	-20.754	-42.850	1,000-10,000
10	Univ. Federal de Uberlândia	Minas Gerais	-18.916	-48.255	Unknown
11	Univ. Federal do Pará	Pará	-1.451	-48.466	10,000-50,000
12	Univ. Federal do Pernambuco	Pernambuco	-8.052	-34.950	10,000-50,000
13	Univ. Federal do Paraná	Paraná	-25.439	-49.266	>100,000
14	Univ. Estadual de Londrina	Paraná	-23.327	-51.183	1,000-10,000
15	Univ. Federal do Rio de Janeiro	Rio de Janeiro	-22.904	-43.216	10,000-50,000
16	Univ. Estadual do Norte Fluminense	Rio de Janeiro	-21.763	-41.283	10,000-50,000
17	Univ. Federal do Rio Grande do Sul	Rio Grande do Sul	-30.034	-51.216	10,000-50,000
18	Univ. Federal de Santa Catarina	Santa Catarina	-27.596	-48.533	1,000-10,000
19	Univ. de São Paulo - Ribeirão Preto	São Paulo	-21.184	-47.800	>100,000
20	Univ. de São Paulo - São Paulo	São Paulo	-23.559	-46.700	10,000-50,000
21	Univ. Federal de Campina Grande	Paraíba	-6.481	-36.133	1,000-10,000
22	Univ. Federal da Paraíba	Paraíba	-7.136	-34.833	10,000-50,000

*We only considered those institutions participating in the proposed Brazilian Pollinators Identification Network.

Table S3 – Spearman's r (lower triangle) and *P*-values (upper triangle) from spatial correlation analyses among the four variables obtained from governmental institutes. Bold values correspond to significant Pearson's correlations.

	HDD	HDI	GRP	RDD
HDD	-	**0.019**	**<0.001**	**0.014**
HDI	**0.303**	-	**0.002**	0.212
GRP	**0.267**	**0.498**	-	0.197
RDD	**0.785**	0.374	0.111	-

Table S4 – Information from the *Megachile* occurrences dataset. n corresponds to the quantity of raw occurrences found per species, considering the 1º grid cells for *Megachile* genus, subgenera, and species. PGPS refers to the proportion of raw occurrences classified as "GPS" occurrences, and PCITY refers to the proportion of raw occurrences classified as "City" occurrences, for each taxa here considered.

Genus	**n**	**PGPS**	**PCITY**	**Subgenus**	**n**	**PGPS**	**PCITY**	**species**	**n**	**PGPS**	**PCITY**
Megachile	105	0.56	0.44	*Incertae sedis*	3	1.00	0.00	*iheringi*	3	1.00	0.00
				Acentron	23	0.63	0.37	*eburnipes*	8	0.78	0.22
								itapuae	2	1.00	0.00
								lentifera	10	0.62	0.38
								tupinaquina	3	0.67	0.33
								verrucosa	3	1.00	0.00
				Austromegachile	33	0.63	0.37	*abnormis*	1	1.00	0.00
								antiqua	2	0.50	0.50
								exaltata	5	0.67	0.33
								facialis	6	0.83	0.17
								fiebrigi	4	0.25	0.75
								habilis	1	1.00	0.00
								oligosticta	1	1.00	0.00
								orbiculata	5	0.50	0.50
								recta	1	0.00	1.00
								susurrans	19	0.60	0.40
								trigonaspis	5	0.80	0.20
				Chrysosarus	32	0.61	0.39	*affabilis*	3	1.00	0.00
								bella	1	1.00	0.00
								diversa	2	1.00	0.00
								guaranitica	5	0.86	0.14
								inquirenda	5	0.38	0.63
								parsonsiae	3	0.67	0.33
								pseudanthidioides	10	0.55	0.45
								tuberculifera	2	0.00	1.00

Genus	n	PGPS	PCITY	Subgenus	n	PGPS	PCITY	species	n	PGPS	PCITY
Megachile	105	0.56	0.44	*Cressoniella*	1	1.00	0.00	*rava*	1	1.00	0.00
				Dasymegachile	8	0.57	0.43	*mitchelli*[1]	3	0.33	0.67
				Grafella[2]	1	1.00	0.00	undetermined species[3]	1	1.00	0.00
				Leptorachina[2]	13	0.63	0.38	*laeta*	13	0.56	0.44
				Leptorachis	42	0.57	0.43	*aetheria*	7	0.50	0.50
								angularis	2	0.50	0.50
								aureiventris	11	0.43	0.57
								crotalariae	1	1.00	0.00
								friesei	7	0.86	0.14
								paulistana	31	0.60	0.40
								rubricrus	1	1.00	0.00
								tenuitarsis	3	0.33	0.67
				Melanosarus	9	0.60	0.40	*brasiliensis*	7	0.57	0.43
								nigripennis	1	1.00	0.00
				Moureapis	29	0.56	0.44	*apicipennis*	16	0.39	0.61
								benigna	3	0.75	0.25
								electrum	2	0.50	0.50
								maculata	16	0.75	0.25
								nigropilosa	6	0.63	0.38
								pampeana	4	0.75	0.25
								pleuralis	1	1.00	0.00
				Neochelynia	17	0.74	0.26	*brethesi*	10	0.82	0.18
								paulista	4	0.50	0.50
				Pseudocentron	52	0.70	0.30	*asuncicola*	2	1.00	0.00
								barbatula	1	0.00	1.00
								botucatuna	5	1.00	0.00
								curvipes	16	0.87	0.13
								framea	11	0.47	0.53
								inscita	5	0.78	0.22
								lobitarsis	1	1.00	0.00

Genus	n	PGPS	PCITY	Subgenus	n	PGPS	PCITY	species	n	PGPS	PCITY
Megachile	105	0.56	0.44	*Pseudocentron*	52	0.70	0.30	*nudiventris*	4	0.83	0.17
								pyrrhogastra	1	1.00	0.00
								rubricata	1	1.00	0.00
								subcingulata	1	1.00	0.00
								terrestris	14	0.84	0.16
								virescens	2	0.00	1.00
				Pseudomegachile	1	0.00	1.00	*lanata*	1	0.00	1.00
				Ptilosaroides	6	0.50	0.50	*neoxanthoptera*	5	0.83	0.17
				Ptilosarus	10	0.62	0.38	*bertonii*	5	0.80	0.20
								xanthura	1	1.00	0.00
				Rhyssomegachile	4	0.75	0.25	*ardua*	1	1.00	0.00
								simillima	2	0.50	0.50
				Sayapis	25	0.70	0.30	*obdurata*	1	1.00	0.00
								zaptlana	24	0.70	0.30
				Schrottkyapis	4	1.00	0.00	*assumptionis*	3	1.00	0.00
				Trichurochile	8	0.56	0.44	*cachoeirensis*[4]	1	1.00	0.00
								gracilis	2	1.00	0.00
								stenodesma	2	0.00	1.00
								thygaterella	4	0.75	0.25
				Tylomegachile	16	0.61	0.39	*orba*	16	0.61	0.39
				Zonomegachile	3	0.67	0.33	*gigas*	3	0.67	0.33
	Total				340			**Total**	396		
	Average				15.45			**Average**	5.21		

[1]*Megachile mitchelli* Raw is a junior homonym of *Megachile mitchelli* (Gupta). A replacement name is needed for the former.

[2]Included in subgenus *Leptorachis* by Michener (2007).

[3]Since this was the only occurrence for the subgenus *Grafella*, this undetermined occurrence was only considered in the analyses involving subgenera.

[4]Described as a subgenus of *Megachile pulchra* Smith.

Table S5 – Average and standard deviations for the TSS values obtained for each one of the modeled *Megachile* taxa. SD refers to the standard deviation value.

Modeled Taxa	**Average TSS value**	**SD**
Genus *Megachile*	0.612	0.037
Subgenera		
Acentron	0.722	0.119
Austromegachile	0.574	0.150
Chrysosarus	0.650	0.101
Leptorachina	0.527	0.146
Leptorachis	0.632	0.112
Moureapis	0.823	0.090
Neochelynia	0.471	0.141
Pseudocentron	0.532	0.072
Sayapis	0.543	0.123
Tylomegachile	0.507	0.194

1.8.2 Supplementary figures

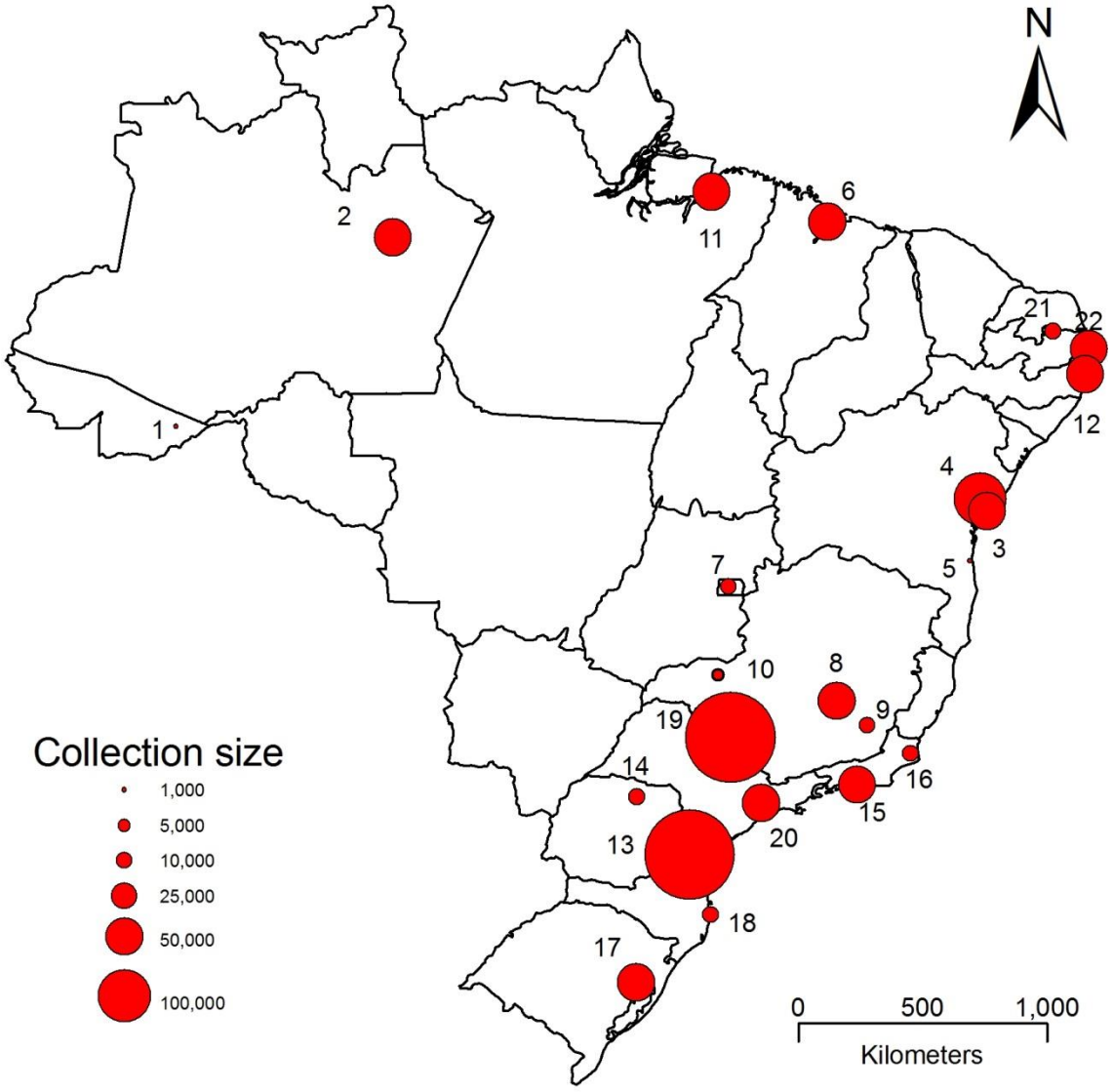

Figure S1 – Spatial distribution of research institutions considered in the spatial analyses and the expected number of bee specimens in their respective entomological collections. Note that the collection size of the institution number 10 (Univ. Federal de Uberlândia) is unknown.

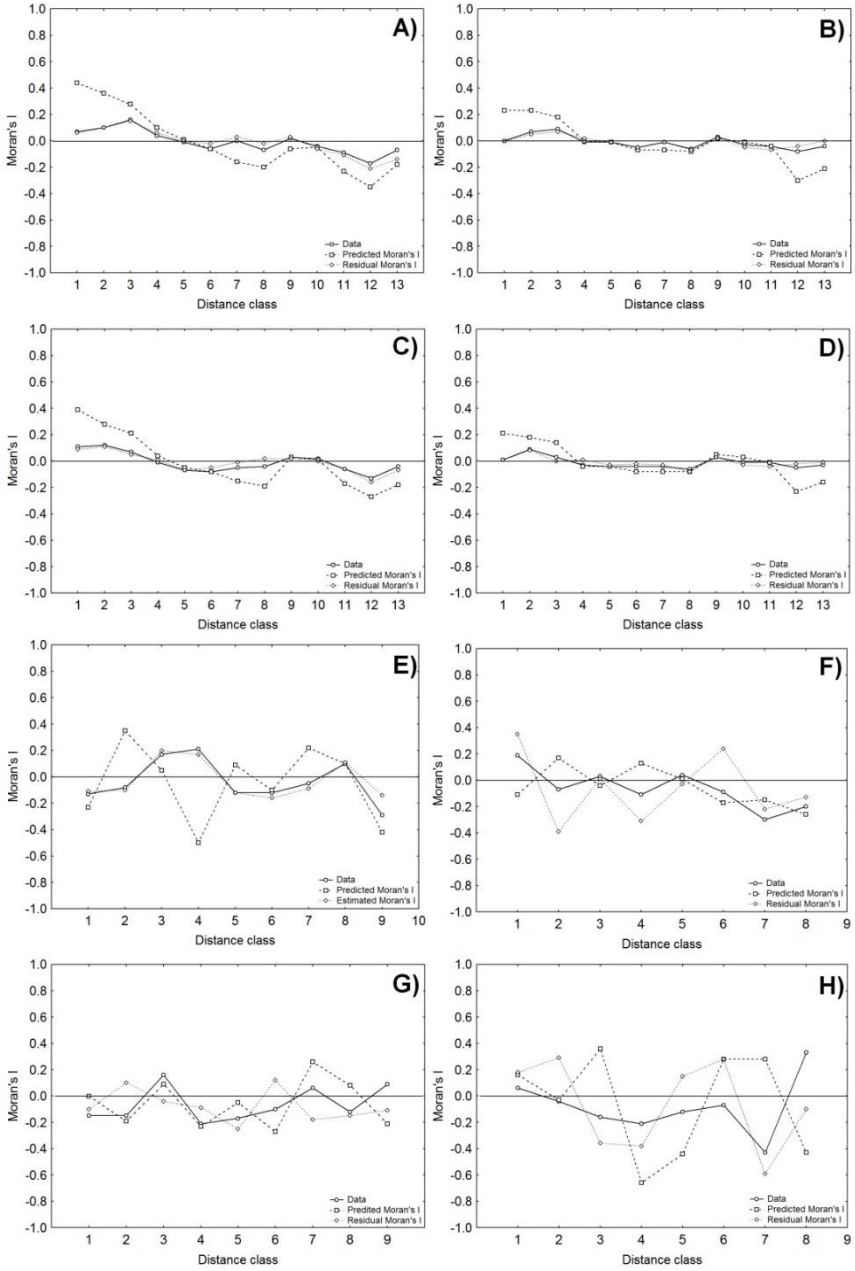

Figure S2 – Residual spatial autocorrelation for A) Observed species richness; B) Observed species occurrences; C) Observed subgenera richness; D) Observed subgenera occurrences; E) Rarefied species richness on 10-sample grid cells; F) Rarefied species richness on 15-sample grid cells; G) Rarefied subgenera richness on 10-sample grid cells; H) Rarefied subgenera richness on 15-sample grid. Opened circles, squares, and triangles refer to the observed, predicted, and residual Moran's *I* values.

1.8.3 Reference list of additional sources holding Megachile *occurrences*

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CAPÍTULO II – Distribution gaps for the Brazilian stingless bees (Hymenoptera, Apoidea, Meliponini): sampling efforts and other biases[‡]

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ABSTRACT

In a world of rapidly intensifying anthropogenic change, effective protection of biodiversity requires knowledge of its patterns. Nonetheless, several intrinsic biases affect the available biological data. Here, we first quantified and mapped such biases present in digitized information available for Brazilian stingless bees (Apidae: Meliponini). We compiled an occurrence dataset with information from available sources, including published revisions and additional specimen records from collaborating institutions. Using a grid with 709 cells 1º covering Brazil, we derived variables known to be causes of biases within biological data. The majority of grid cells containing Meliponini data were in the Brazilian Atlantic coast, reflecting proximity to population centers and research institutions, whereas the majority of grid cells lacking information were in the interior Brazilian regions. Despite generally sparse data for the Amazon, the richest grid cells were from there. Our assessment of the diversity patterns on Meliponini stingless bees in Brazil documents biases and reveals gaps in sampling that should be targets for future surveys. Along with future field surveys, a comprehensive assessment of the diversity patterns on this bee group in the future will also require additional taxonomic revisions in conjunction with expanded digitization and data sharing.

Keywords: Knowledge gaps; Sampling efforts; Biases; Stingless bees.

2.1 INTRODUCTION

In this fast changing-world, humans are now the main drivers of environmental changes and biodiversity loss (Dobrovolski et al. 2013; Tylianakis et al. 2008). The huge efforts necessary to describe, organize, and compile biological data, together with the shortage of specialists of some biological groups (Ebach et al. 2011; Wheeler et al. 2012) imply that only a small fraction of world's biodiversity is currently known to science (Fontaine et al. 2012; Mora et al. 2011). The lack of comprehensive taxonomic and distributional data, known as the Linnean and Wallacean shortfalls (Whittaker et al. 2005), are important obstacles hampering the effective implementation of practical conservation actions (Diniz-Filho et al. 2010; Whittaker et al. 2005) and are the main justifications for the enhancement of standardized biological surveys. This is especially true in tropical countries within which a high but mainly unknown species diversity is being rapidly lost (Bawa et al. 2004; Hong and Lee 2006). Thus, both known and unknown fractions of Earth's biodiversity remain at mercy of the human-caused environmental impacts (Barnosky et al. 2011; Fontaine et al. 2012), which increases the demand for high quality biological data (e.g. ecological, distributional, biogeographical) and the implementation of effective conservation actions (Blagoderov and Smith 2012; Diniz-Filho et al. 2010; Whittaker et al. 2005).

Despite this distressing scenario, the biodiversity information available from museums and other collections, catalogues, publications, monitoring programs, and online datasets, allied with technological novelties (Blagoderov et al. 2012; Blagoderov and Smith 2012) may produce reliable and useful products to direct practical conservation actions and transcend Linnean and Wallacean shortfalls (Newbold 2010; Pyke and Ehrlich 2010; Wheeler et al. 2012). Before its use, data needs to be validated to ensure that data quality standards are met. This includes georeferencing of localities

and careful attention to problems associated with misidentifications, biases towards "easy-to-identify", "-curate", "-digitize" species/samples, and "easy-to-study" biological groups, species-rich sites/regions and/or favorable seasons (Blagoderov et al. 2012; Blagoderov and Smith 2012; Newbold 2010; Pyke and Ehrlich 2010). Recurring biases should be considered, such as under-recording of small-sized or otherwise inconspicuous organisms and/or those occurring in remote and/or sparsely human populated regions as compared large-bodied flagship species from temperate regions (Newbold 2010; Pyke and Ehrlich 2010).

Especially in tropical and poorly sampled countries, using selected taxa as diversity surrogates for others may provide an efficient mean to implement conservation actions, as this approach can reduce the cost of engaging taxonomist qualified to contend with alpha taxonomy. Both higher-taxon and cross-taxon approaches (HTA and CTA, respectively; Balmford et al. 2000; 1996a; Balmford et al. 1996b; Pawar et al. 2007) are important tools in conservation biogeography frameworks (Diniz-Filho et al. 2010), but usually application of these has been used limited to groups with low species richness such as (i.e. mammals and birds; Balmford et al. 2000; Balmford et al. 1996a; 1996b). Few studies analyze the richest biological groups, such as insects in broad-scale analyses (Schuldt and Assmann 2010; Vianna and De Marco Jr 2012).

Despite the extreme diversity of insects and the recognized importance of the ecosystem services they provide (Losey and Vaughan 2006), they are usually disregarded in broad-scale macroecological and conservation biogeography frameworks (Cardoso et al. 2011; Diniz-Filho et al. 2010). Even relatively well-known groups for which extensive biological and ecological data are available (e.g. bees, ants and butterflies) are often excluded due to a lack of available distributional information, especially in tropical regions. As a first step towards elucidating this problem, we

provide a quantitative assessment of distribution patterns for Brazilian stingless bees, based in a large part on newly digitized specimen records and building upon the extraordinarily thorough data-compilation provided by the Meliponini section of Moure's Bee Catalogue (Camargo and Pedro 2007). Specifically our goals were to: 1) evaluate the effects of biases affecting available distributional data for Meliponini; 2) map sampling gaps for the tribe; and 3) test whether overall generic-level information on the stingless bees, or species-level data for selected taxonomically well-known genera may be used as surrogates for Meliponini species-level data overall or the taxonomically poorly-known genera, under the HTA and the CTA surrogacy assumptions. Spatial diversity patterns all Brazilian stingless bees were evaluated in comparison to results for those genera with recent and additional available distributional information, i.e. the subset for which genuine patterns should be discernible.

2.2 MATERIAL AND METHODS

2.2.1 Meliponini, the stingless bees

The stingless bees compose tribe Meliponini (Apidae), a large monophyletic group of highly eusocial insects that abound in warm and humid forests throughout the tropics adjacent subtropics (Michener 2007; Rasmussen and Cameron 2010). In the Americas, these bees occur from northern Mexico (Búrquez 1997) to northern Argentina and on some Caribbean islands. Meliponini are diverse and abundant in warm lowlands, but some species, notably of the Andean *Parapartamona,* are adapted to high elevations, extending their distribution close to 4000 m in the Andes (Camargo and Pedro 2007; Freitas et al. 2009). In the Neotropics, stingless bees provide prominent pollinating services for several wild (Michener 2007; Roubik 1989) and crop plant species (Malagodi-Braga and Kleinert 2004). Addtionally, some Meliponini bees

species also have great socioeconomic importance, as their colonies (especially of in *Melipona*, but also *Frieseomelitta*, *Scaptotrigona*, *Tetragonisca*, and *Tetragona*) yield honey, propolis, and other products harvested and commercialized by local people (Magalhães and Venturieri 2010; Posey 1982; 1983).

These bees have perennial colonies, with varying sizes from a few to thousands of individuals (Michener 2007) may be found in the ground (e.g. *Geotrigona*; Camargo and Moure 1996), preexisting cavities, or even within abandoned termites or ants nests (Camargo and Pedro 2003; Michener 2007; Pedro and Camargo 2003). Nonetheless, exposed nests on tree branches, walls or rock faces may also occur. Usually, these bees secrete wax and mix it with resins and gums to construct their nest walls, but other materials, such as mud or feces, may also be used by some species (Michener 2007).

Currently, there are about 500 described Meliponini species worldwide (Ascher and Pickering 2014), of which 391 are distributed across as many as 33 genera (fewer if some are treated as subgenera; see Michener 2007) occur in the Neotropics (Camargo and Pedro 2007; and its online updates). In areas such as western Amazonia, where the Meliponini are exceptionally diverse (D Roubik and JS Ascher, unpublished), much of the fauna remains undescribed, as much of this region was inaccessible to early collectors. Many undescribed forms exist especially in the small-bodied genera such as *Trgonisca* and *Plebeia*, so the actual number of species is certainly higher. Only some of the Neotropical genera have comprehensive taxonomic revisions (e.g. *Aparatrigona, Camargoia, Celetrigona, Dolichotrigona, Geotrigona, Lestrimelitta, Leurotrigona, Paratrigona, Partamona, Ptilotrigona*; the well-known Meliponini genera hereon). Of the 236 described species recorded from Brazil, at least 78 are endemic, based on the available data. Four *Melipona* species are polytypic, with valid subspecies, whereas

many other former subsepecies have been elevated to specific rank (Camargo and Pedro 2007).

2.2.2 Meliponini occurrence dataset

We compiled available Brazilian records for Meliponini from: 1) publicly accessible online databases (GBIF portal (http://www.gbif.org); CRIA's Species Link (http://www.splink.cria.org.br; Table S1), 2) taxonomic revisions and other literature and unpublished reports (see Supplementary material); and 3) additional newly igitized specimen records from: (a) Division of Invertebrate Zoology database of the American Museum of Natural History (Schuh et al. 2010) captured using the Arthropod Easy Capture Software (Available at: http://sourceforge.net/p/arthropodeasy, v. 1.34, 2013); (b) Laboratório de Bionomia, Biogeografia e Sistemática de Insetos (BIOSIS), from Universidade Federal da Bahia; and (c) Bee Biology and Systematics Lab of USDA-ARS, from the Department of Biology of the Utah University. Data from other research institutions consulted were not digitized, not publicly accessible, or otherwise unavailable.

To minimize biases and improve data quality we followed the procedures described in De Giovanni et al. (2012) and cleared georeferences which (1) had erroneous georeferences, e.g. those mapping in the ocean; (2) were from species not definitively verified from Brazilian localities, such as putative *Trigona fulviventris* and *T. fuscipennis*, which belong to difficult species complexes as yet not adequately resolved (Camargo and Pedro 2007); (3) lacked adequate locality data (i.e. county/municipality information) preventing them from being properly mapped; (4) were duplicates, i.e. records of the same species at the same geographic coordinates, a common occurrence given the eusocial nature of stingless bees; and (5) were identified

only to genus or tribe. Nonetheless, we maintained in the dataset specimens from *Trigona recursa* sensu auct., which may pertain to a complex of related cryptic species, several of which are undescribed (Camargo and Pedro 2007), since this taxonomic entity was very recurrent in our dataset. We used IBGE's gazetteer (2003) and Google Earth (Google Inc. 2013) to obtain city hall coordinates as a proxy geographic information for occurrences with only county information available, corrected occurrences with typos and misspellings, and scrutinized any records from outside the range of a species' documented distribution.

We cross-checked taxonomic and distributional information from Camargo & Pedro (2007 and its online updates) with the "Discover Life bee species guide and world checkliston bee species (Ascher and Pickering 2014) to assess taxonomic nomenclature for Brazilian species, minimize outdated or erroneous identifications, and assemble comprehensive lists for Brazilian states for use in richness analyses. In this dataset, we treated four valid *Melipona* subspecies as operational taxonomic units (OTU hereon). We took the utmost care to filter and exclude doubtful records inconsistent with verified state occurrence records as recorded in revisions and other reliable sources (Camargo and Pedro 2007). Although, such filters may exclude some genuinely correct new species occurrences from the dataset, they offset this by avoiding many more unreliable occurrences present in source datasets.

2.2.3 HTA, CTA, and biases analyses

We built a grid with 709 1º cells (~ 110 km in the tropics) covering Brazil, within which we derived our predictor variables and assessed the effects of potential geographic, spatial, and additional human-related biases in our Meliponini bees occurrence dataset. We obtained data from Brazilian government agencies (Table S1),

for the predictor variables within each grid cell for the following known sources of biases in biological collections (Newbold 2010; Pyke and Ehrlich 2010; Reddy and Davalos 2003): 1) human demographic density (HDD), 2) gross regional product (GRP), 3) human development index (HDI), 4) road density (RDD), and 5) river density (RVD). Additionally, for all grid cell containing Meliponini sampling events, we measured the distance (DIST) from the cell's centroid to the nearest research institution involved with any aspects of melittological research (taxonomy, ecology, and/or life history aspects; Table S2 and Figure S1) and considered the estimated number of bee specimens within their entomological collections. As some socio-economic variables were collinear (Table S3), the final variables set included only HDD, GRP, RVD, and DIST.

Given several the factors that may cause artifactual estimates of the observed Meliponini species richness (e.g., active vs. passive sampling methods; biases related to identification and data basing etc), we used sample-based rarefaction curves to derive rarefied generic/species richness as our response variables within each grid cell (Gotelli and Colwell 2001). We varied our rarefaction factor from a minimum of 50 and a maximum of 100 samples to derive different rarefied richness within our grid cells. We developed a similar approach for the *Partamona* bees, the stingless bee genus with the highest amount of occurrences in our dataset due to the comprehensiveness of recent revisions (Camargo and Pedro 2003; Pedro and Camargo 2003). In comparision to the whole dataset, we were only able to derive *Partamona* rarefied richness considering a minimum of 15 and a maximum was 30 samples per cells, once higher rarefaction factors decreased the amount of grid cells too much, impeding proper statistical analyses given the small sample size. We log-transformed (log+1) these response variables to assure they were normally distributed and had a homogeneous variance.

We assessed the correlation between of higher (rarefied genera richness) and lower (rarefied species richness) or well- vs. poorly-known Meliponini taxa through pair-wise spatial Spearman's correlations to implement both the HTA and CTA frameworks. In all these analyses, we only correlated grid cells with at least 50 and a maximum of 100 samples. Nevertheless, once well-known species had a distribution mainly constrained to the Amazon, while the poorly-known taxa had more wide-spread distributions, we only assessed their rarefied richness correlations in grid cells with 50 and 60 samples (see below)

We measured the effects of the predictor variables on the response variables through Ordinary Least Squares (OLS hereon) regressions. We used eigenvector-based spatial filters (SP filters hereon) as additional predictor variables which could account for the spatial autocorrelation observed in the response variables (Diniz-Filho and Bini 2005). Using this protocol, we also showed (when possible) partial regression coefficients, reporting the amount of variation explained by our predictor variables as well as that explained by the data's spatial structure. We also assessed the effects of spatial autocorrelation (SAC hereon) through autocorrelograms with Moran's *I*. We performed these analyses in two ways: 1) by considering all Meliponini data lumped together and 2) by only considering genus *Partamona*. We performed all these analyses in SAM v4.0 (Rangel et al. 2010).

We checked the quality of the Meliponini occurrences, by classifying them as either "City" (coordinates distant less than 4 km from the nearest city hall coordinates) and or "GPS" (coordinates distant farther than 4 km from the nearest city hall coordinates) records. We tested our data for spatial biases related to the distance of each sampling event to the nearest city/institution involved with bee research. In order to do so at first, we summed up the observed distances of each "GPS" sampling event to the

nearest institution/city to obtain observed distance summed values. Later, we randomly placed the same amount of occurrences onto the geographic space 999 times to obtain randomized distributions of summed distances values to the nearest city/research institution. Thus, we could calculate the probability of randomly obtaining the spatial pattern we observed in our dataset. We weighted both the observed and the randomized values by the amount of occurrences used in each analysis. We did not use "City" records once museum collections usually georeference old records by using city hall coordinates. We also did this analysis for the well-known Meliponini genera.

2.3 RESULTS

From an initial dataset of more than 100,000 occurrences of Brazilian stingless bees, we assembled 10,288 non-redundant records meting data standards, covering 29 genera, and 240 OTUs (230 species and 10 subspecies; Table S4), results similar to those observed in the Moure's Bee Catalogue (Table 1; Camargo and Pedro 2007). There were differences in the state species richness available from the Moure's Bee Catalogue and the one we found here: while for some states we obtained higher species richness, for others we did not reach the reported species richness. On one hand, Distrito Federal (+7 spp.), Rondônia (+6 spp.), Tocantins (+5 spp.) and Pernambuco (+4 spp.) were the ones in which our state species richness was higher than reported in the literature, on the other, Amapá (-15 spp.), and Mato Grosso (-7 spp.) were the states where we were less effective to reach the reported richness from the literature.

The majority of the stingless bee genera occurred within only a few cells, 10 occurred in 50 or fewer grid cells (Figure 1A). Three genera occurring within at least 300 grid cells: *Melipona*, Trigona, and *Partamona* (Figure 1B), and seven other widely recorded genera and the number of grid cells where they occurred are listed in Figure

1B. Most species occurred in 20 or fewer grid cells (Figure 1C), whereas the most widely recorded one species was *Trigona spinipes*, found in 144 grid cells. The other ten most widely recorded Meliponini species are listed in Figure 1D. One of these, *T. recursa* sensu auct.

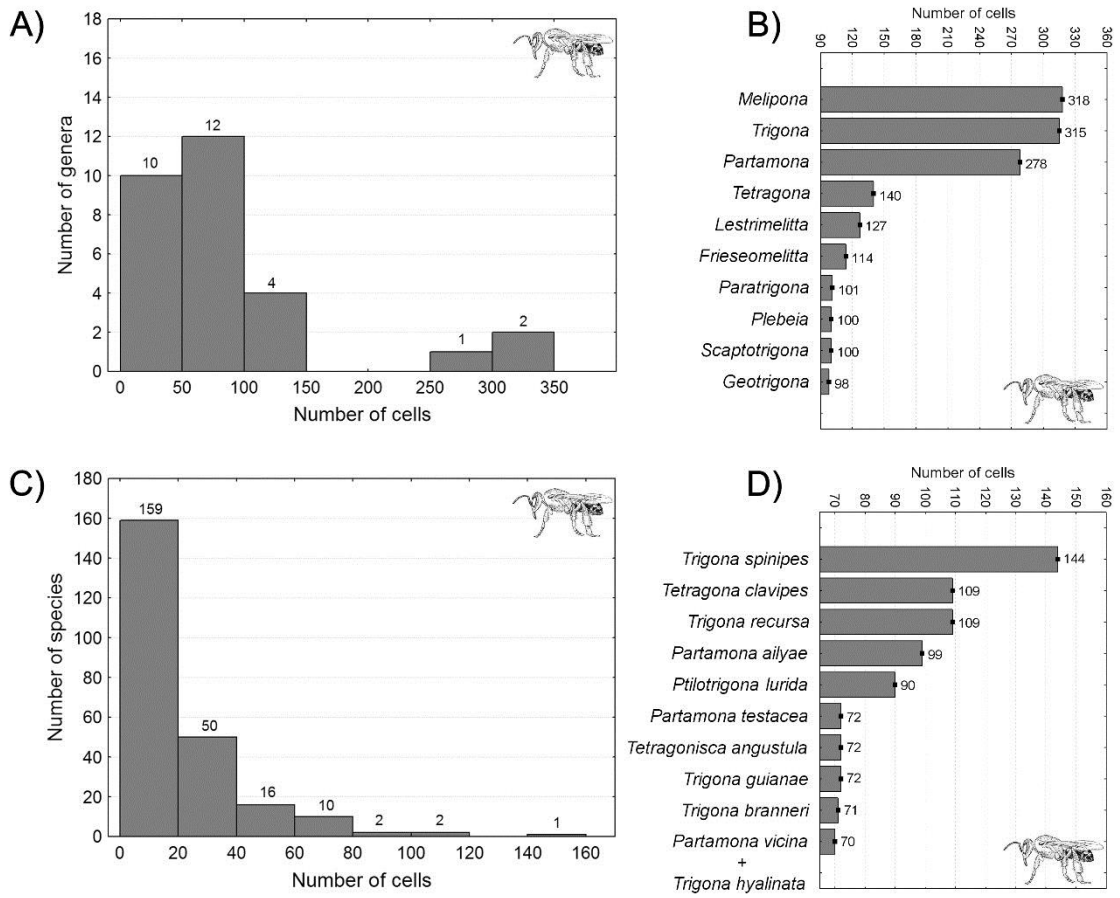


Figure 1 –Brazilian Meliponini data considering their occurrences within the 709 1º grid cells. (A) Generic occurrences by grid cells. (B) The ten most frequent Brazilian Meliponini genera. (C) Species occurrences by grid cells. (D) The eleven most frequent Brazilian Meliponini species. Number above bars in (A) and (C) represent the amount of taxa in a given class category and in (B) and (D) represent the amount of grid cells occupied by a given taxa.

We did not find any information for stingless bee genera in 38.50% of the grid cells (n=273; Figures 2A and 2D). Only 14 grid cells (1.98%) had 16 or more genera recorded. The richest grid cells were sampled mainly within the Brazilian states of Amazonas (n=6), Minas Gerais (n=2), and São Paulo (n=3; Figure 2D), those with renowned institutions involved with bee research (e.g. Instituto Nacional de Pesquisas da Amazônia/INPA, Universidade Federal de Minas Gerais, and Universidadede São Paulo, respectively). Regarding species richness by grid cell, 38.50% (n=273) had no information (Figure 2B and 2E). Many of the richer grid cells (41 to 70 species; 11 of 12) were found in the Amazon and the grid cells surrounding Manaus reached the highest observed richness. Only one grid cell in southeastern Brazil (corresponding to the city of São Paulo) reached a similar observed richness (41 to 70 species). When considering the *Partamona*, 445 grid cells (59%) had no information and of the remaining ones, 23.83% had only 1 or 2 species. The richer ones were mainly distributed in the state of Amazonas, in the core of Amazon forest (7 to 8 species; Figure 2C and 2F). Independent of the taxonomic level considered, we also observed a clear accumulation of sampled grid-cells in eastern Brazil, when compared to western regions (Figs. 2A-2C). Finally, a noteworthy result is the severe lack of information about the Meliponini fauna along the Brazilian Cerrado, interior Amazon regions, and even the eastern coast, which either had none information (white grid cells) or were under sampled (blue grid cells) when compared to the best sampled grid cells in the country.

A total of 45 grid cells satisfied the criteria of 50 records for rarefaction analysis, but this number decreased to only 14 cells if we raised the criterion to 100 records (Table 2; Figure 3). Grid cells with more than 100 samples were mainly

distributed in the Amazon, but there were three of them distributed in São Paulo, and one in Pernambuco (Figure 3F).

Table 1 – Observed Meliponini richness by state retrieved from Moure's Catalogue (Camargo and Pedro 2013), the one obtained in our dataset and the richness differences from the different data sources. The exact location of each state may be found in Figure 3.

State	Moure's Catalogue	This study	Difference
Acre (AC)	61	65	+4
Alagoas (AL)	7	8	+1
Amapá (AP)	54	39	-15
Amazonas (AM)	118	121	+3
Bahia (BA)	45	47	+2
Ceará (CE)	30	26	-4
Distrito Federal (DF)	5	12	+7
Espírito Santo (ES)	37	33	-4
Goiás (GO)	36	34	-2
Maranhão (MA)	52	54	+2
Mato Grosso (MT)	81	74	-7
Mato Grosso do Sul (MS)	24	26	+2
Minas Gerais (MG)	60	57	-3
Pará (PA)	113	110	-3
Paraíba (PB)	18	20	+2
Paraná (PR)	36	34	-2
Pernambuco (PE)	17	21	+4
Piauí (PI)	21	19	-2
Rio Grande do Norte (RN)	8	9	+1
Rio Grande do Sul (RS)	24	26	+2
Rondônia (RO)	74	80	+6
Roraima (RR)	28	31	+3
Santa Catarina (SC)	27	28	+1
São Paulo (SP)	56	59	+3
Sergipe (SE)	7	8	+1
Tocantins (TO)	26	31	+5

Neary 34% of occurrences in the stingless bee dataset were georeferenced by city hall coordinates (Table S4) and these bees were generally sampled near cities (Figs. 4). For Meliponini bees as a group (Figure 4B), and for the well-studied the genera

Geotrigona (Figure 4L), *Lestrimelitta* (Figure 4N), *Leurotrigona* (Figure 4P), and *Paratrigona* (Figure 4R), the sampling events usually occurred near research institutions. However, bees from the genera *Aparatrigona* (Figure 4D), *Camargoia* (Figure 4F), *Celetrigona* (Figure 4H), *Dolichotrigona* (Figure 4J), *Partamona* (Figure 4T), and *Ptilotrigona* (Figure 4V), were usually sampled away from research institutions.

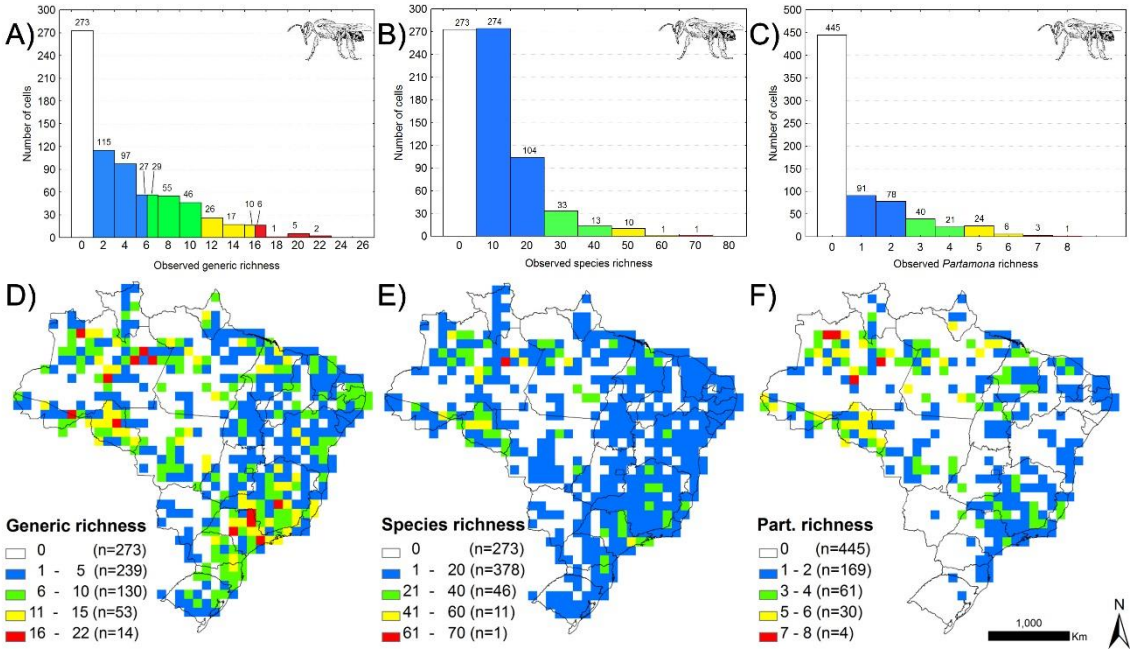
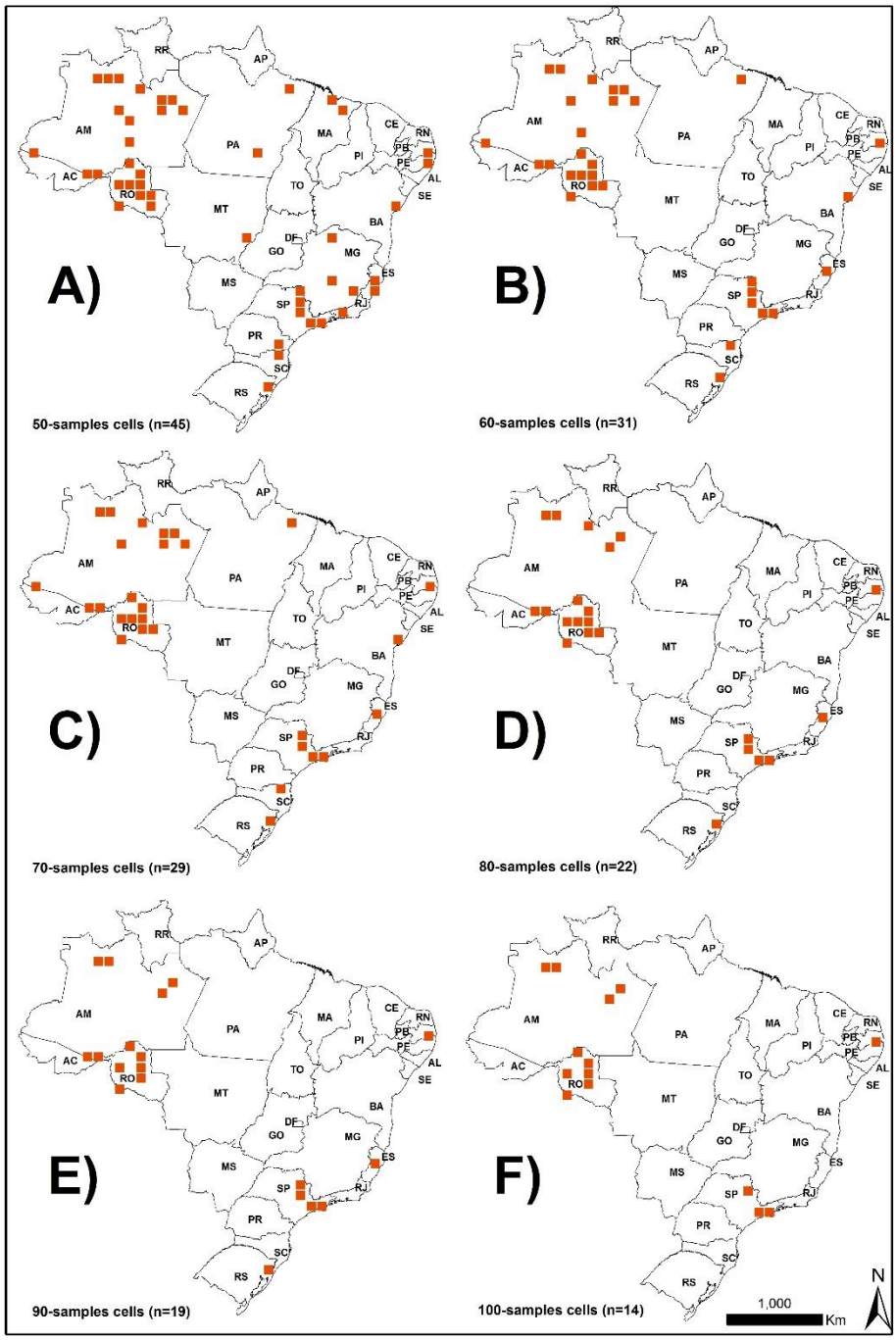


Figure 2 – Data quality and spatial distribution of sampling effort for Meliponini bees in Brazil. (A) Histogram of the generic richness. (B) Histogram of the specific richness. (C) Histogram of *Partamona* species richness. (D) Spatial distribution of the observed generic richness. (E) Spatial distribution of the observed species richness. (F) Spatial distribution of the observed *Partamona* species richness. Numbers in (A), (B), (C), (D), (E), and (F) refer to the number of grid cells within each richness category considered.



1 **Figure 3** – Spatial distribution of rarefied grid cells with A) 50, B) 60, C) 70, D) 80, E)
2 90, and F) 100 samples. The letters within the Brazilian states refer to their known
3 abbreviations.

Table 2 – Higher-taxon (generic vs. species richness) and cross-taxon (well-known vs. poorly known) correlations for grid cells with 50 to 100 samples and 50 to 60 samples. d.f. stands for degrees of freedom.* refer to p<0.001.

	All available data			Well- vs. Poorly-known Meliponini groups		
Variable	**n cells**	**Corrected d.f.**	**Sperman's r**	**n cells**	**Corrected d.f.**	**Sperman's r**
Rarefied richness – 50 samples	45	32.1	0.728*	23	18.041	-0.202
Rarefied richness – 60 samples	31	26.6	0.761*	16	20.991	-0.132
Rarefied richness – 70 samples	29	16.8	0.823*	–	–	–
Rarefied richness – 80 samples	22	27.1	0.737*	–	–	–
Rarefied richness – 90 samples	19	18.8	0.716*	–	–	–
Rarefied richness – 100 samples	14	14.1	0.833*	–	–	–

Table 3 – Multiple regressions results for the Meliponini genera and species rarefied richness within grid cells with at least 70 samples according to ordinary least-squares (OLS). Bold values are statistically significant.

Response variable	**Bias predictors**	**Std. Coeff.**	**Std. Error**	**t**	***p*-value**	**Response variable**	**Bias predictors**	**Std. Coeff.**	**Std. Error**	**t**	***p*-value**
Generic richness 70 samples (R^2=0.038; n=29)	RVD	0.169	0.005	0.874	0.392	**Species richness 70 samples (R^2=0.510; n=29)**	RVD	0.11	0.004	0.784	0.442
	GRP	0.066	<0.001	0.340	0.737		GRP	0.013	<0.001	0.089	0.93
	HDD	-0.425	<0.001	-1.478	0.154		HDD	-0.05	<0.001	-0.341	0.737
	DIST	0.068	0.011	0.306	0.763		DIST	-0.451	0.010	-2.574	**0.018**
	SP filter nº 1	-0.531	0.182	-1.704	0.103		SP filter nº 1	0.824	0.121	4.658	**<0.001**
	SP filter nº 2	-0.350	0.115	-1.775	0.090		SP filter nº 2	-0.382	0.094	-2.759	**0.012**
Generic richness 80 samples (R^2=0.006; n=22)	RVD	0.235	0.005	0.934	0.365	**Species richness 80 samples (R^2=0.474; n=22)**	RVD	0.105	0.005	0.566	0.58
	GRP	0.032	<0.001	0.128	0.900		GRP	0.018	<0.001	0.096	0.925
	HDD	0.022	<0.001	0.078	0.939		HDD	<0.001	<0.001	-0.003	0.998
	DIST	-0.225	0.01	-0.957	0.354		DIST	-0.424	0.011	-2.073	*0.057*
	SP filter nº 1	-0.364	0.105	-1.575	0.136		SP filter nº 1	-0.791	0.124	-3.498	**0.004**
							SP filter nº 2	-0.511	0.093	-3.018	**0.009**
Generic richness 90 samples (R^2=0.035; n=19)	RVD	0.186	0.006	0.654	0.525	**Species richness 90 samples (R^2=0.452; n=19)**	RVD	0.084	0.005	0.401	0.696
	GRP	-0.004	<0.001	-0.014	0.989		GRP	-0.013	<0.001	-0.061	0.952
	HDD	0.052	<0.001	0.168	0.869		HDD	0.017	<0.001	0.074	0.942
	DIST	-0.280	0.012	-1.078	0.302		DIST	-0.459	0.012	-2.05	*0.065*
	SP filter nº 1	0.323	0.117	1.238	0.239		SP filter nº 1	0.776	0.134	3.13	**0.010**
							SP filter nº 2	0.511	0.103	2.677	**0.022**
Generic richness 100 samples (R^2=0.461; n=14)	RVD	0.232	0.004	0.900	0.398	**Species richness 100 samples (R^2=0.468; n=14)**	RVD	-0.024	0.005	-0.100	0.923
	GRP	-0.020	<0.001	-0.088	0.932		GRP	-0.136	<0.001	-0.594	0.571
	HDD	-0.558	0.002	-1.845	0.108		HDD	-0.728	0.002	-2.301	*0.055*
	DIST	-0.812	0.011	-2.924	**0.022**		DIST	-0.715	0.015	-2.358	**0.050**
	SP filter nº 1	0.325	0.098	1.179	0.277		SP filter nº 1	-0.024	0.005	-0.100	0.923

Table 4 – Multiple regressions results for the *Partamona* rarefied species richness within grid cells with at least 15 samples according to ordinary least-squares (OLS). Bold values are statistically significant.

Resp. variable	Bias predictors	Std. Coeff.	Std. Error	t	*p*-value
	RVD	-0.172	0.003	-1.477	0.150
Partamona	GRP	0.020	<0.001	0.168	0.868
15 samples	HDD	-0.014	<0.001	-0.114	0.910
(R^2=0.547; n=37)	DIST	0.138	0.006	1.119	0.272
	Spatial filter nº 1	-0.554	0.084	-4.649	**<0.001**
	Spatial filter nº 2	0.488	0.083	4.138	**<0.001**
	RVD	0.007	0.003	0.049	0.961
Partamona	GRP	0.079	<0.001	0.527	0.607
20 samples	HDD	0.005	<0.001	0.029	0.978
(R^2=0.662; n=21)	DIST	-0.168	0.007	-1.002	0.333
	Spatial filter nº 1	-0.961	0.081	-4.969	**<0.001**
	RVD	0.073	0.004	0.250	0.811
Partamona	GRP	-0.076	<0.001	-0.274	0.793
25 samples	HDD	-0.814	0.016	-0.995	0.358
(R^2=0.474; n=13)	DIST	0.160	0.010	0.532	0.614
	Spatial filter nº 1	0.095	0.243	0.112	0.915
	RVD	0.150	0.007	0.367	0.738
Partamona	GRP	-0.352	<0.001	-0.654	0.560
30 samples	HDD	-0.584	0.016	-0.858	0.454
(R^2=0.130; n=10)	DIST	0.329	0.010	0.915	0.428
	Spatial filter nº 1	-0.299	0.114	-0.534	0.631

Considering the HTA, the generic rarefied richness was positively correlated with the species rarefied richness, with all Spearman's pair-wise correlation coefficients reaching values higher than 0.7 (Table 2). On the other hand, CTA between taxonomically well-known vs. poorly-known stingless bee genera did not show significant correlations.

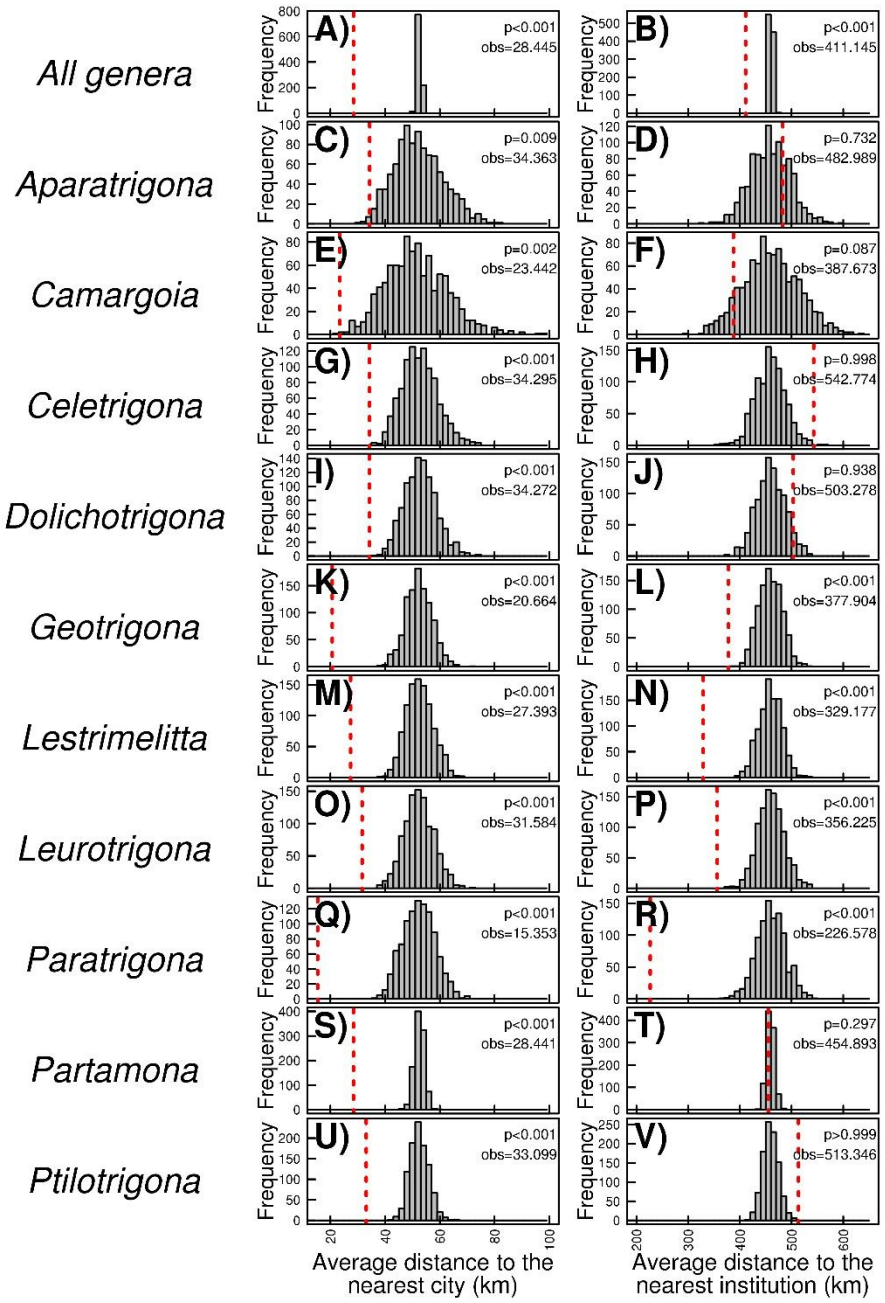


Figure 4 – Histograms for the randomized distances of Meliponini sampling events to the nearest city (left side) and nearest research institution (right side). (A) and (B): all Meliponini sampling events; (C) and (D): *Aparatrigona*; (E) and (F): *Camargoia*; (G) and (H): *Celetrigona*; (I) and (J) *Dolichotrigona*; (K) and (L) *Geotrigona*; (M) and (N) *Lestrimelitta*; (O) and (P) *Leurotrigona*; (Q) and (R) *Paratrigona*; (S) and (T) *Partamona*; (U) and (V) *Ptilotrigona*. The average observed distances (horizontal bars) and individual *p*-values are reported for each histogram.

Only the distance of the sampling events to the nearest research institution involved with bee research (DIST) negatively affected both Meliponini generic and species rarefied richness: the farther away from a research institution the sampling events took place, the lower the estimated rarefied richness (Table 3). However, when we consider the well-studied genus *Partamona*, we did not observe such a relationship (Table 4). In general, the addition of the spatial filters controlled for the spatial autocorrelation found within our estimates (Figures S2 and S3).

2.4 DISCUSSION

In this study, we evaluated the effects of some of the biases affecting the available data for the Brazilian Meliponini bees. We observed that the majority of the grid cells with no data were from western Brazilian regions, while in the Atlantic coast nearly all grid cells had at least one occurrence for the stingless bees. The distance of the sampling records to cities and research centers (for some genera only) were the main sampling bias we observed. Nevertheless, despite a few well-sampled grid cells in eastern Brazil, the majority of the better-sampled grid cells with Meliponini data in our dataset were mainly located within the Amazon, a known diversity center for stingless bees (Freitas et al. 2009). We also observed this pattern for the genus *Partamona*. Finally, although the stingless bee generic rarefied richness showed high correlation with their species rarefied richness, the same did not occur for the comparisons of the rarefied species richness of well- vs. poorly-known Meliponini species.

Fragmentary distributional data is a common feature across biological datasets from tropical regions (Ballesteros-Mejia et al. 2013; Kamino et al. 2011; Soberón et al. 2007). With respect to Brazil, the accumulation of biological data in the Atlantic coast is a frequent pattern observed for insect groups (tiger moths; Ferro and Melo 2011;

odonates; De Marco and Vianna 2005; Vianna and De Marco Jr 2012), "well-known" vertebrates (mammals; Patterson 1994; Bernard et al. 2011; herpetofauna; Costa et al. 2007; birds; da Silva 1995), and plant species (Sousa-Baena et al. 2013a). The historical concentration of human occupation in the Atlantic coastal areas of Brazil and the resultant high frequency of research institutions (Figure S1) may account for the relatively few grid cells with no Meliponini data we found in Central Brazil and the Cerrado savanna or in the Amazon. Especially for this Brazilian biome, there was a north-south longitudinal stripe lacking grid cells intensively sampled. Despite the fact this trend was caused by overall surveys under sampling, the fauna within this biome may be naturally less diverse when compared to other vegetational formations, such as the Amazon and the Atlantic rainforests. However, even some Brazilian regions with high human densities in the eastern coast also had several grid cells lacking a good knowledge on their stingless bees' fauna. The effects of the researchers' activity area and samplings performed near cities, as observed here, especially for some well-known Meliponini genera are often reported as sources of biases in biological data (Newbold 2010; Pyke and Ehrlich 2010; Reddy and Davalos 2003).

The spatial patterns we observed for the Brazilian stingless bees reflect the activities of the most active Brazilian researchers, including Padre J.S. Moure, D. Urban in Curitiba (Engel et al. 2012; Urban 2003), J.M.F. Camargo (Pedro 2009), S.R.M. Pedro in Ribeirão Preto, P. Nogueira-Neto in São Paulo, and F.A. Silveira in Belo Horizonte, and their students and colleagues. Usually, the overlapping distributions of species with centers of high human density and renowned taxonomic expertise result in higher probabilities of the local or regional species pool to be studied and described (Gaston and Blackburn 1994). Nonetheless, at least for the well-known Meliponini taxa, researchers actively sampled specimens and described species far away from their

homes and institutions, a pattern confirmed by our randomization tests. As the Meliponini fauna is still largely unknown in many portions of the Brazilian Amazon, especially those away from large rivers, certainly a great bee biodiversity is still to be discovered. Government incentives for colonization and road-building process deep in the Amazon may help on the discovery of new stingless bees, in the near future, but also considerably increase the ecological risks related to human activities.

Even though the Amazonian region is generally undersampled (Freitas et al. 2009), the areas where it was most sampled were some of the best-sampled and richest grid-cells in our dataset. Species richness for the genus *Partamona* also showed similar patterns, with the richest grid cells occurring mainly in the Amazon (Camargo and Pedro 2003; Pedro and Camargo 2003). Such pattern also arose for the taxonomically well-revised Meliponini groups (e.g. *Aparatrigona*, *Camargoia*, *Celetrigona*, *Dolichotrigona*, and *Ptilotrigona*), strictly centered on the Amazon or northeastern Brazilian regions, but rare or entirely absent from southern and eastern Brazil. Similar patterns may also emerge in the future for poorly-known Meliponini groups, which general includes small bodied-species sizes, when they receive comprehensive taxonomic reviews and their true distributional patterns are thoroughly documented. A lack of taxonomic revisions and identification resources for several Meliponini genera also prevents routine identification of such numerous, relatively large-bodied and conspicuous genera, as *Scaptotrigona*, and as result most material in collections remains as unidentified or misidentified specimens and is not digitized or otherwise available for analyses. This difficulty in making reliable species identification certainly impedes the effectiveness of any practical future conservation action (Kim and Byrne 2006).

The restricted distribution of the well-known genera to the Amazon in comparison with the poorly-known obscure ones, distributed in broader spatial extents,

is the main reason for the low correlation between the two taxa under the CTA assumptions. Such taxon- and scale-dependency of CTA and HTA analyses was already criticized elsewhere (Rosser and Eggleton 2012). Still, the effectiveness of the well-known Meliponini genera as biodiversity surrogates for the poorly-known ones remains to be tested in more restricted and finer spatial scales within the Amazon. Once new taxonomic revisions for the Meliponini are completed, and new data is added to our dataset, such analysis should be re-run. On the other hand, the high effectiveness of the rarefied richness of higher Meliponini taxa (genera) as surrogates for the rarefied richness of lower ones (species) were corroborated for the broad spatial scales we used, as expected by the HTA theory (Balmford et al. 2000; Balmford et al. 1996a; 1996b) and already observed for other Brazilian insect taxa (e.g. Vianna and De Marco Jr 2012). Despite, criticisms raised by Rosser and Eggleton (2012) on the effectiveness of the HTA, this framework is being increasingly used elsewhere and with different organisms (Groc et al. 2010; Heino et al. 2003; Lin et al. 2012; Ricketts et al. 1999; Schuldt and Assmann 2010).

Our results show that the available distributional data on the Brazilian Meliponini is far from complete and has obvious geographic biases. Nonetheless, it is far more comprehensive than available digitized information for Brazilian solitary bees, such as *Megachile* (Silva et al. submitted). Differing life-history traits certainly contribute to the striking difference we found in the amount of distributional data between both groups. Stingless bee species have large and often conspicuous nests and considerable higher recruitment rates to food resources from perennial colonies, so their detectability in the field are certainly far higher than that for *Megachile* and other solitary species. Visual conspicuousness, body coloration, body size, and behavioral traits are certainly important determinants affecting insects detectability (Dennis et al.

2006; Gaston et al. 1995; Gaston 1991; Nemésio 2012). Additionally, for some Meliponini bee species, socioeconomic aspects also inspire studies and data acquisition, given the harvest of honey, propolis, and other products, by local people (Magalhães and Venturieri 2010; Posey 1982; 1983).

Although sampling biases mapped here are some of the main reasons that explain the fragmentary distributional patterns we observed, other less-appreciated factors also contribute. Although researchers may have extensively sampled an area, resulting in an accumulation of many specimens and data to be processed, insufficient financial and/or personnel resources for identification and curation may severely delay the species-level documentation for the majority of the sampled material (Fontaine et al. 2012). Additionally, the lack of resources to capture the data available on specimens' labels of from many collections elsewhere, as well as to deliver such data to biodiversity portals (e.g. GBIF, CRIA's Species Link) also constitutes a severe obstacle to the assessment of bees' (and other biological groups) biodiversity (Costello et al. 2013; Ebach et al. 2011; Wheeler et al. 2012).

Finally yet importantly, historical sampling biases towards areas that provide putatively fruitful samples (Newbold 2010; Pyke and Ehrlich 2010), result in the specimen accumulation of already well-known species from already well-known sites. Such museum-related biases certainly affect taxonomists' ability to process, curate, identify, and describe eventual new taxa sampled at poorly known areas also generate biased spatial and taxonomic information and decrease the effectiveness of practical conservation actions. Nonetheless, obscure new occurrences, which can be costly to obtain, when allied with species distribution models, may 1) increase species' range to areas it was previously unexpected (Almeida et al. 2010; Silva et al. 2013); 2) guide future field surveys (Sousa-Baena et al. 2013a; 2013b); and even 3) help on the

discovery of previously unknown species (Raxworthy et al. 2003) or new populations for rarer (Silva et al. 2013) or threatened ones (De Siqueira et al. 2009).

Although museum's collections house an irreplaceable biological information, access to such data is usually difficult to obtain, and dependent on inherent sociopolitical pressures. Concerns about data ownership and academic priority (Wheeler et al. 2012), and lack of mechanisms to ensure proper credit for empirical workers, are important obstacles affecting proper description of biological diversity patterns. Collections require more reliable funding if they are to efficiently delivery publication-quality digitized specimens to major biodiversity online portals. This entails considerable investments in specimen curation and identification, in addition to digitalization itself. Optimal use of data will require improved cooperation among data providers and aggregators (Boakes et al. 2010; Wheeler et al. 2012). We are well aware that many additional Meliponini specimens potentially available for our study were not accessible to us, thereby reducing our ability to properly evaluate this bee group.

In this study, we mapped the available biological information for the Brazilian Meliponini bees, and the sampling effort invested on their sampling within Brazilian. Even though our data we is far from complete, even with respect to material identified in collections, this assessment may provide useful information of current sampling gaps needing new surveys for the improvement of the distributional data on these bees and support practical conservation actions. Given the fast and intense environmental changes in mega-diverse but poorly sampled tropical countries (Bawa et al. 2004; Hong and Lee 2006), similar analyses with other groups, including conspicuous flagship taxa such as orchid bees (e.g. tribe Euglossini) and other widely sampled insect groups.

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2.7 SUPPLEMENTARY MATERIALS

2.7.1 Supplementary tables

Table S1 – Internet addresses of datasets and shapefiles used in our study.

Data source	Web address
Global Biological Information Facility	http://www.gbif.org
Species Link	http://splink.cria.org.br
Brazilian Transport Ministry	http://www.transportes.gov.br/index/conteudo/id/36604
Brazilian Agency of Geography and Statistics (IBGE)	http://www.ibge.gov.br/home/download/geociencias.shtm
Natiaonal Water Agency (ANA)	http://www.ana.org.br
AMNH-IZ Database (as mapped on Discover Life)	http://www.discoverlife.org/mp/20m?kind=AMNH_BEE

Table S2 – List of renowned Brazilian collections* involved in bee research that were used in this study and their estimated number of bee specimens.

Institution Number	Institution Name	Brazilian state	Latidude	Longitude	Expected number of bee specimens
1	Univ. Federal do Acre	Acre	-9.953	-67.850	<1,000
2	Instituto de Pesquisas da Amazônia	Amazonas	-3.098	-60.016	10,000-50,000
3	Univ. Federal da Bahia	Bahia	-13.001	-38.500	10,000-50,000
4	Univ. Estadual de Feira de Santana	Bahia	-12.564	-38.750	1,000-10,000
5	Univ. Estadual de Santa Cruz	Bahia	-14.814	-39.150	<1,000
6	Univ. Federal do Maranhão	Maranhão	-2.522	-44.287	10,000-50,000
7	Univ. de Brasília	Distrito Federal	-15.736	-47.866	<1,000
8	Univ. Federal de Minas Gerais	Minas Gerais	-19.871	-43.950	10,000-50,000
9	Univ. Federal de Viçosa	Minas Gerais	-20.754	-42.850	1,000-10,000
10	Univ. Federal de Uberlândia	Minas Gerais	-18.916	-48.255	Unknown
11	Univ. Federal do Pará	Pará	-1.451	-48.466	10,000-50,000
12	Univ. Federal do Pernambuco	Pernambuco	-8.052	-34.950	10,000-50,000
13	Univ. Federal do Paraná	Paraná	-25.439	-49.266	>100,000
14	Univ. Estadual de Londrina	Paraná	-23.327	-51.183	1,000-10,000
15	Univ. Federal do Rio de Janeiro	Rio de Janeiro	-22.904	-43.216	10,000-50,000
16	Univ. Estadual do Norte Fluminense	Rio de Janeiro	-21.763	-41.283	10,000-50,000
17	Univ. Federal do Rio Grande do Sul	Rio Grande do Sul	-30.034	-51.216	10,000-50,000
18	Univ. Federal de Santa Catarina	Santa Catarina	-27.596	-48.533	1,000-10,000
19	Univ. de São Paulo - Ribeirão Preto	São Paulo	-21.184	-47.800	>100,000
20	Univ. de São Paulo - São Paulo	São Paulo	-23.559	-46.700	10,000-50,000
21	Univ. Federal de Campina Grande	Paraíba	-6.481	-36.133	1,000-10,000
22	Univ. Federal da Paraíba	Paraíba	-7.136	-34.833	10,000-50,000

*We only considered those institutions participating in the proposed Brazilian Pollinators Identification Network.

Table S3 – Spearman's r (lower triangle) and *P*-values (upper triangle) from spatial correlation analyses among the four variables obtained from governmental institutes. Bold values correspond to significant Pearson's correlations.

	HDD	HDI	GRP	RDD
HDD	-	**0.019**	**<0.001**	**0.014**
HDI	**0.303**	-	**0.002**	0.212
GRP	**0.267**	**0.498**	-	0.197
RDD	**0.785**	0.374	0.111	-

Table S4 - Information from the Meliponini occurrences dataset. PGPS refers to the proportion of raw occurrences classified as "GPS" occurrences, and PCITY refers to the proportion of raw occurrences classified as "City" occurrences, for each taxa considered.

Genus	**n**	**PCITY**	**PGPS**	**Species**	**n**	**PCITY**	**PGPS**
Aparatrigona	57	0.263	0.737	*impunctata*	57	0.263	0.737
Camargoia	28	0.107	0.893	*camargoi*	9	0.222	0.778
				nordestina	12	0.083	0.917
				pilicornis	7	0.000	1.000
Celetrigona	107	0.280	0.720	*euclydiana*	3	0.000	1.000
				hirsuticornis	24	0.208	0.792
				longicornis	70	0.314	0.686
				manauara	10	0.200	0.800
Cephalotrigona	71	0.338	0.662	*capitata*	58	0.414	0.586
				femorata	12	0.000	1.000
Dolichotrigona	172	0.180	0.820	*browni*	50	0.180	0.820
				clavicornis	5	0.200	0.800
				longitarsis	46	0.174	0.826
				mendersoni	12	0.167	0.833
				moratoi	9	0.444	0.556
				rondoni	40	0.125	0.875
				tavaresi	10	0.100	0.900
Duckeola	42	0.119	0.881	*ghilianii*	33	0.152	0.848
				pavani	9	0.000	1.000
Friesella	42	0.548	0.452	*schrottkyi*	42	0.548	0.452
Frieseomelitta	260	0.327	0.673	*dispar*	8	0.500	0.500
				doederleini	69	0.275	0.725
				flavicornis	11	0.091	0.909
				freiremalai	1	1.000	0.000
				languida	21	0.429	0.571
				longipes	7	0.286	0.714
				meadewaldoi	32	0.344	0.656
				paranigra	1	0.000	1.000
				portoi	19	0.000	1.000
				silvestrii	5	0.400	0.600
				trichocerata	36	0.306	0.694
				varia	51	0.490	0.510
Geotrigona	239	0.385	0.615	*aequinoctialis*	20	0.300	0.700
				fulvohirta	8	0.750	0.250
				kwyrakai	2	0.000	1.000
				mattogrossensis	29	0.069	0.931

Genus	n	PCITY	PGPS	Species	n	PCITY	PGPS
Geotrigona				*mombuca*	68	0.338	0.662
				subfulva	1	0.000	1.000
	239	0.385	0.615	*subgrisea*	2	0.500	0.500
				subnigra	8	0.000	1.000
				subterranea	90	0.556	0.444
				xanthopoda	8	0.500	0.500
Lestrimelitta	251	0.406	0.594	*ciliata*	3	0.333	0.667
				ehrhardti	31	0.516	0.484
				glaberrima	1	0.000	1.000
				glabrata	10	0.200	0.800
				limao	75	0.440	0.560
				maracaia	6	0.000	1.000
				monodonta	12	0.083	0.917
				nana	1	0.000	1.000
				rufa	10	0.200	0.800
				rufipes	75	0.427	0.573
				similis	4	0.250	0.750
				sulina	17	0.588	0.412
				tropica	8	0.500	0.500
Leurotrigona	152	0.329	0.671	*gracilis*	24	0.042	0.958
				muelleri	113	0.425	0.575
				pusila	15	0.067	0.933
Melipona	1613	0.386	0.614	*amazonica*	19	0.263	0.737
				asilvai	52	0.577	0.423
				bicolor bicolor	38	0.684	0.316
				bicolor schencki	29	0.655	0.345
				brachychaeta	4	0.750	0.250
				bradleyi	8	0.000	1.000
				capixaba	10	0.600	0.400
				captiosa	12	0.250	0.750
				compressipes	11	0.182	0.818
				crinita	26	0.308	0.692
				dubia	5	0.200	0.800
				eburnea	6	0.333	0.667
				fasciculata	48	0.104	0.896
				flavolineata	34	0.353	0.647
				fuliginosa	70	0.243	0.757
				fulva	24	0.167	0.833
				fuscopilosa	16	0.313	0.688
				grandis	106	0.151	0.849
				illustris	31	0.194	0.806
				interrupta	26	0.308	0.692
				lateralis	22	0.227	0.773
				mandacaia	40	0.475	0.525
				marginata carioca	16	0.813	0.188
				marginata marginata	32	0.781	0.219
				melanoventer	75	0.173	0.827

Genus	n	PCITY	PGPS	Species	n	PCITY	PGPS
Melipona	1613	0.386	0.614	*mondury*	60	0.783	0.217
				nebulosa	22	0.318	0.682
				obscurior	23	0.652	0.348
				ogilviei	6	0.000	1.000
				orbignyi	10	0.900	0.100
				paraensis	34	0.206	0.794
				puncticollis	19	0.263	0.737
				quadrifasciata anthidioides	86	0.698	0.302
				quadrifasciata quadrifasciata	61	0.574	0.426
				quinquefasciata	78	0.385	0.615
				rufiventris	72	0.417	0.583
				schwarzi	36	0.139	0.861
				scutellaris	95	0.600	0.400
				seminigra abunensis	123	0.130	0.870
				seminigra merrillae	17	0.353	0.647
				seminigra seminigra	17	0.471	0.529
				subnitida	63	0.365	0.635
				titania	2	0.500	0.500
Mourella	39	0.615	0.385	*caerulea*	39	0.615	0.385
Nannotrigona	123	0.463	0.537	*chapadana*	5	0.600	0.400
				dutrae	3	0.000	1.000
				melanocera	9	0.333	0.667
				minuta	2	0.500	0.500
				punctata	3	0.000	1.000
				schultzei	9	0.444	0.556
				testaceicornis	91	0.484	0.516
Nogueirapis	38	0.132	0.868	*butteli*	27	0.185	0.815
				minor	11	0.000	1.000
Oxytrigona	105	0.400	0.600	*ignis*	10	0.300	0.700
				mulfordi	4	0.500	0.500
				obscura	39	0.128	0.872
				tataira	52	0.615	0.385
Paratrigona	188	0.548	0.452	*catabolonota*	1	1.000	0.000
				compsa	2	0.500	0.500
				crassicornis	1	1.000	0.000
				euxanthospila	3	0.000	1.000
				haeckeli	7	0.857	0.143
				incerta	2	0.500	0.500
				lineata	88	0.511	0.489
				lineatifrons	4	0.250	0.750
				melanaspis	1	0.000	1.000
				myrmecophila	2	0.000	1.000
				pannosa	8	0.125	0.875
				peltata	7	0.571	0.429
				prosopiformis	9	0.889	0.111
	188	0.548	0.452	*subnuda*	50	0.640	0.360
Partamona	2437	0.324	0.676	*ailyae*	359	0.178	0.822

Genus	n	PCITY	PGPS	Species	n	PCITY	PGPS
Partamona				*auripennis*	45	0.267	0.733
				batesi	30	0.167	0.833
				chapadicola	52	0.404	0.596
				combinata	183	0.328	0.672
				criptica	43	0.744	0.256
				cupira	96	0.688	0.313
				epiphytophila	84	0.321	0.679
				ferreirai	65	0.123	0.877
				gregaria	31	0.226	0.774
				helleri	283	0.311	0.689
				littoralis	18	0.278	0.722
				mourei	67	0.239	0.761
				mulata	30	0.667	0.333
				nhambiquara	197	0.168	0.832
				nigrior	2	0.000	1.000
				pearsoni	81	0.136	0.864
				rustica	27	0.593	0.407
				seridoensis	94	0.617	0.383
				sooretamae	34	0.735	0.265
				subtilis	13	0.538	0.462
				testacea	346	0.159	0.841
				vicina	256	0.207	0.793
Plebeia	384	0.526	0.474	*alvarengai*	2	0.000	1.000
				catamarcensis	16	0.688	0.313
				droryana	74	0.500	0.500
				emerina	54	0.759	0.241
				flavocincta	65	0.338	0.662
				grapiuna	1	1.000	0.000
				julianii	4	0.750	0.250
				lucii	3	1.000	0.000
				margaritae	5	0.200	0.800
				meridionalis	1	0.000	1.000
				minima	15	0.267	0.733
				nigriceps	13	0.923	0.077
				phyrnostoma	3	1.000	0.000
				poecilochroa	8	0.750	0.250
				remota	64	0.469	0.531
				saiqui	31	0.516	0.484
				variicolor	3	0.000	1.000
				wittmanni	18	0.667	0.333
Ptilotrigona	347	0.161	0.839	*lurida*	339	0.147	0.853
				pereneae	8	0.750	0.250
Scaptotrigona	244	0.500	0.500	*affabra*	3	0.000	1.000
	244	0.500	0.500	*bipunctata*	78	0.590	0.410
				depilis	39	0.410	0.590
				fulvicutis	8	0.375	0.625
				polysticta	27	0.370	0.630

Genus	n	PCITY	PGPS	Species	n	PCITY	PGPS
Scaptotrigona				*postica*	48	0.375	0.625
				tricolorata	2	0.000	1.000
				tubiba	16	0.563	0.438
				xanthotricha	23	0.870	0.130
Scaura	317	0.240	0.760	*atlantica*	10	0.100	0.900
				latitarsis	152	0.270	0.730
				longula	26	0.462	0.538
				tenuis	129	0.171	0.829
Schwarziana	130	0.446	0.554	*mourei*	14	0.429	0.571
				quadripunctata	116	0.448	0.552
Schwarzula	109	0.220	0.780	*coccidophila*	56	0.125	0.875
				timida	53	0.321	0.679
Tetragona	528	0.144	0.856	*clavipes*	268	0.179	0.821
				dorsalis	58	0.052	0.948
				essequiboensis	5	0.200	0.800
				goettei	142	0.127	0.873
				handlirschii	11	0.000	1.000
				kaieteurensis	8	0.125	0.875
				quadrangula	11	0.091	0.909
				truncata	21	0.190	0.810
Tetragonisca	164	0.530	0.470	*angustula*	145	0.490	0.510
				fiebrigi	12	0.833	0.167
				weyrauchi	7	0.857	0.143
Trichotrigona	5	0.000	1.000	*extranea*	5	0.000	1.000
Trigona	1956	0.281	0.719	*albipennis*	28	0.321	0.679
				amalthea	8	0.125	0.875
				amazonensis	119	0.160	0.840
				branneri	156	0.167	0.833
				braueri	10	0.500	0.500
				chanchamayoensis	94	0.213	0.787
				cilipes	68	0.191	0.809
				crassipes	88	0.159	0.841
				dallatorreana	74	0.176	0.824
				dimidiata	13	0.077	0.923
				guianae	213	0.160	0.840
				hyalinata	136	0.449	0.551
				hypogea	56	0.268	0.732
				lacteipennis	11	0.273	0.727
				pallens	108	0.185	0.815
				pellucida	15	0.000	1.000
				recursa	208	0.269	0.731
	1956	0.281	0.719	*sesquipedalis*	1	1.000	0.000
				spinipes	424	0.450	0.550
				truculenta	58	0.500	0.500
				williana	68	0.279	0.721
Trigonisca	144	0.368	0.632	*bidentata*	4	0.250	0.750
				ceophloei	2	0.000	1.000

Genus	n	PCITY	PGPS	Species	n	PCITY	PGPS
Trigonisca				*dobzhanskyi*	20	0.100	0.900
				duckei	2	0.500	0.500
				extrema	4	0.000	1.000
				flavicans	4	0.500	0.500
				fraissei	5	0.000	1.000
				graeffei	1	0.000	1.000
				hirticornis	7	0.286	0.714
				intermedia	8	0.375	0.625
				meridionalis	12	0.500	0.500
				nataliae	18	0.500	0.500
				pediculana	37	0.622	0.378
				rondoni	1	0.000	1.000
				unidentata	2	0.000	1.000
				variegatifrons	5	0.200	0.800
				vitrifrons	11	0.182	0.818

2.7.2 Supplementary figures

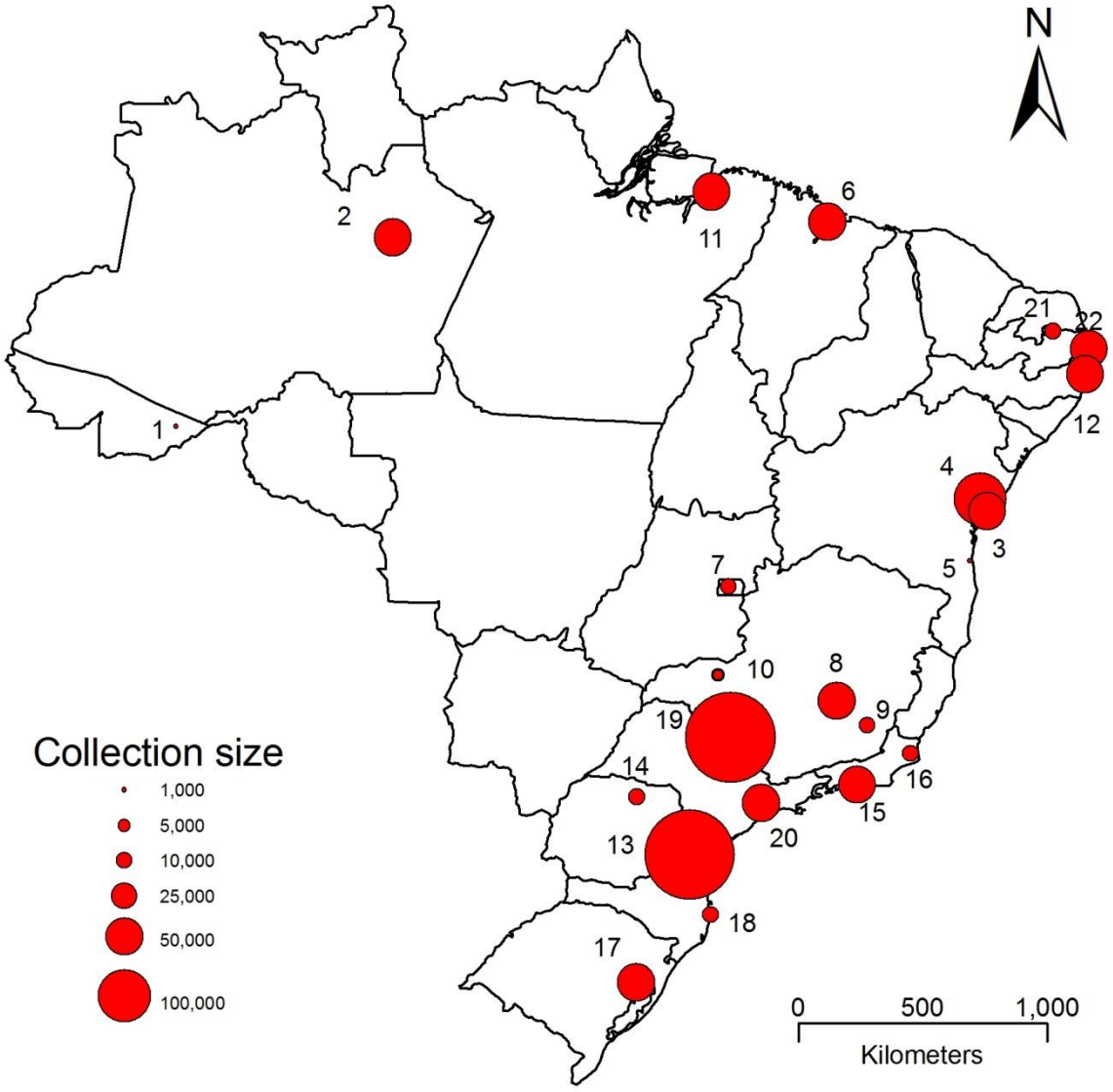

Figure S1 – Spatial distribution of research institutions considered in the spatial analyses and the expected number of bee specimens in their respective entomological collections. Note that the collection size of the institution number 10 (Univ. Federal de Uberlândia) is unknown.

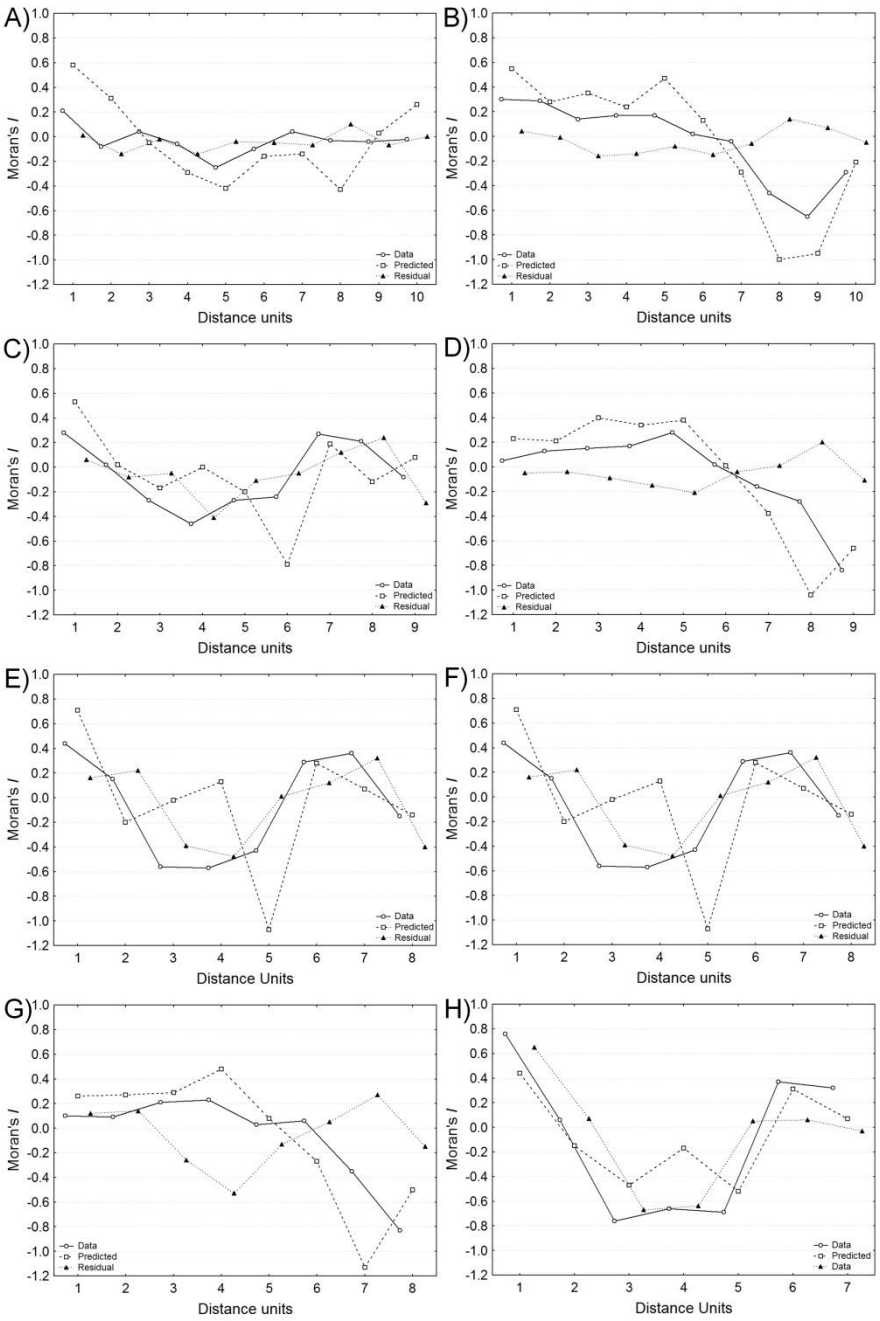

Figure S2 – Residual spatial autocorrelation obtained from the OLS analyses for the Meliponini generic (A, C, E, G) and specific (B, D, F, H) rarefied richness, considering grid cells with 70 (A, B), 80 (C, D), 90 (E, F), and 100 (G, H) samples. Opened circles, squares, and triangles refer to the observed, predicted, and residual Moran's *I* values, respectively.

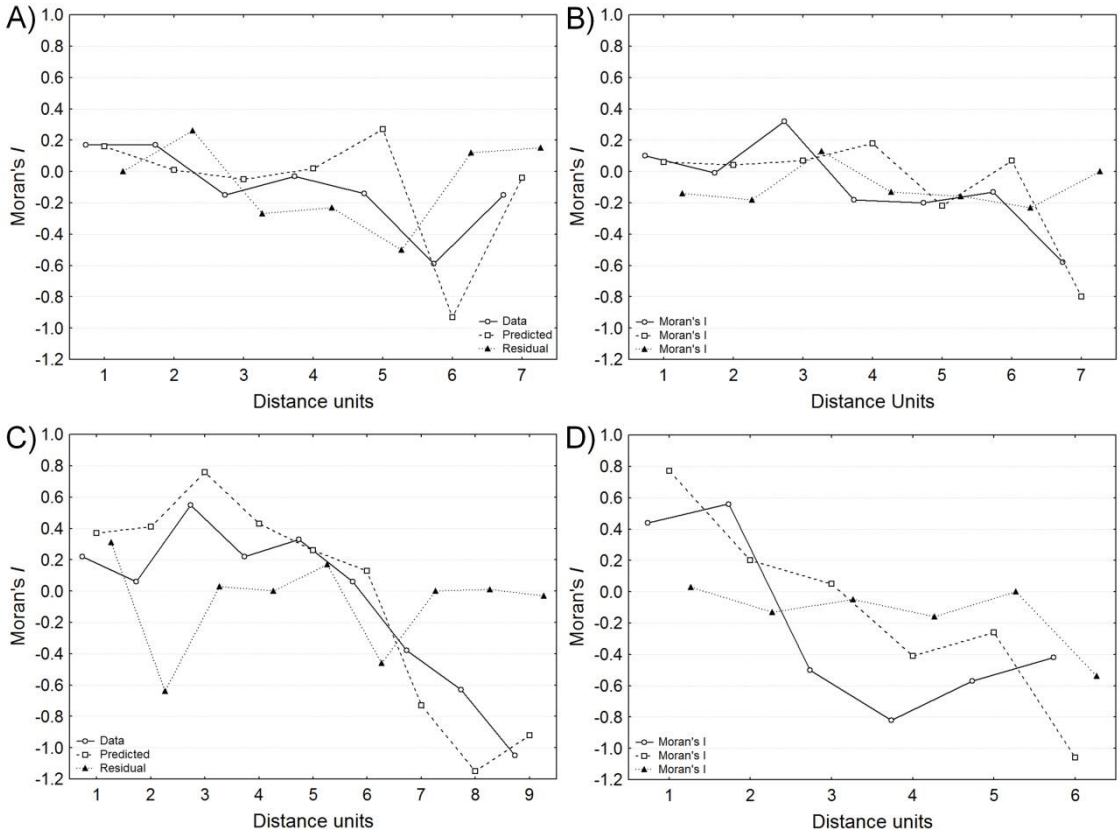

Figure S3 – Residual spatial autocorrelation obtained in the OLS analyses for the species richness of the *Partamona* genus considering grid cells with (A) 15 samples, (B) 20 samples, (C) 25 samples, and (D) 30 samples. Opened circles, squares, and triangles refer to the observed, predicted, and residual Moran's *I* values, respectively.

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- Coleção de Insetos da PUCRS
- Illinois Natural History Survey
- Coleção Entomológica Paulo Nogueira Neto – IB/USP
- Coleção Entomológica Pe. Jesús Santiago Moure (Hymenoptera) - UFPR
- Bee Biology and Systematics Laboratory
- Coleção de Entomologia do Labortório de Biologia Vegetal
- Coleção Entomológica Moure & Costa - EBDA
- Coleção Entomológica do Depto. de Sistemática e Ecologia - UFPB
- Laboratório de Ecologia e Biogeografia de Insetos da Caatinga - UFCG
- Coleção Entomológica dos Campos Gerais do Paraná - UEPG
- Coleção Entomológica da UFPE - UFPE

- Field Museum of Natural History – Brazilian records
- Coleção Entomológica "Adolph Hempel" do Instituto Biológico – IB
- Coleção Hymenoptera INPA – INPA
- Coleção Entomológica MHNCI – Museu de História Natural Capão da Imbuia
- Coleção Camargo – FFCLRP/SP
- Coleção Entomológica da UFES

Occurrences were also gathered from the Division of Invertebrate Zoology database of the American Museum of Natural History (http://www.discoverlife.org/mp/20m?kind=AMNH_BEE**) captured using the Arthropod Easy Capture Software (Available as a downloadable file from:** http://sourceforge.net/p/arthropodeasy**, version: 1.34, 2013, last accessed 06/26/13).**

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Original article

Amazonian species within the Cerrado savanna: new records and potential distribution for *Aglae caerulea* (Apidae: Euglossini)

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Abstract – Given human-related changes, quality distributional data are required for consistent conservation. Still, the lack of proper biogeographic information is a major setback for many groups. Here, we use new occurrences for *Aglae caerulea* in the Cerrado to model its potential distribution. We used Maximum Entropy (MaxEnt) and Genetic Algorithm for Rule-Set Production (GARP) algorithms in different modeling runs and both previous and new *A. caerulea* occurrences to predict this species distribution. Models which used only the previous *A. caerulea*'s records did not predicted the new Cerrado records, while those where we used the latter did predict the new ones as minimally suitable. *A. caerulea* distribution significantly increased towards the Cerrado according to both MaxEnt and GARP algorithms. Gallery forests are important dispersal alternatives for several species dwelling the Amazon and the Atlantic forest. Niche models of other rare Euglossini bees are advised to better evaluate their distributions.

***Aglae caerulea* / Amazon / Cerrado / dispersal corridor / Wallacean shortfall / species distribution modeling**

1. INTRODUCTION

In a continuously changing world, which is directly and indirectly affected by human activities (Tylianakis et al. 2008; Dobrovolski et al. 2011), high-quality distributional data are essential to help on the task of setting priorities and efficient conservation actions (Myers et al. 2000; Whittaker et al. 2005; Brooks et al. 2006). Still, the Wallacean shortfall, i.e., lack of proper biogeographic information, is one of the major setbacks hampering conservation actions (Bini et al. 2006). Such situation is even worse in megadiverse but poorly sampled tropical regions (Newbold 2010; Kamino et al. 2011), which usually lack extensive biogeographic information but suffer deep and fast environmental changes (Bawa et al. 2004; Hong and Lee 2006).

Beside their diversity, insects and other terrestrial invertebrates play several important

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ecosystemic roles (e.g., pollination, plague control, nutrient cycling). However, they have been usually neglected in conservation actions (Diniz-Filho et al. 2010a; Cardoso et al. 2011). Even insect groups with extensive taxonomic, biological, and ecological data available (e.g., ants, bees, odonates, and butterflies) lack consistent biogeographic data (Diniz-Filho et al. 2010a; Vianna and De Marco Jr 2012). Despite such problems, Diniz-Filho et al. (2010a) provided an optimistic view on how to use theoretical approaches and modern methods to conserve insects, such as ecological niche models (ENM). Based on statistically or derived response surfaces, ENMs relate presence records of a given species to the available predictor variables from those places where it was sampled to predict environmentally suitable areas for its occurrence (Guisan and Zimmermann 2000). Consequently, it is possible to fill gaps in the biogeographic knowledge concerning species distribution and improve the implementation of conservation actions (Nóbrega and De Marco Jr 2011).

Considering that species distribution is delimited by the intersection of environmentally suitable, biologically available, and biogeographically/historically reachable habitats (Soberón 2007), ENMs are useful tools in the attempt to overcome Wallacean shortfall and implement insect-oriented biogeography conservation plans (Diniz-Filho et al. 2010a). ENM techniques have been used quite often to study insects, particularly due to the following reasons: (1) determine potential distribution of taxa given new occurrences (Almeida et al. 2010), (2) assess suitable areas for future samplings (Diniz-Filho et al. 2010b), (3) pinpoint areas for the implementation of new conservation units (Nóbrega and De Marco Jr 2011), and (4) determine areas prone to invasion of alien species (Mata et al. 2010) or suitable for species distribution under different global warming scenarios (Giannini et al. 2012).

Considering new distributional data for the orchid bee *Aglae caerulea* Lepeletier and Serville (Apidae: Euglossini) outside its previously known core Amazonian distribution (see below), here we use both previous and new distribution data to deal with two questions. Initially, we assess whether previous occurrences of *A. caerulea* are sufficient to predict the new information obtained for the Cerrado biome and a doubtful Panamanian record (Moure 1967; Cameron 2004; Michener 2007). If they do, dispersal of *A. caerulea* from its core distribution can be considered the only process accounting for the new data. If they do not, we evaluate whether the inclusion of the new occurrences increases the total distribution for this species, pinpointing new suitable areas outside the Amazon for *A. caerulea*. Second, considering all *A. caerulea* occurrences, we evaluate its possible dispersal paths from its core distribution in the Amazon basin through the Cerrado, with particular attention to the role of riparian areas of large rivers.

2. MATERIAL AND METHODS

2.1. *A. caerulea* and its known distribution

Different from the other Euglossini bees, the rarely sampled *A. caerulea* has a long (23–25 mm long), slender, and flattened body and slender hind legs (Cameron 2004). The only bionomical observations available for this species indicate that it parasitizes nests of *Eulaema* bees (Myers 1935). Given its rareness in entomological collections and in Euglossini surveys using scent baits, it is considered to be a rare species in nature (Cameron 2004). Its distribution has been considered to be mostly restricted to the Amazon basin (Cameron 2004; Michener 2007). Nevertheless, this species has been lately sampled outside its Amazon core distribution in four different occasions (Anjos-Silva et al. 2006, and three new occurrences for the state of Goiás, Brazil, sampled by Silva, DP). Additionally, Moure (1967) reported its presence in Panama. Nonetheless, such occurrence has been flagged as uncertain since no other specimen of *A. caerulea* was sampled in that country again, even after decades of new surveys after the date of the first record (Cameron 2004).

We also compiled *A. caerulea* records from museum collections [(1) DZUP—Coleção Entomológica Padre J.S. Moure, Universidade Federal do Paraná, Curitiba, PR, Brazil; (2) RPSP—Coleção Camargo, Universidade de São Paulo, Ribeirão Preto, SP, Brazil;

(3) MZUSP—Muzeu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil; (4) COENTOL—Coleção Entomológica do Departamento de Biologia, Universidade do Estado de Mato Grosso, Cáceres, MT, Brazil], online data bases [(1) Discover Life Bee Species Guide and World Checklist (http://www.discover-life.org); (2) Species Link (http://splink.cria.org.br)], and literature (Morato 2001; Otero and Sandino 2003; Anjos-Silva et al. 2006). A total of 41 occurrences for *A. caerulea* were compiled, most of them in the Amazon basin, but with two records from the Choco region, in western Ecuador and southwestern Colombia. For records lacking the exact sampling site information, we used Google Earth (Google Inc. 2012) to find city center coordinates as a proxy information for sampling sites. The geographical coordinates of the three new *A. caerulea* occurrences found in Brazil may be found in the Supplementary Materials section (Table S1).

2.2. Environmental data

We derived seven environmental variables to be used in our ENM procedures and produce *A. caerulea* distribution models. Six of them [annual temperature, temperature seasonality (coefficient of variation), mean temperature of the driest quarter, annual precipitation, precipitation seasonality (coefficient of variation), and precipitation of the warmest quarter] were obtained from WorldClim (Hijmans et al. 2005; http:\\www.worldclim.org). The last variable (terrain slope) was derived from Hydro-1K global digital elevation model (http://eros.usgs.gov). We selected these variables since they were already used as climate predictors in other studies which modeled insect distributions (e.g., Almeida et al. 2010; Serra et al. 2012). Once some of our occurrences were related to city center coordinates instead of actual GPS coordinates, we re-scaled all variables to a 5-min resolution (0.0833º ≈ 8 km).

In order to define the location of the new *A. caerulea* occurrences in the species environmental space, we performed a principal components analysis (PCA) with all variables. Once all environmental variables had different units, prior to the analysis, we standardized them. We considered the Kaiser–Guttmann criterion (eigenvectors with eigenvalues higher than 1; Peres-Neto et al. 2005) to retain the most important PCA eigenvectors. The cutoff loading to consider an environmental variable as influent in the PCA analysis was 0.6.

2.3. Modeling procedures and model evaluation

We divided the occurrence dataset into three categories: (1) "Previous" (n=36), (2) "Cerrado" (n=4), and (3) "Doubtful" Panamanian record (n=1). In a first modeling run, we randomly split the previous and mostly Amazonian occurrences into 70 %:30 % training/testing subsets and evaluated whether the training subset was able to predict the newer and the doubtful *A. caerulea* occurrences. In a second modeling run, we included all the new Cerrado occurrences in the training subset and reevaluated *A. caerulea* distribution considering a testing subset composed by 30 % of all *A. caerulea* occurrences (except the newer and the Panamanian ones). Finally, we used all occurrences to predict the species distribution. The doubtful occurrence was never used in any of the modeling procedures. The modeling procedures are summarized in Figure S1.

We trained *A. caerulea* distribution models with two widely used algorithms: Maximum Entropy implemented in MaxEnt (Phillips et al. 2006; Phillips and Dudik 2008) and the Genetic Algorithm for Rule-Set Production (GARP; Stockwell and Peters 1999) implemented in openModeller Desktop v.1.1.0 (Munoz et al. 2011). MaxEnt is a machine-learning presence/pseudo-absence method which is very reliable when occurrence dataset have few and/or biased records (Pearson et al. 2007). We only modeled *A. caerulea* distributions with linear and quadratic features selected, to produce simpler biological models (Elith et al. 2011). GARP is a non-deterministic algorithm based in a random set of mathematical rules which may be interpreted as the limiting environmental conditions determining species occurrences (Stockwell and Peters 1999). Defining the area within which the species may potentially reach is an important step, while modeling species distribution, once the potential area the species may reach, is an important feature which affects the development of its ecological niche (Barve et al. 2011). Here, we trained the *A. caerulea*'s distribution models using the whole extent of South America as the species maximum potential ranges. Although different biogeographic regions may be contemplated within this region (e.g., Amazon basin, Cerrado, Mata Atlântica; Nemésio

and Silveira 2007), once the species was already sampled in two of those, to train the models considering the whole South American continent was advised and methodologically indicated.

Following Liu et al. (2011), we used both area under the receiver–operator curve (AUC) and true skilled statistics (TSS) to assess models performance. The AUC is a threshold-independent statistics varying from 0 to 1. Values around 0.5 represent distribution models no better than random and values around 1 represent a perfect fitting between the observed and the predicted species distribution. Acceptable distribution models are those with values higher than 0.7. TSS is a threshold-dependent statistics which varies from −1 to +1 (Allouche et al. 2006). TSS values near 0 or negative represent distributions no better than random, while values equal to +1 represent a perfect agreement between the observed and the predicted distribution. We used 10,000 random pseudo-absences during model evaluation procedures.

We used the lowest predicted suitability value associated with a given observed presence record (lowest presence threshold—LPT; Pearson et al. 2007), to determine *A. caerulea* distribution generated by each modeling algorithm. Ecologically speaking, the LPT identifies the pixels predicted to be as minimally suitable for the species occurrence as its actual observed records. For the final *A. caerulea* distribution, we used a single mean consensus map between both modeling algorithms in order to determine *A. caerulea* distribution, considering the LPT values that each independent model (Maximum Entropy and GARP) obtained when all occurrences (including the new Cerrado records) were used. This consensus method considers the separated values in each grid cell for all predictions obtained from different modeling algorithms to determine the mean modeled species distribution. This method was considered to be one of the most robust while determining the agreement of species distributions (Marmion et al. 2009). For the sake of discussing the distribution of *A. caerulea*, considering its known occurrences and the known Euglossini sampling effort in South American, we also show the ensemble distribution obtained from the threshold derived from the "receiver–operator curve" (ROC; Liu et al. 2011). While LPT minimizes omission but maximizes commission errors, ROC balances both errors and produces smaller distributions when compared LPT.

3. RESULTS

We retained three eigenvectors from our PCA analysis (Figure 1; Table S2). Nevertheless, we only show the results comparing the first two eigenvectors because such interpretation is simpler and the other comparisons (PC1 vs. PC3 and PC2 vs. PC3) had similar results (Figure S2A–B). All new occurrences from Cerrado were separated from all previously known occurrences for *A. caerulea*. On the other hand, the doubtful Panamanian occurrence was always among the previous records for the modeled species (Figures 1 and S2A–B).

The four new *A. caerulea* occurrences considerably increased its distribution range, especially considering their distances to the nearest occurrence records previously sampled in the Amazon [~2,000 km for the occurrences in Goiás and ~1,000 km for the one sampled by Anjos-Silva et al. (2006)]. Generally, the distribution models produced only with the previous occurrences showed a fair to good performance when considering both TSS and AUC values, respectively (Table I).

The doubtful Panamanian record was predicted as suitable for *A. caerulea* in all models (Figure 2). On the other hand, the models using only the previous occurrences as the training subset had a low predictive power regarding the new occurrences for the Cerrado savanna (Figure 2a–b). The model generated only with the previously known *A. caerulea* occurrences predicted areas in northern Peru, southeastern Colombia, northeastern Ecuador, southern Venezuela, and Amazonas and Para states in Brazil as suitable for *A. caerulea*.

The inclusion of the new Cerrado records had a great effect on models performance (Table I), with overall decreases in both AUC and TSS values. Although the new occurrences were predicted as minimally suitable in both modeling algorithms, they increased *A. caerulea* potential distribution by almost 30 and 50 %, according to GARP and MaxEnt, respectively (Figure 2c–d). After their inclusion, we observed additional range increases towards the Cerrado savanna and Bolivia. The Panamanian

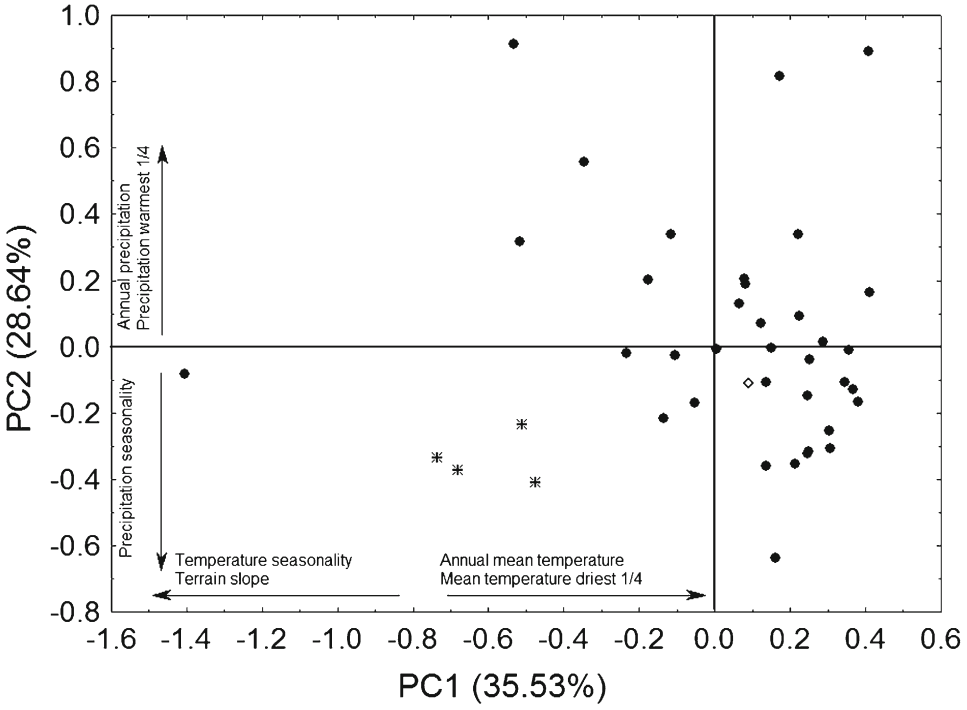

Figure 1. Principal components analysis results showing the separation of the new Cerrado occurrences (*asterisks*) from the previous ones (*black circles*) recorded for *A. caerulea*. Note that the doubtful Panamanian occurrence (*diamonds*) is suitable for *A. caerulea* occurrence. The *arrows* represent which environmental variables were positively and negatively related to each retained eigenvector. The *percentages* represent the amount of variation explained by each eigenvector.

occurrence was still predicted as suitable in both modeling algorithms and in the *A. caerulea* consensus map (Figure 3a, b).

Considering the consensus maps, although the LPT threshold minimally predicted the new occurrences records for *A. caerulea* within the Cerrado biome (Figure 3a), it also increased its distribution into arid areas in northwestern Venezuela and northern Colombia, where the species is assumed to be absent. On the other

Table I. Performance of *A. caerulea* models considering training subsets without and with the new occurrences from the Cerrado. The doubtful Panamanian occurrence was not used in the models.

	Amazonian occurrences (70:30)		All occurrences (70:30)		All occurrences (100:100)	
Modeling algorithm	AUC	TSS	AUC	TSS	AUC	TSS
MaxEnt	0.769	0.609	0.699	0.424	0.816	0.532
GARP	0.839	0.598	0.769	0.422	0.858	0.487

Numbers in brackets refer to the proportion of occurrences used in the training/test subsets in all modeling procedures

TSS values consider the LPT threshold, *SD* standard deviation

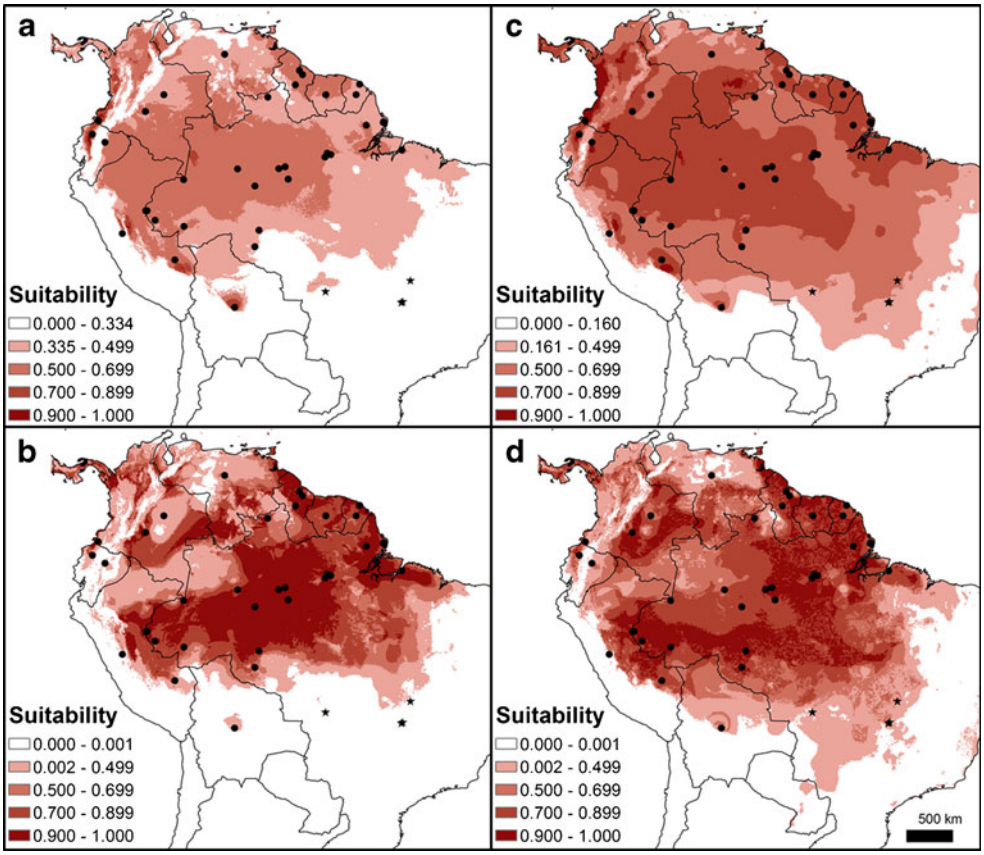

Figure 2. Distribution models generated by MaxEnt (**a**, **c**) and GARP (**b**, **d**) using only the previous (*left*) or both the previous and the newer occurrences from the Cerrado (*right*) in the training subset to predict *A. caerulea* potential distribution. *Circles* refer to the previous *A. caerulea*'s known records; *stars* refer to the new occurrences found in the Cerrado Biome; *question marks* refer to the doubtful Panamanian occurrence.

hand, although the ROC threshold minimized *A. caerulea* distribution in those areas, it did not predict the new occurrences sampled in the Cerrado as suitable for *A. caerulea* distribution. Nevertheless, neighboring areas near those new occurrences were predicted as suitable (Figure 3b).

4. DISCUSSION

In this study, we presented three new occurrences for *A. caerulea*, a rare Euglossini bee species from South America, and modeled its distribution considering these additional records. We showed that the doubtful Panamanian occurrence (Cameron 2004) is suitable as an occurrence record and that *A. caerulea* distribution range, previously believed to be restricted mostly to the Amazon basin (Cameron 2004), also includes some portions of the Brazilian Cerrado. These results have important implications for understanding the dispersal and distribution of Euglossini bees in South America.

As the second largest biome and the largest savanna in South America (Ab'Saber 1977), the Cerrado separates two important biomes: the Amazon and the Atlantic forests. Despite its usual xeric-like environment, it commonly bears evergreen gallery forests near rivers and streamlets. Studies with plants (Méio et al. 2003),

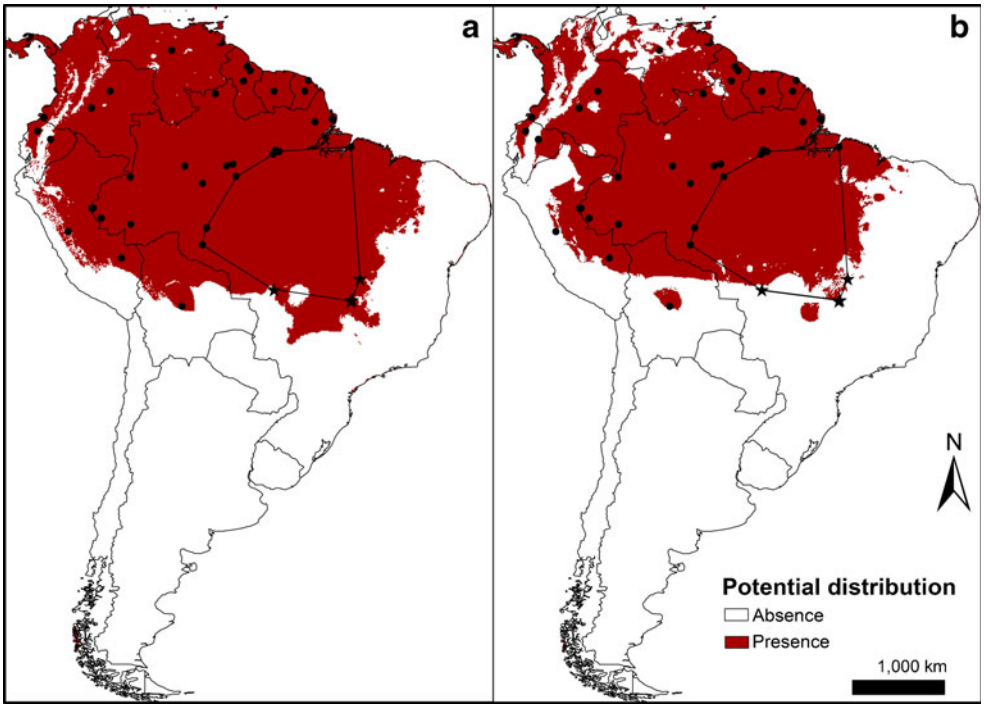

Figure 3. Mean ensemble forecast produced by MaxEnt and GARP considering both **a** LPT and **b** ROC thresholds. Note that semi-desert areas in northern Colombia and northwestern Venezuela are not predicted as suitable when we consider only the ROC threshold. The depicted polygon in **a** and **b** refers to areas where future surveys for *A. caerulea* in gallery forests should take place. *Circles* refer to the previous *A. caerulea*'s known records; *stars* refer to the new occurrences found in the Cerrado Biome; *question marks* refer to the doubtful Panamanian occurrence.

birds (Silva 1996), butterflies (Brown Jr 1987; 1992), mammals (Redford and Da Fonseca 1986), and solitary bees (Aguiar and Melo 2007) have already suggested the importance of the gallery forest while facilitating dispersal of species dwelling either in the Amazon or in the Atlantic Forest. In Cerrado, gallery forests provide important habitat conditions which allow Euglossini bees (and insects associated with mesic environments) to easily disperse (Moura and Schlindwein 2009). They also provide humidity for the development and establishment of orchid plant species, which are generally used by the males of Euglossini bees as scent sources (Dressler 1982). Such dependence on the gallery forest to disperse in the Cerrado may be the reason why other insects species previously thought only to inhabit in the Amazon were recently sampled in Cerrado (see Almeida et al. 2010 for an example). Although large rivers within the Cerrado (e.g., Araguaia and Paranã rivers) may act as important dispersal barriers for non-flying organisms (Cáceres et al. 2008), such barriers may not restrict the dispersal of Euglossini bees, given their excellent flight capacities and uncommon vagility (Janzen 1971).

The distribution model trained only with the previous, mostly Amazonian, occurrences did not predict the newer Cerrado records and even the model with all occurrences predicted the observed Cerrado occurrences as minimally suitable for *A. caerulea*. The newer records appear to be outliers in the environmental niche parameters of the known *A. caerulea* records, which explain the low predictive power for these occurrences. Similar results were

also observed for the modeled distribution of other Amazonian species sampled within the Cerrado (Almeida et al. 2010), as well as for other Euglossini bees sampled outside their previously known ranges (Hinojosa-Díaz et al. 2009).

At first, these results may indicate that *A. caerulea* populations in Cerrado are in fact sink populations (Pulliam and Danielson 1991; Pulliam 2000), since the suitability in these areas support the prediction of the occurrence under the LPT threshold (but at minimal values) and was predicted as absent under the ROC threshold. Considering the distribution of habitat suitability, only sites deep in the Amazon (areas with high habitat suitability) would be considered as source populations. Nevertheless, the predicted suitability may not correspond to the true habitat suitability, as perceived by *A. caerulea* bees. For instance, Anjos-Silva et al. (2006) sampled eight *A. caerulea* bees in a gallery forest within the Cerrado, with vegetational features similar to both the Amazon and the Atlantic forest (sensu lato) (Pinto and Oliveira-Filho 1999). In Cerrado gallery forests, either minimally or not predicted as suitable, we sampled two specimens of *A. caerulea* (Silvânia County, Goiás state). Therefore, the dependence on gallery forests of Euglossini bees (Moura and Schlindwein 2009) may significantly increase *A. caerulea* habitat suitability within the Cerrado, a biome which naturally harbor low Euglossini bees diversity (Nemésio and Silveira 2007).

A biased sampling effort in different habitats (Kamino et al. 2011) may underestimate species distribution, affecting the predicted suitability in the new occurrence records (Almeida et al. 2010). Therefore, in order to validate both models and generate thresholds for binary prediction based in true absences instead of computer-generated pseudo-absences, future surveys should be performed either in areas where model suitability was low or where the species does not occur.

Considering the known Euglossini sampling effort in South America, the arid areas in northern Colombia and northwestern Venezuela, as well as the dry forests in northwestern Peru and southern Ecuador, are good candidates for further evaluation of the models, since they seem too dry to be considered suitable for the occurrence of *A. caerulea* (GAR Melo, unpublished data). Nevertheless, considering the strong association of Euglossini with mesic environments, future sampling surveys in the humid formations found in those dry areas should be considered in order to validate model predictions, independently of the thresholds and modeling algorithms used. Future field surveys should also take place in gallery forests found in the area comprehending the southeastern Para and Amazonas states, as well as northern Mato Grosso and Tocantins states, areas predicted as suitable in the consensus maps considering both the LPT and the ROC thresholds (polygon shown in Figure 3a, b).

Although standardized sampling protocols may be considered inefficient on sampling rare species, the continuous use of ENM techniques, whenever new occurrences for rare species are discovered, may improve our knowledge on their distribution range. Such strategy for rare species has been used with success elsewhere (Raxworthy et al. 2003; Pearson et al. 2007; De Siqueira et al. 2009) and should be used continuously as it will optimize to a large extent the amount of resources invested in field surveys (Guisan et al. 2006). Similar approaches to this study should also be considered to other South American Euglossini species sampled outside their previously known distributions (Anjos-Silva 2008; Silva and Rebêlo 2009), in order to properly assess the distribution patterns of these species and pinpoint not-sampled but potentially fruitful areas for future surveys. This suggestion is particularly appropriate for areas of poor knowledge on Euglossini diversity, such as those in the Brazilian Cerrado (Nemésio and Silveira 2007). Despite plenty of studies on Euglossini bees in humid environments from South America (e.g., Mata Atlântica and the Amazon Forest), very few systematic studies have been carried out in dry areas of the continent, as well as in gallery forests within these biomes, which may bear a still unknown Euglossini diversity. Therefore, we advise future surveys of Euglossini bees to be conducted in gallery forests of such environments in order to fill a

gap on our current knowledge of the distribution patterns of orchid bees.

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Espèces amazoniennes à l'intérieur du Cerrado: nouvelles observations et répartition potentielle pour *Aglae caerulea* (Apidae: Euglossini)

Amazonie / savanne / corridor de dispersion / modélisation / répartition des espèces

Artyen aus dem Amazonasgebiet in der Cerrado-Savanne: Neue Funde und Angaben zum potentiellen Vorkommen von *Aglae cearulea* (Apidae: Euglossini)

Amazonien / Cerrado / Verbreitungskorridor / Wallace'scher Fehler / Modellerstellung zur Artenverteilung

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3.7 SUPPLEMENTARY MATERIAL

3.7.1 Supplementary tables

Table S1 – List of *A. caerulea* new occurrences sampled in the Brazilian state of Goiás. Longitude and latitude coordinates are in decimal degrees. The specimens are currently found in the Entomological collection of the Universidade Federal de Goiás (UFG).

County Name	Longitude	Latitude
Silvânia	-48.49167	-16.49819
Silvânia	-48.37900	-16.39758
Alto Paraíso de Goiás	-47.6088	-14.3152

Table S2 – PCA loadings considering all *A. caerulea* occurrences, including the doubtful one from Panamá. Lines with bold values represent the selected eigenvectors.

Eigenvector	Eigenvalue	Proportion of explained variation	Accumulated proportion
PC1	**2.487**	**0.3553**	**0.3553**
PC2	**2.005**	**0.2864**	**0.6417**
PC3	**1.161**	**0.1659**	**0.8076**
PC4	0.689	0.0984	0.9060
PC5	0.455	0.0650	0.9710
PC6	0.191	0.0273	0.9983
PC7	0.012	0.0017	1.0000

3.7.2 Supplementary figures

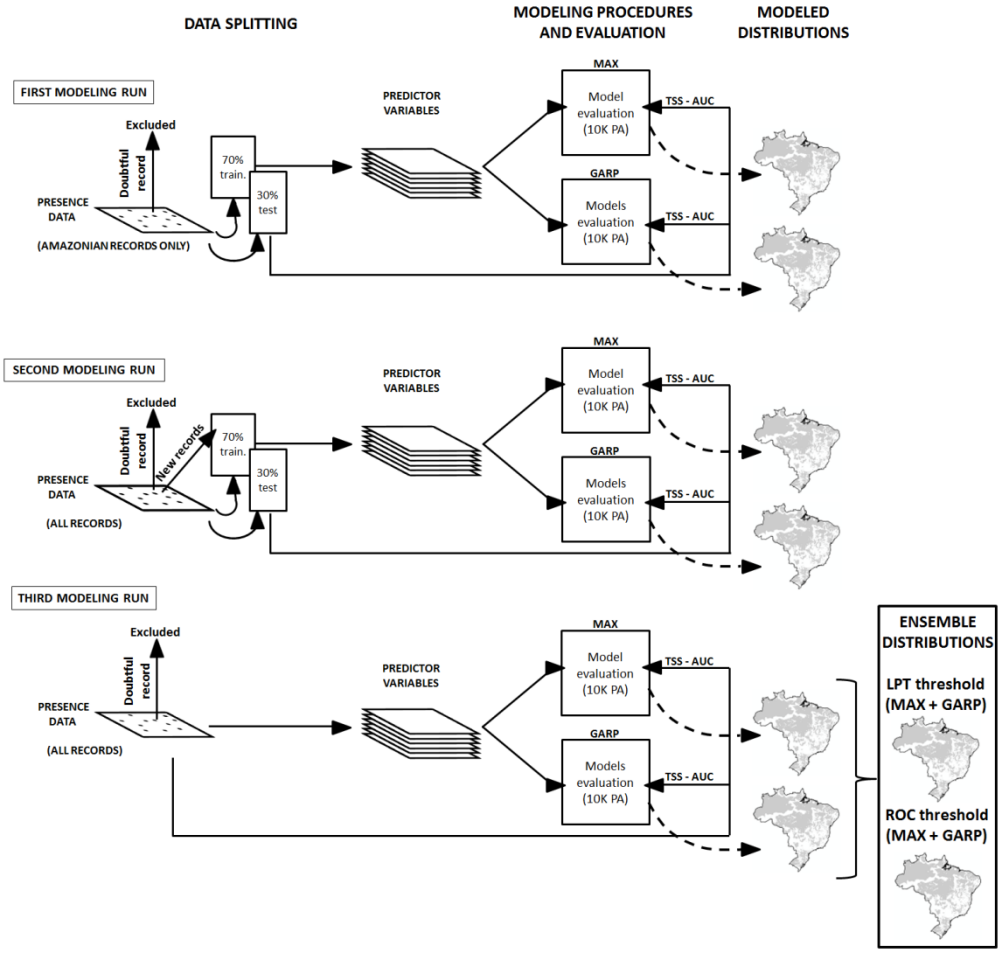
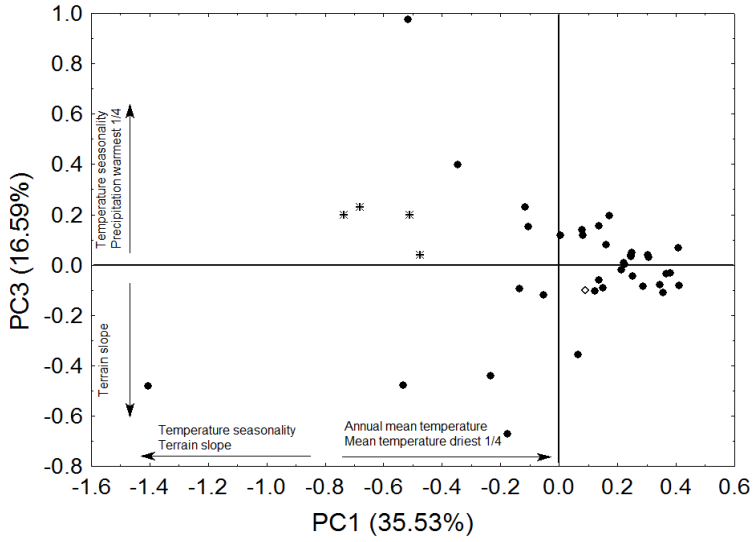
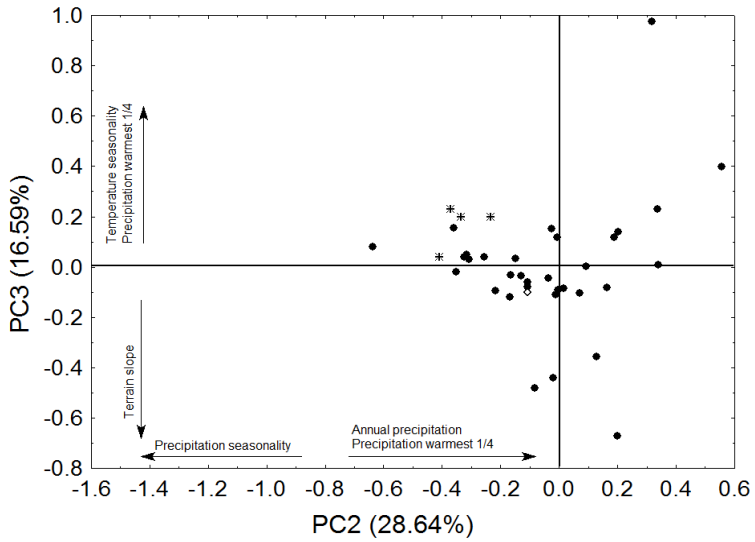


Figure S1 – Flowchart of *A. caerulea* modeling distribution modeling procedures. Train. stands for training. The Panamanian uncertain occurrence was not used in any of the modeling runs we performed. MAX stands for Maxent.

A)





B)

1 **Figure S2** – Principal Components Analysis results showing the separation of the new
2 Cerrado occurrences (✳) from the Amazonian ones (●) recorded for *A. caerulea*. Note
3 that the doubtful Panamanian occurrence (◊) is suitable for the species occurrence. The
4 arrows represent which environmental variables were positively and negatively related
5 to each eigenvector retained. The percentages represent the amount of variation
6 explained by each eigenvector. A) PC1 vs. PC3 comparison. B) PC2 vs. PC3
7 comparison.

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Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species *Lithurgus huberi* in South America

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ABSTRACT

The wood-boring bee *Lithurgus huberi* Ducke (Apidae: Megachilinae: Lithurgini) is arguably an exotic species to South America. This solitary bee is the only representative in the Western Hemisphere of the Old World genus *Lithurgus*, and likely a conspecific with the Indo-Australian species *Lithurgus atratus*. *L. huberi* appears to have reached the continent at least 100 years ago, when it was discovered and described. Because this species seems to be oligolectic on pollen of Convolvulaceae flowers in South America, we attempted to integrate this biotic interaction (plant–bee relationships) to our species distribution model (SDM) procedures to predict its potential distribution in South America. The modeled distribution of seven *L. huberi*'s host plant species did not improve the algorithms' ability to predict its distribution, but it produced constrained ranges. These results suggest that our biotic variables are not independent of the abiotic variables used (mostly related to climate). We employed five modeling algorithms, Envelope Score, GARP, Mahalanobis Distance, Support Vector Machines, and MaxEnt, but only the former two showed a good performance when predicting the occurrence of both, the host plant species and *L. huberi*. Our results indicate that this exotic pollinator is mainly distributed in eastern, northeastern, central, and southwestern South America, with few suitable areas in the Amazon region. We also highlight suitable areas for future surveys and present new occurrence records.

1. Introduction

The world is undergoing fast and intense environmental changes caused, directly or indirectly, by human activities (MEA, 2005; Sala, 2000). Habitat loss and fragmentation, deposition of anthropogenic fixed nitrogenous substances, and the increasing atmospheric CO_2 concentration with its associated climatic changes, are considered to be worldwide drivers of environmental change (Tylianakis et al., 2008). Introduction of exotic species are also recognized as a major cause of environmental changes (Pejchar and Mooney, 2009; Tylianakis et al., 2008) and economic losses elsewhere (Pimentel et al., 2001, 2005). Therefore, practical tools to predict exotic species invasions are of the greatest importance for both science and society (Jiménez-Valverde et al., 2011; Thuiller et al., 2005), especially if we consider that human activities greatly increase species migratory abilities, allowing them to overcome their natural migratory barriers (Jiménez-Valverde et al., 2011).

The invasion of exotic species is often characterized by three stages (Richardson et al., 2000): species' introduction, naturalization, and spread. In the first stage, the species arrive within its new ranges. In the second, some individuals from self-sustaining populations arrive and establish other populations in the new geographic range. Given the appropriate conditions, such populations

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will increase the species' range, and eventually, in the third stage, they will spread, causing a new range expansion.

A wide array of environmental features may be changed after the establishment of exotic species in a new area, such as biogeochemical cycles (Ashton et al., 2005), which have inherent effects on important ecosystem processes (Bradley et al., 2010; Mangla et al., 2010; Pejchar and Mooney, 2009; Traveset and Richardson, 2006). Those changes may decrease the availability of important resources for native species (Asner et al., 2008; Iponga et al., 2008) and also affect species–specific interactions (Traveset and Richardson, 2006). Thus, cultural (*e.g.* tourism, aesthetic beauty), provisioning (*e.g.* food, fuel, water), and/or regulating ecosystem services (*e.g.* climate regulation, disease regulation, pollination) may be affected during the invasion process of exotic species.

In the context of pollination services, it is well known that many angiosperms rely on animal species for seed production (Herrera and Pellmyr, 2002; Traveset and Richardson, 2006). Depending on the degree of specialization, they may be generalists, which are visited by several pollinators, or extremely specialized species, which rely on a narrow suite of specific pollinators. In the latter case, the introduction of a pervasive exotic pollinator is expected to decrease the quantity and quality of pollen grains exchanged among different individuals, with subsequent fitness losses (Traveset and Richardson, 2006). Generalist invasive pollinators may easily become integrated to plant–pollinator systems in the exotic range (Traveset and Richardson, 2006) and may cause negative results for plant communities, given the establishment of fragile and loose interactions between invader pollinators and the plant species, but also for pollinator as well (Butz-Huryn, 1997; Santos et al., 2012).

When considering all factors determining either the success or failure of exotic species in new ranges, it is usually expected that the abiotic component of their ecological niche exerts a major effect on their distribution (Jiménez-Valverde et al., 2011; Soberón and Peterson, 2005; Soberón, 2007). However, while the biotic component of their niche is usually not considered in macroecological studies (Hortal et al., 2010; Pearson and Dawson, 2003), interspecific interactions with plant species are very important to pollinators, since they mainly depend on plants to survive in their environments. Therefore, the potential effects of such components, while determining the distribution of a given species, should be carefully considered whenever possible. Some attempts to contemplate interactions between pollinators and their specific host plants in macroecological scales have already been explored (Araújo and Luoto, 2007; Giannini et al., 2013a; Heikkinen et al., 2007; Meier et al., 2010; Preston et al., 2008; Rouget et al., 2001), however, as far as we know, no study has assessed the effects of the host plant species distribution on the distribution of an exotic species.

Other similar studies have already tried to include the biotic components of species niche while evaluating their distributions. Usually, biotic interactions between different species are considered by including them as predictor variables of the focus modeled species layers, corresponding to the modeled distribution of its interacting species (Giannini et al., 2013a; Heikkinen et al., 2007). Nonetheless, only the inclusion of known presence/absence data of interacting species (Araújo and Luoto, 2007; Giannini et al., 2013a), their abundances (Pellissier et al., 2010), or even land cover types (González-Salazar et al., 2013) may also be used as biotic predictor variables potentially determining the distribution of a species. Although such methods may seem simple at first, considering the broad spatial scale used in species distribution modeling, they can certainly provide us with a deeper understanding of important biological interactions occurring in local and/or regional scales, especially if we consider community ecology frameworks (Guisan and Rahbek, 2011; Meier et al., 2010; Pellissier et al., 2010). Considering the biotic portion of the species' niche, while dealing with their potential distributions, is of utmost importance, especially in a rapidly changing world (Adler and HilleRisLambers, 2008).

Herein, we constructed species distribution models to examine the potential distribution of the exotic bee species *Lithurgus huberi* Ducke (Apidae: Megachilinae: Lithurgini) in South America. Given the discovery of new occurrence records for this species (see below), the main goals in this study were: (1) to evaluate the capability of several species distribution modeling algorithms on predicting new occurrences using only the older ones; (2) to evaluate how the modeled distribution of its host plant species may affect the final distribution of *L. huberi*; and (3) to highlight unsurveyed but suitable areas for the occurrence of *L. huberi* in South America, with the aim of directing future studies.

2. Materials and methods

2.1. The modeled species

L. huberi was described by Ducke (1907) from Maranhão, Brazil, and is the only representative of this Old World genus of solitary bees in the Americas. The nesting biology, cocoon, and floral associations of *L. huberi* have been documented by Camillo et al. (1994, 1983), Mello et al. (1987), and Pick and Schlindwein (2011). The species is univoltine and, as in other members of the genus, *L. huberi* has a wood-nesting habit that facilitates dispersion across great distances. Nests are built inside dead dry logs, and are initiated between March and June (Camillo et al., 1983, 1994; Gonzalez et al., 2013a,b; Michener, 1965, 2007; Snelling, 1983). Also, as in other *Lithurgus*, it appears to be oligolectic on plants with large pollen grains. While it has been observed to collect pollen from Asteraceae, and especially Malvaceae, in its natural range (Michener, 2007), in its invaded range, this species has been collected on flowers of Convolvulaceae (particularly on *Ipomoea* and *Merremia*) and Malvaceae (*Sida* sp. and *Gossypium* spp.; Camillo et al., 1983, 1994; Pick and Schlindwein, 2011). Given morphological similarities with *Lithurgus atratus*, an Indo-Australian species presumably composed of at least eight species that have been suggested to represent a single taxonomic unit (Michener, 1965), Snelling (1983) was the first to hypothesize that *L. huberi* was exotic to South America. Nonetheless, a recent study by Gonzalez et al. (2013b) suggested that those species are in fact two independent taxonomic units, a classification that has also been previously adopted by other authors (*e.g.* Moure and Melo, 2007). Following Colautti and MacIsaac (2004), *L. huberi* can be classified as a widespread but locally rare exotic species (Stage IVa species).

2.2. L. huberi and host plant species occurrences dataset

To predict the potential distribution of *L. huberi* in South America, we gathered a total of 56 occurrence records for this species from the following sources: (1) literature records (see Supplementary Material for complete list of published papers holding *L. huberi* occurrence information), (2) online databases such as CRIA Species Link (http://splink.cria.org.br) (the only institution in CRIA Species Link bearing *L. huberi* occurrences was Coleção Entomológica da Universidade Federal do Pernambuco), Global Biodiversity Information Facility (http://www.gbif.org), Inter-American Biodiversity Information Network (IABIN; http://iabin.databasin.org), and Discover Life Bee Species Guide and World Checklist (http://www.discover-life.org), and (3) museum collections [(i) Coleção Entomológica Padre J.S. Moure, Universidade Federal do Paraná, Curitiba, PR, Brazil; (ii) Coleção Entomológica Paulo Nogueira-Netto, Universidade de São Paulo, São Paulo, SP, Brazil;

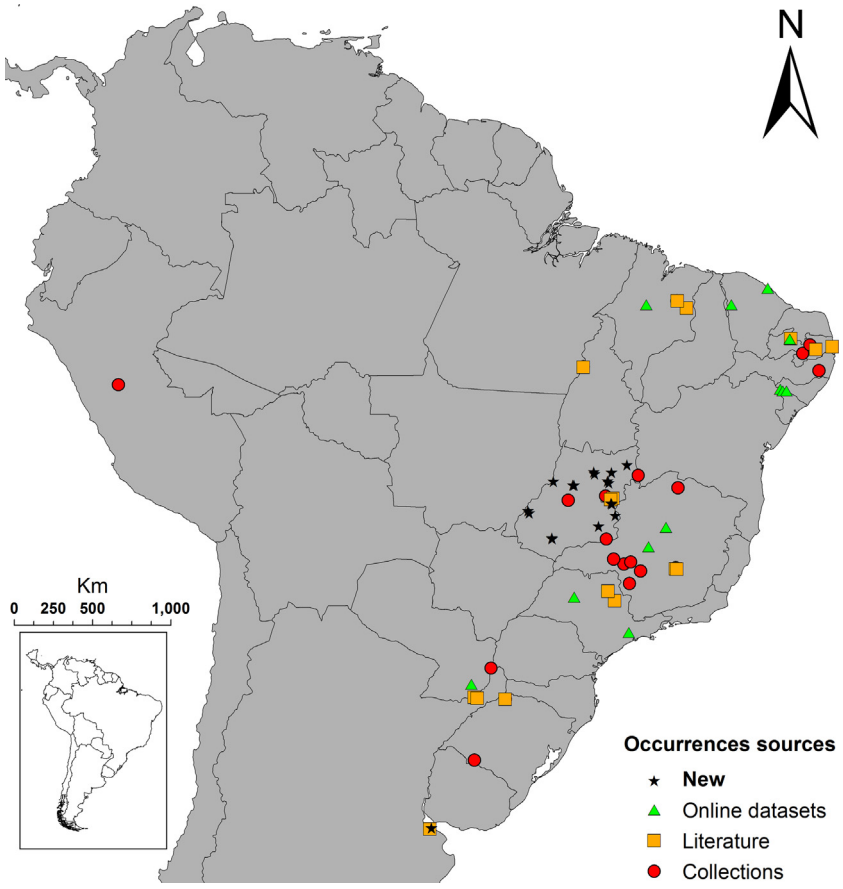

Fig. 1. Occurrence records for *Lithurgus huberi* in South America, including data sources and new records reported in this study.

(iii) Coleção Entomológica da Universidade Federal do Pernambuco (retrieved from CRIA Species Link)]. Additionally, we gathered 18 new occurrence records taken from field surveys in the Brazilian state of Goiás and in Argentina (Table S1). In some localities in Brazil, more than 30 individuals of *L. huberi* were sampled, thus suggesting high density populations of this species (DPS, pers. obs.). All *L. huberi* occurrences are depicted in Fig. 1.

To evaluate how the modeled distribution of *L. huberi* is affected by the distribution of the host plant, we gathered data on the occurrences of all plant species recorded to be used by *L. huberi* as pollen resources in South America (Camillo et al., 1983, 1994; Pick and Schlindwein, 2011). All available information for *Ipomoea nil* (L.) Roth, *Ipomoea bahiensis* (L.) Roth, *Ipomoea purpurea* (L.) Roth, *Ipomoea indica* (Burm. F.) Merril, *Ipomoea cairica* (L.) Sweet, *Ipomoea asarifolia* (Desr.) Roemer & Schultes, and *Merremia aegyptia* (L.) Urban were gathered from CRIA Species Link and GBIF. We disregarded those obtained both for *Sida* spp. and *Gossypium* spp. because the species–specific relationships of the bee with these plants are unspecific and were not fully addressed in the literature, as far as we are aware of. The complete list of institutions holding occurrences for these plant species can be found in the Supplementary Material.

We used Google Earth (Google Inc., 2013) to acquire proxy geographical information from city hall coordinates for those records of bees and flowers that did not have exact geographical information. Given the grid resolution used in this study (see below), of the initial 56 old occurrences gathered for *L. huberi*, only 48 remained as unique. All 18 new occurrences for *L. huberi* remained when considering this grid resolution. The amount of unique occurrences for all modeled host plant species are listed in Table S2.

2.3. Modeling algorithms as predictive tools

Species Distribution Models (SDM hereon) are considered good tools for predicting the distribution of exotic species (Araújo and Peterson, 2012; Jiménez-Valverde et al., 2011). Based on the observed occurrences of the modeled species, these tools correlate the environmental variables of these known locations to create a multidimensional environmental space. Then, based on such environmental space and the known species location, niche parameters can be estimated and the species potential distribution can be projected into the geographical areas with environmental features similar to those of the observed occurrences (Araújo and Guisan, 2006). These tools have also been widely used to predict the distribution of species unknown to science (Raxworthy et al., 2003), predict new records for rare ones (Almeida et al., 2010; De Siqueira et al., 2009; Silva et al., 2013), guide and optimize future surveys (Raxworthy et al., 2003), and to indicate areas with high predicted species richness as priority targets for future conservation actions (Loyola et al., 2012; Nóbrega and De Marco Jr., 2011).

2.4. Environmental layers, modeling procedures, distribution thresholds, and evaluation

We used all 19 available layers from WorldClim's climatic variables dataset (Hijmans et al., 2005) to derive principal components (PCs hereon) that we employed as environmental layers during the modeling procedures. From the 19 PCs produced, we selected seven, which accounted for more than 98% of the variation on the original environmental variables set (Table 1), and used them as new variables. This method is recommended to decrease

Table 1
Summary of the Principal Component Analysis which generated the principal components (PC) used as environmental layers. Each cell value represents the individual loadings of each variable in each of the PCs. The PCs, individual, and accumulated proportions of each PCs are also shown.

Environmental variables	Principal components						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Annual mean temperature	0.271	0.225	−0.130	0.043	−0.054	−0.018	0.019
Annual precipitation	0.262	−0.221	−0.025	−0.214	0.174	0.089	−0.095
Isothermality	0.237	0.011	0.345	−0.074	−0.232	−0.493	−0.217
Maximum temperature warmest period	0.194	0.316	−0.345	−0.017	0.134	−0.076	−0.043
Mean diurnal range	−0.179	0.219	−0.075	−0.541	0.039	−0.474	−0.320
Mean temperature coldest quarter	0.286	0.183	−0.006	0.037	−0.097	−0.028	−0.040
Mean temperature driest quarter	0.277	0.160	0.013	0.162	0.020	−0.021	−0.112
Mean temperature warmest quarter	0.232	0.262	−0.305	0.076	0.049	−0.006	0.090
Mean temperature wettest quarter	0.234	0.255	−0.234	−0.057	−0.119	−0.023	0.189
Minimum temperature coldest period	0.294	0.123	−0.007	0.165	−0.060	0.013	0.024
Precipitation coldest quarter	0.202	−0.222	0.068	0.101	0.604	−0.288	0.129
Precipitation driest period	0.143	−0.397	−0.227	−0.019	−0.130	−0.325	0.272
Precipitation driest quarter	0.154	−0.396	−0.221	−0.023	−0.099	−0.296	0.231
Precipitation seasonality	−0.039	0.328	0.409	−0.328	0.069	−0.053	0.749
Precipitation warmest quarter	0.155	−0.211	−0.199	−0.502	−0.430	0.323	0.072
Precipitation wettest period	0.267	−0.082	0.124	−0.274	0.298	0.249	−0.103
Precipitation wettest quarter	0.268	−0.090	0.113	−0.278	0.294	0.246	−0.129
Temperature annual range	−0.250	0.118	−0.315	−0.258	0.216	−0.090	−0.076
Temperature seasonality	−0.250	−0.009	−0.389	0.024	0.245	0.049	0.193
Proportion explained by each PC	0.554	0.197	0.092	0.059	0.039	0.026	0.015
Accumulated variation proportion	0.554	0.751	0.843	0.902	0.941	0.966	0.981
Principal Components eigenvalues	55.356	19.750	9.203	5.905	3.888	2.558	1.481

the collinearity among environmental variables, but also to avoid model overfitting that may result in biologically unreliable species potential distributions (Jiménez-Valverde et al., 2011). The grid of all variables was 2.5 arc-min resolution (0.041 ≈ 4 km). We also used *L. huberi*'s host plant distributions as environmental layers (see below).

Given the overall biases and uncertain nature of species distribution models, different algorithms may result in different patterns of species distribution (Barry and Elith, 2006; Diniz-Filho et al., 2009; Rocchini et al., 2011). In order to provide the most reliable potential distribution possible, we evaluated *L. huberi* and its host plant species distributions considering five different modeling algorithms: (1) Envelope Score, a quantitative version of BIOCLIM (Nix, 1986; Piñero et al., 2007); (2) GARP with best subsets (Stockwell and Peters, 1999); (3) Mahalanobis Distance (Farber and Kadmon, 2003); (4) Support Vector Machines (SVM hereon; Schölkopf et al., 2001; Tax and Duin, 2004); and (5) Maximum Entropy (Phillips and Dudik, 2008; Phillips et al., 2006). While Envelope Score and Mahalanobis distance are simpler models that usually need presence data only to produce the species' potential distributions, MaxEnt, SVM, and GARP are artificial intelligence methods that are generally more complex, and correctly predict the species known occurrences more often (Rangel and Loyola, 2012). We used the software MaxEnt to run Maximum Entropy (Phillips et al., 2006), and openModeller Desktop for the other four modeling algorithms (Muñoz et al., 2011).

In our first modeling experiment, we divided the occurrences of all host plant species into ten 75–25% training–testing subsets. With the training subsets, we produced distributions of all host plant species using all modeling algorithms. With the testing subsets, the distributions predicted by each algorithm were evaluated. With the two best modeling algorithms, we used all available occurrences for each host plant species to produce their final distributions. Here, we considered as the host plants distributions the binary maps of presence/absence generated by each modeling algorithm. Later, we used these distributions obtained from each modeling algorithm to produce a summed distribution map for each plant species. In addition to the individual host plant distribution, we also created a stacked layer where the resulting individual host plant distribution for each host plant species were summed up. We used either all single or stacked host plant distribution layers (SEP and STK treatments, see below) in different treatments to determine *L. huberi*'s potential distribution (see Fig. 2A).

As we did for the host plant species distributions, we randomly divided all *L. huberi*'s old occurrences into ten 75–25% training–testing subsets. We used the training subsets with the previously selected PCs to produce *L. huberi*'s distributions with the four modeling algorithms. Then, we evaluated the resulting distributions with the testing subsets. Additionally, using a paired *t*-test, we assessed what proportion of the 18 new occurrences for *L. huberi* was predicted with each of the two best modeling algorithms. As a second independent model evaluation procedure, we pooled all old *L. huberi*'s occurrences to obtain its potential distribution according to the two best modeling algorithms, and evaluated these distributions using all new *L. huberi*'s occurrences as a testing subset. We used the two best modeling algorithms in all the following modeling experiment (see Fig. 2B).

In the second modeling experiment, all available *L. huberi* records were divided into ten 75–25% training–testing subsets. For the first treatment, we only used the PCs as environmental layers (PCONLY hereon) and we evaluated the resulting *L. huberi*'s distributions produced by the two best modeling algorithms with the testing subsets. Finally, we used all available *L. huberi* records with the same two best algorithms to produce the *L. huberi* final distribution and its summed final distribution. Our second and third treatments for this second modeling experiment were similar to the first one, except for slight differences. For the second treatment, we used all separated distributions of *L. huberi*'s host plant species as environmental layers, along with the PCs already used in the first treatment (SEP treatment hereon). For the second treatment, we only used the stacked host plant species layer as an environmental predictor, along with the PCs as environmental variables (STK treatment hereon), as already used for both PCONLY and SEP treatments. During all modeling procedures the algorithms were trained for the entire South American continent. Although the resulting host plant species distribution are very similar and consequently collinear, the different treatments used to predict *L. huberi*'s potential distribution (PCONLY vs. SEP vs. STK) would allow us to account for the effects produced by different environmental variables with different similarity levels.

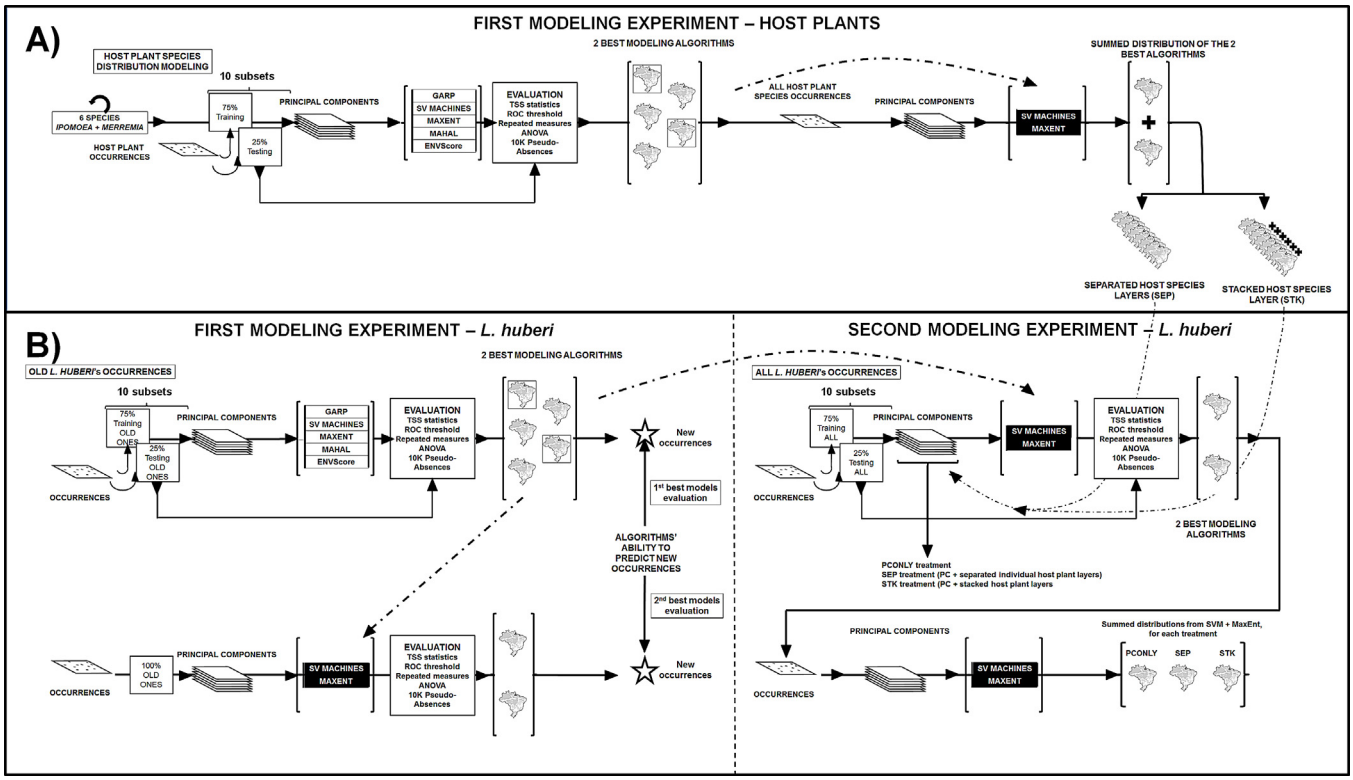

Fig. 2. Flowchart of all modeling procedures performed on this study. (A) Modeling procedures used to determine the host plant species distributions; (B) Modeling procedures used to determine *L. huberi*'s distribution in both the first and second modeling experiments. Black boxes are those algorithms which performed better during the first modeling experiment.

Despite the usual recommendation of using the LPT threshold (Pearson et al., 2007) to generate the presence/absence distribution matrices of the modeled exotic species (Jiménez-Valverde et al., 2011; Pearson et al., 2007), we chose to cut the modeled suitability matrices using the ROC threshold, which balances both omission and commission errors while determining the modeled distribution ranges. However, for comparison purposes, we also showed its current distribution considering the LPT threshold for all algorithms used to determine its final distribution under the ROC threshold in all modeling experiments. Following Liu et al. (2011), we only used True Skilled Statistics (TSS; Allouche et al., 2006) values to assess model performance. The TSS is a threshold-dependent statistics that varies from −1 to +1, where negative and around zero values regard distributions no better than a random distribution, while values near +1 represent perfect agreement between the observed and the modeled distributions. Acceptable models considering this statistics are those which reach at least 0.5, and excellent TSS values reaching a minimum of 0.7, an interpretation somehow similar to that employed with the *Area Under the Receiver-Operator Curve* statistics (AUC; Fielding and Bell, 1997). In all model evaluation procedures we used 10,000 random pseudo-absences (PAs hereon). We used repeated measures ANOVAs (Fig. 2A and B) to determine the two best modeling algorithms while modeling the host plant species distributions and during the evaluation of the best environmental layer in predicting *L. huberi* distribution.

3. Results

In the first modeling experiment, TSS values for Envelope Score always showed the lowest values, independent of the species considered. The TSS values for all other modeling algorithms, for all species including *L. huberi*, were always higher than 0.5 (Fig. 3A), except for the modeled distributions of the host plants *I. nil* and *I. purpurea* obtained with Mahalanobis distance and GARP, which had TSS values below 0.5, under the ROC threshold. Despite a few exceptions (*e.g. I. asarifolia*, *I. bahiensis*), for which only SVM showed higher predictive performance, both SVM and MaxEnt were the algorithms that obtained the highest TSS values (Fig. 3A). Therefore, we selected them to model both the host plants' and *L. huberi*'s final distributions in South America. In general, considering the ROC threshold, all host plant species distributions were frequent in northeastern and southeastern South America, with a few species also showing suitable areas in central and northwestern South America (Bolivia, Paraguay, Peru, Ecuador, Colombia, and Venezuela). Suitable areas for the occurrence of those host plant species were not observed in core Amazonian areas (predicted distributions are depicted in Figure S1).

Under the ROC threshold, no differences in the algorithms' ability to predict the 18 new occurrences for *L. huberi* were observed between SVM and MaxEnt (paired *t*-value: 0.138; d.f.: 9; *p*-value: 0.892; MaxEnt: 0.594 ± 0.187, mean ± standard error; SVM: 0.605 ± 0.193). In the second independent model evaluation, while SVM predicted all new occurrences, MaxEnt only predicted half of them, similar to what was predicted in the first model evaluation procedure. Nonetheless, this bigger proportion of occurrences correctly predicted by SVM was mainly caused by a model overprediction of the species potential distribution in South America (TSS values for SVM and MaxEnt were 0.356 and 0.385, respectively in the independent model evaluation).

Considering the different treatments used to determine *L. huberi*'s distribution in the second modeling experiment, MaxEnt showed a constant performance with no substantial increase/decrease in TSS values in all procedures, with values around 0.5 and 0.7 (Fig. 3B). Such variation in TSS values is

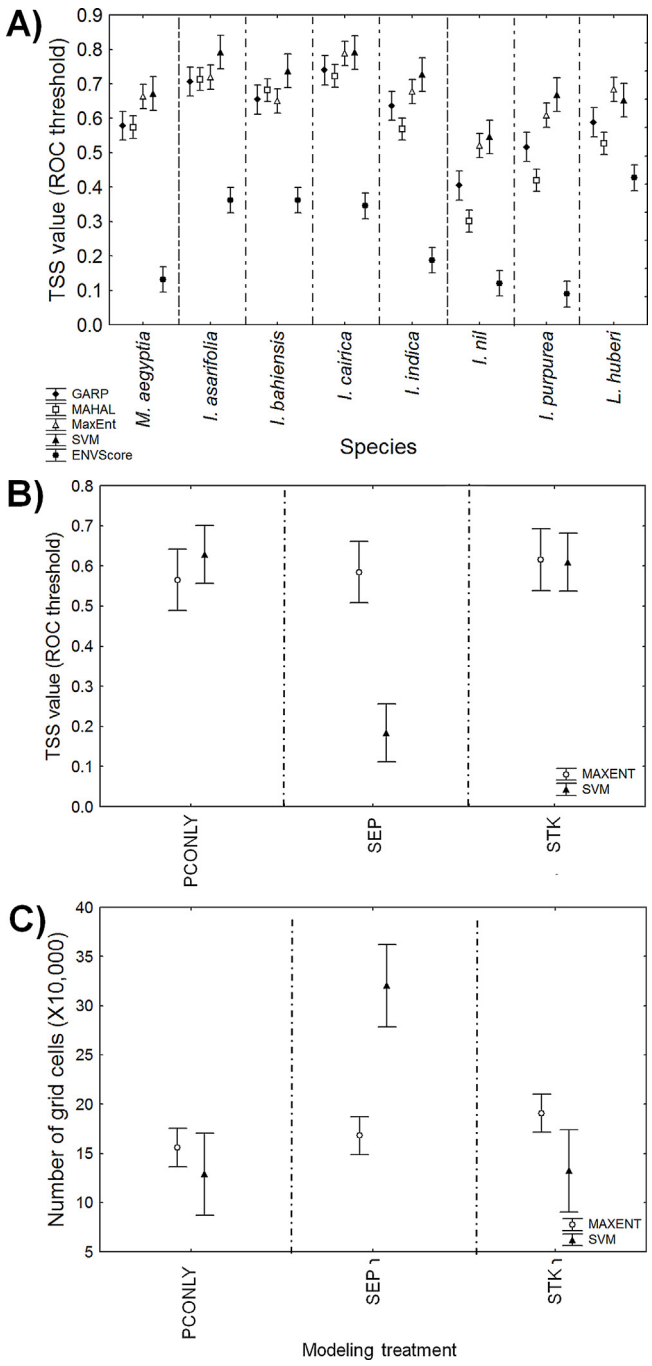

Fig. 3. Results of the second modeling experiment. (A) Evaluation of the four algorithms used to determine the distribution of the seven host plant species as well as of *L. huberi* in the first modeling experiment; (B) Evaluation of both MaxEnt and Support Vector Machines (SVM), the chosen algorithms to determine the final distributions for *L. huberi*, in the second modeling experiment. (C) *L. huberi*'s range sizes according to each algorithm in the second modeling experiment. Mid-points refer to means and bars represent 95% confidence intervals.

not negligible, and may have been caused by the use of all the different 10 random subsets of *L. huberi* occurrences used during the modeling procedures. Nonetheless, the algorithm SVM also showed a similar trend, at least for both the PCONLY and STK treatments. However, its performance showed a substantial decrease for the SEP treatment, with TSS values ranging between 0.1 and 0.3 (Fig. 3B). Although the total size of *L. huberi*'s resulting distributions were larger for both SEP and STK treatments, when compared to those produced with the PCONLY treatment, those

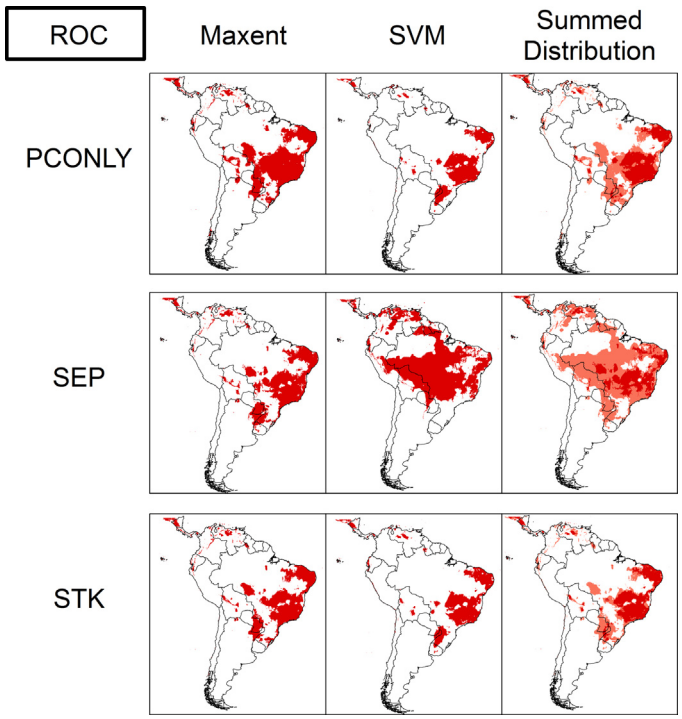

Fig. 4. Final individual distributions for *Lithurgus huberi* produced by each modeling algorithm according to each modeling treatment and its related summed distributions, considering the ROC threshold.

distributions produced with MaxEnt were more cohesive, with less dispersed suitable patches for *L. huberi* occurrence in South America (Figs. 3C and 4, first column). We observed a similar trend for SVM in the STK treatment (Figs. 3C and 4, second column). On the other hand, the SEP treatment showed a substantial increase in range size (Figs. 3C and 4).

Fig. 4 shows the resulting final distributions for *L. huberi* produced by each modeling algorithm under each treatment, as well as, their summed distributions under the ROC threshold. In general, *L. huberi* distribution was mainly predicted to occur in northeastern and southeastern South America, similar to the predicted distribution of its host plant species. Even so, for both modeling algorithms used, we observed disjunct distributions in central, southern, and northern areas of South America. As observed for its host plant species, *L. huberi* was not predicted to occur in core Amazonian areas. The only distribution that showed different results was that produced with SVM in the SEP treatment, which had a greater predicted range for *L. huberi* than that observed for MaxEnt (Fig. 4, second row). Finally, *L. huberi* distribution determined by the LPT threshold (Figure S2), especially when considering the SVM algorithm, showed a large increase in its predicted range, which certainly does not correspond to its distribution in South America. Based on a 350 km buffer around the known occurrences predicted by our models from the STK treatment, we suggest that future sampling efforts should be focused on: (1) Brazilian states of Goiás, Minas Gerais, and São Paulo in central-eastern South America; (2) Brazilian states in northeastern South America, and (3) southern Brazilian regions, Paraguay, and some areas in northern Argentina (Fig. 5).

4. Discussion

In this study, we attempted to integrate biotic interactions (plant–bee relationships) to our SDM procedures when predicting the potential distribution of *L. huberi* in its invaded range in

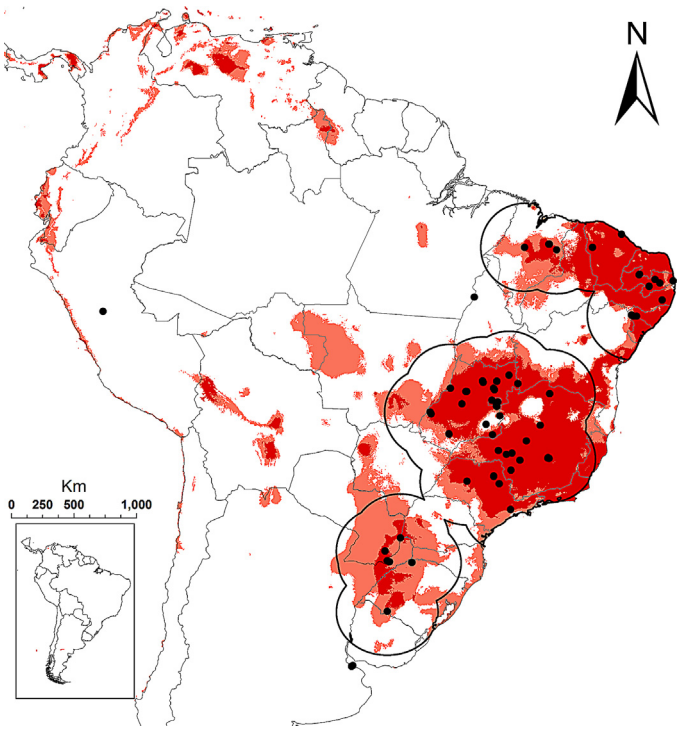

Fig. 5. Areas suggested for future surveys of *Lithurgus huberi* in South America, according to the summed distribution of MaxEnt and SVM algorithms considering the stacked modeled distribution of host plants produced by the STK treatments (Fig. 4, third column, last map). Known records for *L. huberi* are depicted as black circles.

South America. We also presented new occurrence records for *L. huberi* in Brazil ($n = 17$) and Argentina ($n = 1$). Of the five initial modeling algorithms, SVM and MaxEnt showed a good performance when predicting the occurrence of both, the host plant species and the bee. The inclusion of the host plant species distributions as variables when modeling the distribution of *L. huberi* did not increase the algorithms ability to predict its distributions, and in fact, for the SVM algorithm, model performance decreased. Nonetheless, when considering the STK treatment, both algorithms produced more constrained distributions, with lesser amounts of scattered suitable patches for *L. huberi* occurrence in South America. Our modeling procedures show that this exotic species is mainly distributed in eastern, northeastern, central, and southwestern South America, with a few suitable areas in the Amazon region. Such distribution pattern resembles that obtained from modeling all seven host plant species considered in the present study.

Generally, species distribution is determined by the intersection of the biotic, the abiotic, and the historic/migration elements that are available for the species (the BAM diagram; Soberón and Peterson, 2005; Soberón, 2007). However, biotic interactions are usually disregarded in macroecological analyses as effective variables determining the distributions of modeled species because they are assumed to exert only local effects (*e.g.* community assembly rules). This contrasts with abiotic variables (*e.g.* climate), which are thought to be the main responsible factors for determining species distribution at broader scales (Hortal et al., 2010; Pearson and Dawson, 2003; Willis and Whittaker, 2002). Nonetheless, the omission of biotic interactions from the SDM does not necessarily mean that they do not have any role in determining species distribution at broader scales (Meier et al., 2010).

Given such concerns and criticisms regarding the true effects of biotic variables at broader scale analyses (Guisan and Rahbek, 2011; Wisz et al., 2013), several studies have improved the models' ability to predict the species distribution. These studies have considered different kinds of biotic variables and different biological scenarios into the modeling procedures (Araújo and Luoto, 2007; Heikkinen et al., 2007; Meier et al., 2010; Preston et al., 2008; Rouget et al., 2001). In general, the contribution of biotic predictors on models' performance of focus species final distributions also varied. For instance, Heikkinen et al. (2007), Araújo and Luoto (2007), and Meier et al. (2010), found positive effects by including biotic variables in determining the target species' potential distribution. Pellissier et al. (2010) obtained results which ranged from highly positive, mildly positive, no effect, to even negative effects while evaluating the effect of including the abundance of *Empetrum hermafroditum* as a predictor variable affecting the distribution of other 34 subordinate species. Our results indicate that the biotic variables we used (the distributions of host plant species) are not independent of the abiotic variables (mostly related to climate) considered in the modeling procedures, as they did not improve the algorithms' ability to determine the modeled distribution of *L. huberi*. Nonetheless, our results are different from those found by other studies (Araújo and Luoto, 2007; Giannini et al., 2013a; Heikkinen et al., 2007; Meier et al., 2010), which indicated that biotic interactions are important variables determining the distributions of several target species.

In our case, given the dependency of insects and plants on climate conditions (Chown and Terblanche, 2006; Hutchinson, 1957), such variables would be the main factor responsible for both known and modeled distributions of *L. huberi* and its host plant species. Additionally, because *L. huberi* seems to be oligolectic on the pollen of those plants, the observed occurrences that we obtained for both, the bee and the host plant species, might already be the resulting intersection of the abiotic and biotic components regulating their niche (Soberón and Peterson, 2005; Soberón, 2007). Consequently, even though the use of the host plant species distribution to determine *L. huberi*'s distribution may produce a more concise distribution, may not necessarily improve the algorithm's prediction ability. At least for *L. huberi* and its host plant species, our results agree with the widely established theory that climate is the main variable determining the species distribution at a broad scales (Hortal et al., 2010; Pearson and Dawson, 2003). Such influence of climate on the distribution of both plant species and pollinators has also been shown for other intimate bee–plant species systems, namely between *Curcubita* (Curcubitaceae) plants and *Peponapis* bees (Apinae: Eucerini) (Giannini et al., 2011, 2010) and *Centris* (Apinae: Centridini) bees and oil-producing plants (Giannini et al., 2013b).

Exotic species may experience niche shifts after establishing in a new area (Broennimann et al., 2007; Da Mata et al., 2010; Fitzpatrick et al., 2007; Mukherjee et al., 2012), with a tendency to occupy regions that are climatically different from those where they naturally occur. However, a study involving another invasive megachiline species, *Anthidium manicatum* Linnaeus, showed that its invasive range seems to be restricted to areas environmentally similar to its original Eurasian range (Strange et al., 2011). The niche similarity in South America, when compared to its native distribution range, is smaller than that observed for North America, which suggests ongoing niche shifts. The relationship of *L. huberi* with species of Convolvulaceae species seems to have emerged only after its arrival in South America, since species of *Lithurgus* are known to visit only flowers of Asteraceae and, especially, Malvaceae as pollen sources in their native ranges (Michener, 2007). Such new relationship seems possible given that oligolectic bees can shift hosts (*e.g.* Wcislo and Cane, 1996; Williams, 2003), and it may also indicate that this species is becoming naturalized in South America after more than 100 years when it was first detected. However, our understanding on the floral preferences of *L. huberi* are limited to a few observations in Brazil (Camillo et al., 1983, 1994; Pick and Schlindwein, 2011; Pires et al., 2006), and to properly answer

the question whether *L. huberi* suffered niche shift or not, further macroecologic analyses on its distributional patterns in both native and invaded ranges are required (*e.g.* Broennimann et al., 2012; Warren et al., 2008).

The use of additional flower resources not accounted in this study as important biotic predictor variables may exert significant effects in the determination of *L. huberi*'s distribution in its invaded range. Thus, given its putative relationships with species of Malvaceae in its original range, further natural history and ecological studies across its South American range might be necessary to determine whether this bee also rely on such sources of pollen in its invaded range, as scarce observations from its native range suggest. In the event *L. huberi* is observed collecting pollen from other plant species not considered here, the methods we used here should be reconsidered, with the inclusion of these new biotic interactions as a potential new predictor variables determining its distribution in South America. Other possible determinants of *L. huberi* distribution not considered here are the plant species it uses as nesting substrate, namely *Euphorbia carinatum*, *Euphorbia pulcherrima* (Euphorbiaceae), *Spathodea campanulata* (Bignoniaceae), and *Eucalyptus* sp. (Myrtaceae) (Camillo et al., 1994). Particularly important is the later species, which is now widely planted in Brazil for timber and charcoal. The abundance of *Eucalyptus* in Brazil, as well as other nesting substrates and also pollen from other sources not considered in our study, might also affect the distribution of *L. huberi*, especially in areas not predicted as suitable in our models.

Different species distribution models have different mechanistic features, and usually tend to produce results with inherent peculiarities (Diniz-Filho et al., 2009; Rangel and Loyola, 2012), and such difference may be observed even for the models we considered as the best ones to represent a given species potential distribution. Although both MaxEnt and SVM showed some differences while representing *L. huberi*'s distribution, with only a ~60% prediction rate of the bee's known occurrences, in general they were the algorithms that attained the best predictions of both the bee's and its host plant species' distributions, when compared to the others. Considering the fact the insect species' known distributions usually lack deep distributional knowledge, especially in the neotropical region (Ballesteros-Mejia et al., 2013; Kamino et al., 2011; Soberón et al., 2007), even algorithms that reached only a 60% prediction rate may generate interesting and useful species distributions to be evaluated in new field surveys. Using known occurrences for some leaf-tailed geckos in Madagascar allied with SDM procedures, Raxworthy et al. (2003) were able to find both new occurrences for the known modeled species, as well as, new-to-science leaf-tailed geckos species. In a similar way and given new distributional information on the orchid bee *Aglae caerulea*, Silva et al. (2013) pinpointed suitable areas for future surveys of the species in the Brazilian Cerrado Savanna.

Given the modeled distribution of *L. huberi* in South America, based on both SVM and MaxEnt algorithms, the areas depicted in Fig. 5 are suggested as suitable for future surveys. These areas correspond to northeastern Brazil, southeastern Brazil, and northeastern Argentina/southern Brazil. Although the third region was not predicted as suitable, according to the SVM algorithm, many of its known occurrences were located in this third area, and, therefore, it should be considered in future surveys. Similar approaches have been used before and yielded fruitful results. Eventually, in case future occurrences for *L. huberi* are obtained, especially in areas not predicted as suitable for species in this study, new distribution evaluation for *L. huberi* are advised (Guisan et al., 2006). The main justifications to be considered for such process are threefold: (1) optimization to a larger extent of the resources invested in field surveys, (2) the discovery and improvement of *L. huberi* known and potential distribution, and (3) the proper evaluation of the modeling methods employed in the present study.

5. Conclusions

In this study we modeled the distribution of seven host plant species recorded in the literature for *L. huberi* and used them as a biotic variable in determining the potential distribution of this exotic pollinator in South America. We also presented new occurrence records for this species in Brazil and Argentina, some of which appear to support high population densities of *L. huberi* (DPS, pers. obs.). Although the modeled host plant distributions did not improve the algorithms' ability to predict the distribution of *L. huberi*, similar studies with other host plants as well as with other biological contexts should be sought to properly evaluate biotic variables on SDM procedures. The modeled distribution of *L. huberi*, either using ROC or LPT thresholds, suggests that this species is able to colonize most of South America. Future surveys should focus on some of the areas indicated in Fig. 5 to evaluate the true invasive potential of this species. Biological studies across the invaded range of this species are also suggested to improve our knowledge of the documented floral association with Convolvulaceae as well as to detect any host shift.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2013.11.016.

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4.8 SUPPLEMENTARY MATERIALS

4.8.1 Supplementary tables

Table S1 – List of all the new occurrence records for *L. huberi* sampled in Brazil and Argentina.

Locality, state, country	Longitude	Latitude
Água Fria de Goiás, Goiás, Brazil	-47.799	-14.924
Alto Paraíso de Goiás, Goiás, Brazil	-47.642	-14.317
Aruanã, Goiás, Brazil	-50.989	-14.831
Baliza, Goiás, Brazil	-52.444	-16.529
Ensenada, Buenos Aires Province, Argentina	-58.003	-34.787
Cristalina, Goiás, Brazil	-47.669	-16.095
Cristalina, Goiás, Brazil	-47.637	-16.143
Cristalina, Goiás, Brazil	-47.428	-16.809
Doverlândia, Goiás, Brazil	-52.377	-16.659
Niquelândia, Goiás, Brazil	-48.662	-14.297
Niquelândia, Goiás, Brazil	-48.621	-14.409
Nova Roma, Goiás, Brazil	-46.763	-13.891
Pires do Rio, Goiás, Brazil	-48.399	-17.418
Rio Verde, Goiás, Brazil	-51.080	-18.092
Rio Verde, Goiás, Brazil	-51.065	-18.143
Rubiataba, Goiás, Brazil	-49.868	-15.058
Rubiataba, Goiás, Brazil	-49.799	-15.053
Santa Cruz de Goiás, Goiás, Brazil	-47.871	-14.824

Table S2 – Number of unique occurrences for each *L. huberi* host plant species modeled, considering a grid-resolution of 4km in South America.

Host plant species	n
Ipomoea asarifolia	213
Ipomoea bahiensis	198
Ipomoea cairica	190
Ipomoea indica	281
Ipomoea nil	391
Ipomoea purpurea	291
Merremia aegyptia	290

4.8.2 Supplementary figures

FIGURE S1

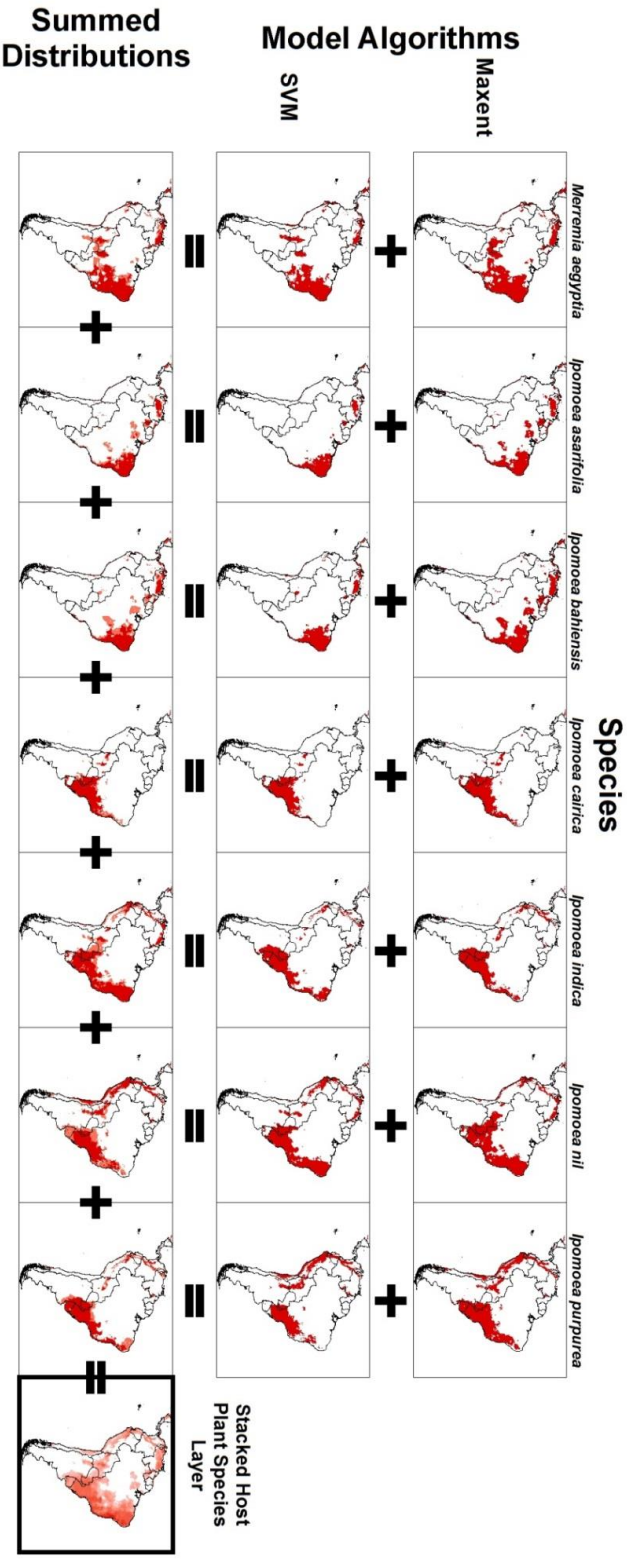

Figure S1 – Separated and stacked *L. huberi*'s host plant species modeled distributions considering each individual modeling algorithm and their summed distributions.

Figure S2

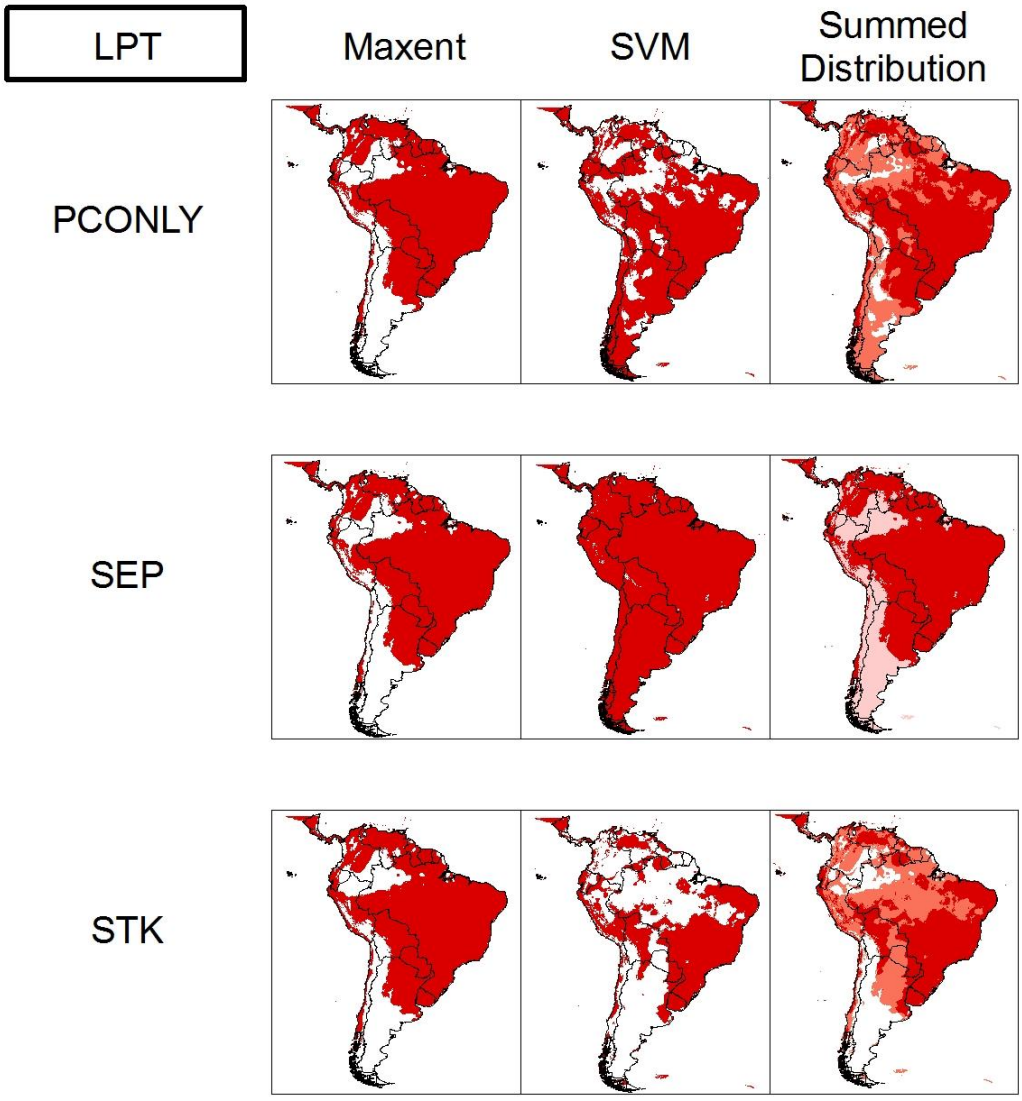

Figure S2 - Final distributions for *L. huberi* produced by each modeling algorithm according to each modeling treatment from the second modeling experiment (PCONLY, SEP, and STK) and their related summed distributions, considering the LPT threshold.

4.8.3 Reference list of additional sources holding Meliponini occurrences

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4.8.3 List of institutions holding Ipomoea *and* Merremia *occurrences*

- Administración de Parques Nacionales, Argentina
- Biodiversity International
- CEPLAC – Comissão Executiva do Plano da Lavoura Cacaueira
- CPAP – Embrapa Pantanal Botânica
- CPATSA – Embrapa Semi-Árido
- CPQBA – Coleção de Plantas Medicinais e Aromáticas
- CVRD – Herbário da Reserva Natural Vale
- EBDA – Empresa Baiana de Desenvolvimento Agrícola
- ESALQ – Escola Superior Agrícola "Luiz de Queiroz"
- Fairchild Tropic Botanic Garden
- FAPESP – Fundação de Apoio à Pesquisa do Estado de São Paulo
- FEMACT – Fundação Estadual do Meio Ambiente e Recursos Hídricos
- Field Museum
- HFSL – INCT Herbário Virtual
- FUNED – Herbário Virtual de Minas Gerais
- FURB – Herbário Dr. Roberto Miguel Klein, Universidade Regional de Blumenal
- GBIF-SPAIN – Global Biodiversity Information Foundation from Spain
- GBIF-SWEDEN – Global Biodiversity Information Foundation from Sweden
- Herbarium of the University of Aarhus
- HPL – Herbário do Jardim Botânico Plantarum
- IAC – Instituto Agronômico de Campinas
- IF – Instituto Florestal
- IFAM-CMZL – Instituto Federal do Amazonas, Campus Manaus Zona Leste
- INPA – Instituto Nacional de Pesquisa da Amazônia
- CONICET – Instituto de Botânica Darwinion
- IPA – Herbário Dárdano de Andrade Lima, Embrapa, Recife, Pernambuco
- IRD – Institute of Research for Development
- JBRJ – Instituto de Pesquisas do Jardim Botânico do Rio De Janeiro
- MBM – Herbário do Museu Botânico Municipal, Curitiba, Paraná
- MCN/FZBRS – Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul
- Missouri Botanical Garden
- MNHN – Museum National d'Historie Naturelle
- PUCRS – Pontifícia Universidade Católica Rio Grande do Sul
- SYSTAX
- NYBG – New York Botanical Garden
- UEFS – Universidade Estadual de Feira de Santana
- UEL – Universidade Estadual de Londrina
- UEM – Universidade Estadual de Maringá
- UEMA – Universidade Estadual do Maranhão
- UEPA – Universidade Estadual do Pará
- UESB – Universidade Estadual do Sudoeste da Bahia
- UFG – Universidade Federal de Goiás
- UESC – Universidade Estadual de Santa Catarina
- UFBA – Universidade Federal da Bahia
- UFC – Universidade Federal do Ceará
- UFERSA – Universidade Federal do Semi-Árido
- UFES – Universidade Federal do Espírito Santo
- UFJF – Universidade Federal de Juiz de Fora
- UFMG – Universidade Federal de Minas Gerais
- UFMS – Universidade Federal de Mato Grossos do Sul
- UFPB – Universidade Federal da Paraíba
- UFPI – Universidade Federal do Piauí
- UFPR – Universidade Federal do Paraná

- UFRGS – Universidade Federal do Rio Grande do Sul
- UFRN – Universidade Federal do Rio Grande do Norte
- UFRPE – Universidade Federal Rural do Pernambuco
- UFS – Universidade Federal de Sergipe
- UFSC – Universidade Federal de Santa Catarina
- UFU – Universidade Federal de Uberlândia
- UnB – Universidade de Brasília
- UNESPRC – Universidade Estadual de São Paulo, Campus Rio Claro
- UNESPSJRP – Universidade Estadual de São Paulo, Cmapus São José do Rio Preto
- UNICAMP – Universidade Estadual de Campinas
- UNIVASF – Universidade Federal do Vale do São Francisco
- Universidad de La Salle
- University of Alabama – Biodiversity and Systematics Department
- Herbarium of The University of Arizona
- UNIVILLE – Universidade da Região de Joinville
- United States National Plant Germplasm System
- USP – Universidade Estadual de São Paulo
- UTFPR – Universidade Tecnológica Federal do Paraná

CAPÍTULO V – Are the large-body orchid bees *Eulaema nigrita* and *Eufriesea auriceps* (Apinae: Euglossini) good indicators of habitat loss in the Brazilian Cerrado Savanna?[4]

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Running title: Are orchid bees good indicators of habitat loss in Cerrado?

[4] Formatted according to *Neotropical Entomology*.

ABSTRACT

Habitat loss, landscape fragmentation, and agriculture intensification constitute the main threats to bees. As the organisms responsible for almost one third of the food produced worldwide, there are growing concerns on bees' response to human-related disturbances. Among all bee groups, orchid bees (Apidae: Euglossini) compose an interesting group to test landscape-related hypotheses. In here, we tested the effect of landscape features (amount of anthropic areas and isolation) on the probability of occurrence and the abundances of both *Eulaema nigrita* and *Eufriesea auriceps* in the Cerrado savanna. As large-bodied bees with potential high dispersal abilities, we expected that the abundance of both species would be affected by landscape features in different local spatial scales. In general, we did not observe any effect of landscape features on the probability of occurrence and the abundances of both species in our sampling sites. As large-bodied bees and with potential high dispersal abilities, these bee species may be less sensitive to fragmented landscapes or even positively affected by the increase of anthropic habitats. Since we sampled many *El. nigrita* specimens in highly preserved Cerrado savanna areas, we believe that at least for this biome, this species may not be a good indicator of landscape disturbance.

Keywords: Habitat loss; Fragmentation; Disturbed areas; Indicator species; Cerrado savanna; orchid bees

5.1 INTRODUCTION

Agriculture intensification is accepted as a severe cause of worldwide biodiversity loss (Brittain et al. 2010; Robinson and Sutherland 2002), together with habitat loss and fragmentation (Dobrovolski et al. 2011; Tylianakis et al. 2008). Unfortunately, future scenarios on global economy suggest that given increasing demands on food production (Cirera and Masset 2010; Kearney 2010), these problems will continue to affect biodiversity in the 21th century (Foley et al. 2011; Rockström et al. 2009), along with other human-related processes (Rockström et al. 2009; Tylianakis et al. 2008). Once croplands and pastures currently encompass more than 38% of the planet's surface (Foley et al. 2011; Foley et al. 2005), it is reasonable to rank them as the greatest worldwide "biomes" on Earth, and the main causes conservation conflicts elsewhere (Dobrovolski et al. 2013), mainly in tropical regions, those with the highest deforestation rates since the 1980's (Foley et al. 2011; Hansen et al. 2013).

Depending on the combination of life-history traits they possess, species inhabiting areas affected by habitat loss and changes in landscape structure may either perish or flourish (Davies et al. 2004; Henle et al. 2004). From metapopulation perspectives, both habitat amount, expressed by the available habitat patches, and the isolation between them are important determinants of a given species success or failure to persist within a given landscape (Hanski 1994; Moilanen and Hanski 1998). Therefore, the higher the amount of habitat available for the species and the higher the connectivity, the higher the species' expected abundance and occupancy rates in the available habitat patches and the whole landscape, once species' colonization and extinction rates are directly affected by both variables (Fahrig 2013; Hanski 1994).

Considering a theoretical framework (MacArthur and Levins 1964), generalist species may perceiving the landscapes as finer-grains, allowing them to easily cope with

different landscape features, and easily percolating through any given landscape. Otherwise, specialists may perceive their surroundings as coarser-grains, hampering their movements, inhibiting their movements, and persistence in the changing landscapes (MacArthur and Levins 1964). Additionally, such contrasting landscape perception between different species may also vary according to the spatial scale analyzed, and strong and consistent relationships of species features, may not hold in other finer- or coarser- spatial scales, given the so called "scale effect" (Jackson and Fahrig 2012).

Bees compose one of the insect groups most potentially affected by decreases in habitat quality and habitat loss. Depending on the considered species, these organisms show a wide variety life-history traits, such as different nest locations (above vs. below-ground), sociality degree (solitary, parasocial, communal, highly eusocial, cleptoparasites), the exploration of their food resources (specialists/oligolecy vs. generalists/polylecy), and body-sizes (Michener 2007; Williams et al. 2010). Since they are responsible for the pollination of a great proportion of all the food consumed by humans (Klein et al. 2007), and given worldwide reports of bee abundance and species richness decreases due to habitat loss and agriculture intensification (Biesmeijer et al. 2006; Brittain et al. 2010; Brosi et al. 2008; Williams et al. 2010; Winfree et al. 2009), the effects of habitat loss on these insects are of growing public concern worldwide (Bartomeus et al. 2013; Biesmeijer et al. 2006; Burkle et al. 2013).

Orchid bees (Apidae: Euglossini) are one of the most remarkable bee groups existent, not only because of their day-glow metallic coloration but also because of the visits male orchid bees pay to several orchid species to collect fragrances, supposed used as precursors of their sexual pheromones (Dressler 1982; Eltz et al. 2006), in return, for the pollination of the Neotropical orchids (Dressler 1982). Such attraction to

plant fragrances allowed the development of aromatic artificial fragrances (Dodson et al. 1969), facilitating their consequent and community studies (Ackerman 1983; Janzen et al. 1982; Morato 1998). Despite some taxonomic issues (Nemésio 2012), this group of bees is very diverse, currently comprising almost 250 species endemics to the Neotropics (Nemésio and Rasmussen 2011). Additionally, some species of these bees have been recorded to have high daily-dispersal abilities (Janzen 1971; Raw 1989; Wikelski et al. 2010), features, make of them a unique component to be considered while addressing questions related to habitat loss, agriculture intensification, landscape and fragmentation (Brosi 2009; Nemésio and Vasconcelos 2013).

Small habitat patches, even those embedded within urban areas, were proven to maintain minimal viable population of some of orchid-bee species (Nemésio and Silveira 2010; Nemésio and Silveira 2007a). However, other studies have shown that these bees are negatively affected by habitat loss, especially by changes in landscape structure and the decreasing sizes of remnant vegetation fragments (Becker et al. 1991; Brosi 2009; Brosi et al. 2008; Nemésio 2013; Powell and Powell 1987; Tonhasca Jr et al. 2002). Otherwise, some species have also been shown to be positively affected by habitat loss. For instance, *Eulaema nigrita* Lepeletier (1841) is a species known to be associated to disturbed and anthropic matrices, what further allows it to increase its abundance (Morato 1998; Nemésio and Silveira 2006; Peruquetti et al. 1999; Tonhasca Jr et al. 2002). This species occurs from southern Mexico to southern Brazil and northern Argentina (Moure 1967) and pollinates several different plant species (Dressler 1982; Zucchi et al. 1969). Other orchid bees are usually associated with forest formations and have their peak abundances and diversity in forested areas (Dressler 1982; Nemésio and Silveira 2007b), apparently depending on the size of remnant vegetation available to maintain their population sizes (Nemésio and Silveira

2007a).Contrary to *El. nigrita*, the populations of some *Eufriesea* species (e.g. *Ef. violacea*) are believed to be negatively affected by reductions in the sizes of original vegetation patches (Sofia and Suzuki 2004), and consequent genetic effects on the individuals inhabiting fragmented landscapes (Freiria et al. 2012; Sofia et al. 2005).

Given this context, the generalist orchid bee, *El. nigrita*, would also be positively affected by the amount of disturbed areas found in the Cerrado. On the contrary, once other *Eufrisea* species seem to be negatively affected by human-related landscape disturbances (Sofia et al. 2005; Sofia and Suzuki 2004), *Eufriesea auriceps* Friese 1899 was expected to be negatively affected habitat loss in Cerrado. Therefore, here we aimed to test the effect of habitat loss and habitat isolation on these two orchid bees. Specifically we addressed the following questions: 1) If these species are affected by the structure of our sampled Cerrado's landscapes, in what local spatial scale of our sampling sites, does the amount and isolation of anthropic areas most influence the probability of occurrence of both species?; and 2) In what local spatial scale of our sampling sites, does the amount and isolation of anthropic areas influence their abundances? As general expectations, for we expected that *El. nigrita* would be either positively or not affected by the amount and isolation of anthropic areas while *Ef. auriceps* would be negatively affected by the features of our sampling sites.

5.2 MATERIAL AND METHODS

5.2.1 The Cerrado savanna, study areas, and sampling methods

The Cerrado is the second largest Brazilian biome and it is considered as one of the 25 worldwide biodiversity hotspots (Myers et al. 2000). Originally, it covered almost a quarter of the country's political territory (IBGE 2004), but according to last estimates, 39-55% of its range has been converted from its original vegetation types to

soya, maize, and sugar-cane plantations and pastures for extensive cattle-raising enterprises (Carvalho et al. 2009; Klink and Machado 2005; Klink and Moreira 2002).

We selected our sampling areas considering both a macro- and a micro-regional scales. In the macro-regional scale, we gridded the state of Goiás, in the core Cerrado area, with 25 x 25 km cells considering a land-use classification of the year 2002 for the whole biome (Sano et al. 2008). Then, we eliminated all grid cells with overlapping boundaries with the state political borders (Figure 1A). Later, we calculated two different metrics, vegetation remnants isolation (log) and the amount of vegetation remnants using FRAGSTATS v3.3 (McGarigal and Marks 1995), and evaluated their correlation within the remaining grid cells (Figure 1B). In the third step, we selected eight grid cells which resembled the overall correlation pattern for all landscapes to be sampled (Figures 1C and 1D). At the micro-regional scale, within the eight sampled grid cells, we selected areas near either natural vegetation or crop plantation matrices (n=49) to sample the orchid bees.

Once these bees are generally associated with humid habitats, streamlets and rivers generally serve as dispersal corridors, especially in drier areas such as the Cerrado and the Caatinga (Moura and Schlindwein 2009), all samplings occurred near streamlets we found within each grid cell. The sampled specimens of both *El. nigrita* and *Ef. auriceps*, were sampled from February-April/2011 and March-April/2012 (late wet season) in 49 sites from the Cerrado savanna from the state of Goiás.

In each sampling area, we delimited a 250m transect, where in every 50m intervals, we settled up a sampling station. Each sampling station was composed of five scent traps made of 2l PET bottles, within which one cotton ball was soaked with one of the following five aromatic scents: vanillin, eucalyptol (cineol), eugenol, methyl salicylate, or methyl cinnamate. Each scent trap was installed 5m apart from each other,

and in tree branches with at least 1.5m height. Three funnel-shaped entrances in the sides of the scent traps allowed the access of the bee specimens to their interior. We added 200ml of soap water in the bottom of each scent trap to guarantee that the trapped bees did not escape until they were sampled. Each site had six traps of each aromatic scent, totaling 30 traps per sampling site. The scent traps remained at each sampling site for 48h.

The strict use of scent baits sampling, without additional hand-netting surveys, is criticized elsewhere (Nemésio and Morato 2006; 2004; Storck-Tonon et al. 2009) for underestimating local species richness towards large-bodied Euglossini bees, which are less prone to escape from the scent traps than are small-bodied species (e.g. *Euglossa* bees). However, once we dealt with only large-bodied species in this study and given the small amount of time we had to develop this study, only the use of scent traps would allowed us to cover so many sampling sites within the same seasons in which we performed our surveys (Mattozo and Faria 2011).

5.2.2 Sampling sites landscape classification

We obtained Landsat Thematic Mapper (TM hereon) images for the year 2010 form the website of the Instituto Nacional de Pesquisas Espaciais (INPE; http://www.inpe.br) to classify our sampling sites. These images have 30 x 30 m resolution and were composed by up-to seven different spectral bands. From the final composite images used to classify the soil use of our sampling sites, we georeferenced and registered to landscape mosaics for further soil classification considered the bands TM3, TM4, and TM5. We classified each image considering the scale 1:25,000. The main classes we used to classify our landscapes were: (1) riparian vegetation, (2) Cerrado vegetation remnants, (3) anthropic areas, and (4) water. Later, the classes (1)

and (2) were lumped together and the final classes we used in our analyses were: original Cerrado vegetation, anthropic areas, and water.

We manually classified the different soil uses of the surrounding landscapes of each sampling sites considering circular buffers from the sampling GPS coordinates with increasing and nested radii of 250 m, 500 m, 750 m, 1,000 m, 1,250 m, 1,500 m, 1,750 m, 2,000 m, which are known to be relevant for bee communities as foraging distances (Gathmann and Tscharntke 2002; Greenleaf et al. 2007; Steffan-Dewenter et al. 2002; Taki et al. 2007). We considered these different and nested buffers surrounding each sampling site as possible multiple scales affecting both probability of occurrence and abundances of *El. nigrita* and *Ef. auriceps*.

5.2.3 Statistical analyses

We used logistic regressions to test whether the probabilities of occurrence of *El. nigrita* and *Ef. auriceps* were determined by the amount of anthropic areas and isolation of the anthropic patches surrounding each of our sampling sites, considering the eight different spatial scales covered by the circular buffers around our sampling sites. We also performed multiple linear regressions in all eight spatial scales to test whether both species abundances were also determined by the isolation and the amount of anthropic areas surrounding our sampling sites.In order to assess the multi-scale landscape effect on the abundances of *El. nigrita* and *Ef. auriceps*, we retained both the R^2 and p-values. We also repeated these procedures considering the amount of remnant Cerrado vegetation and their isolation, considering Fahrig's (2013) Habitat Amount Hypothesis. Consequently our expectations regarding both *El. nigrita*' and *Ef. auriceps*' probabilities of occurrence and abundance would be inversed, in relation to those predicted to the amount of anthropic areas and their isolation rates: with *El. nigrita*

showing either no effects or being negatively affected by the amount of remaining Cerrado vegetation and *Ef. auriceps* being positively affected by increasing amounts of remnant Cerado vegetation. The data was tested for both normality and homogeneity of variances, and it was transformed whenever necessary (Zar 2010).

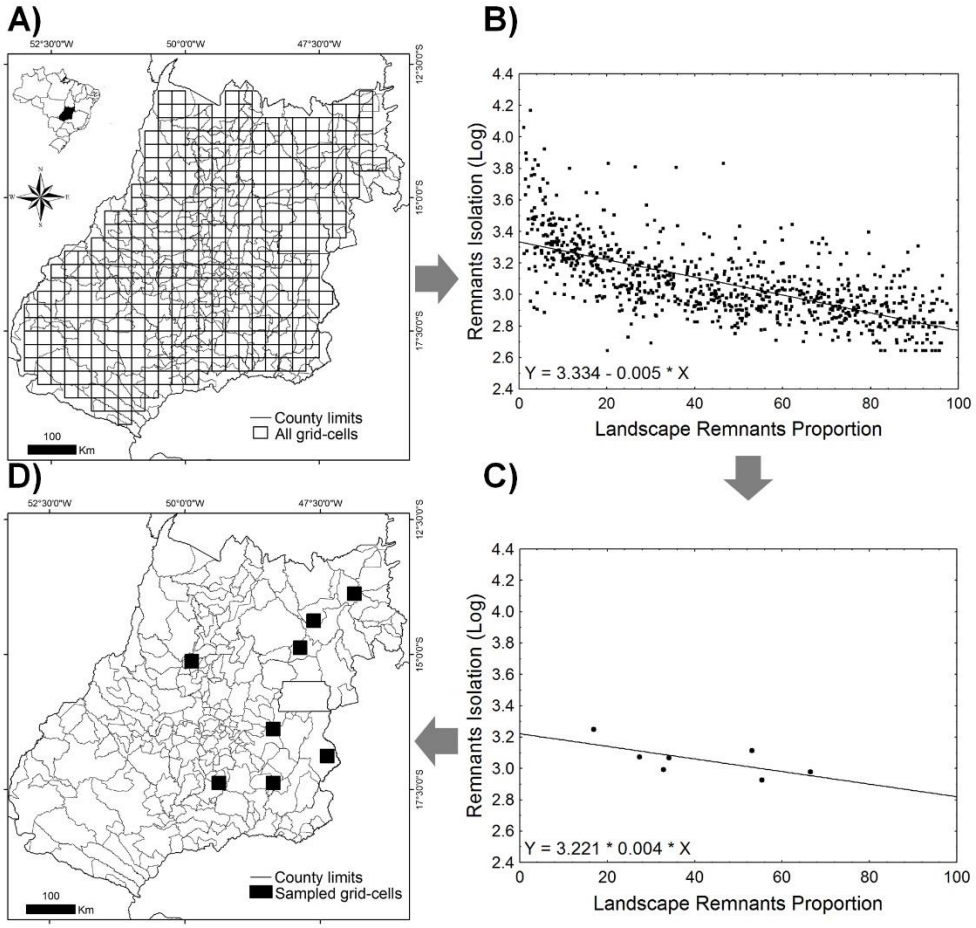

Figure 1 – Visual representation of the process involved with the selection of the sampled landscapes. A) The state of Goiás with all initial 25 km x 25 km grid cells. B) Gradient between landscape remnants proportion and remnants isolation found for the whole state. C) Gradient between landscape remnants proportion and landscape remnants isolation found for the sampled grid cells. D) Spatial distribution of all sampled grid cells within Goiás. The fitted correlations in B) and C) are expressed by inset equations in both steps.

5.3 RESULTS

We sampled a total 506 specimens of *El. nigrita*, mainly using vanillin and eucalyptol and a few individuals were captured with eugenol and methyl cinnamate. No bees were captured with methyl salicylate. Regarding *Ef. auriceps*, we sampled a total of 91 specimens, mainly using vanillin. A few individuals were also attracted by eugenol, methyl cinnamate and methyl salicylate.

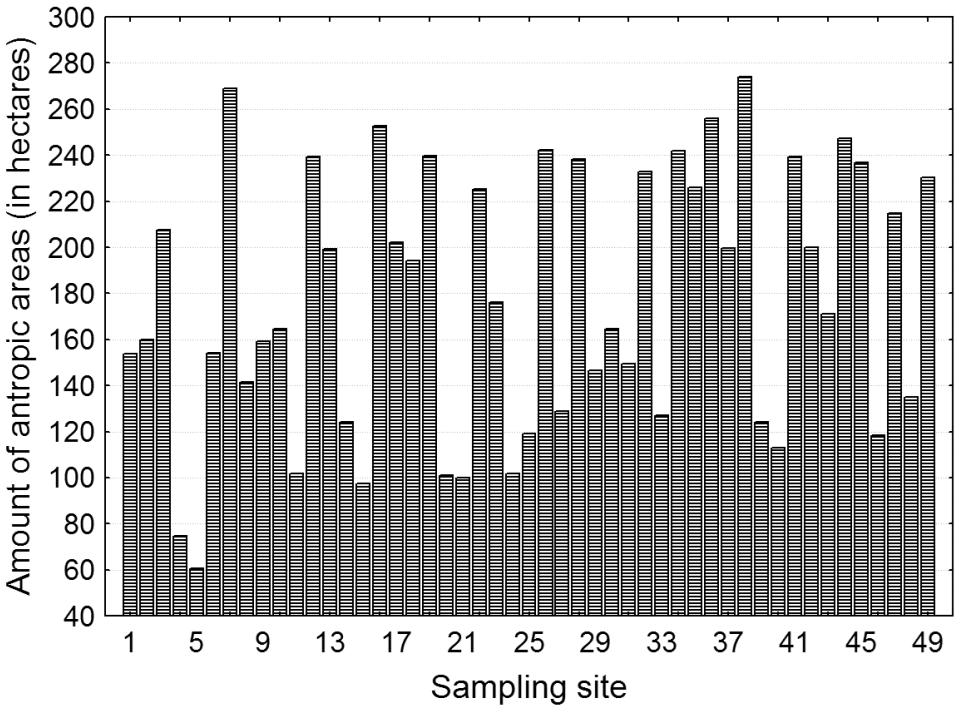

Figure 2 – Amount of anthropic areas within all the 49 sampling sites where we sampled both *El. nigrita* and *Ef. auriceps* in the state of Goiás, considering the broader buffer we used in our analyses (2,000 m).

Both of our predictor variables were negatively correlated in all local spatial scales but the one, at 250 m (2,000 m: r = -0.62; 1,750 m: r =-0.57; 1,500 m: r =-0.52; 1,250 m: r =-0.56; 1,000 m: r =-0.59; 750 m: r =-0.48; 500 m: r =-0.30). Therefore, we only used the amount of anthropic areas as our predictor variable. Our sampling sites

showed varying quantities of the amount of anthropic areas within the buffers with 2,000 m radius, with highly disturbed (more than 200 ha within the buffer) and highly preserved (less than 70 ha of anthropic areas within the buffer) sites (Figure 2).

Table 1 – Logistic regression analysis of the effects of amount of anthropic matrix on the probability of occurrence of *Ef. auriceps*. In all regressions, degrees of freedom were equal to 1.

Spatial scale	Chi-square	p-value
2,000 m	1.864	0.172
1,750 m	1.735	0.187
1,500 m	1.736	0.187
1,250 m	2.407	0.120
1,000 m	2.340	0.126
750 m	1.953	0.162
500 m	1.831	0.176
250 m	0.314	0.575

Our data did not corroborate any of our previous expectations for *El.* nigrita, once it was present in 48 of our 49 sampling sites in the Cerrado savanna, what implies that the amount of anthropic areas did not affect its probability of occurrence in those areas at all. On the other hand, *Eufrisea auriceps* occurred in only 29 of our 49 sampling sites. Still, its probability of occurrence was not affected by the amount of anthropic areas within each different local multiple spatial scales of our sampling sites (Table 1). In general, our predictor variable also did not show any effect on the abundances of *El. nigrita* in any of our local spatial scales (Table 2). Nonetheless, *Ef. auriceps*' abundances were positively affected by the amount of anthropic areas found at the 500 m scale (R^2=0.115; p=0.04), contrasting our initial predictions that that this species would be negatively affected by the amount of anthropic areas in our sample

sites. Although we expected broader scales showing the higher explanation of both species abundances, in general, we did not observe any effect for any of the buffers, either the smaller or the broader ones. When we considered the amount of remnant vegetation affecting both species, our results were practically the same, with both species not responding to the amount of remnants in any of the local spatial scales we considered (Tables S1 and S2).

Table 2 – Regression analyses results of the effects of amount of anthropic matrix on the abundances of both *El. nigrita* and *Ef. auriceps* in multiple spatial scales. Bold values are significant at $\alpha = 0.05$. SE: Standard Error.

	Eulaema nigrita					***Eufriesea auriceps***				
Spatial scale	**B**	**SE of B**	**t-value**	***p*-value**	**R^2**	**B**	**SE of B**	**t-value**	***p*-value**	**R^2**
2,000 m	-0.018	0.068	-0.273	0.785	<0.001	0.026	0.026	1.006	0.323	<0.001
1,750 m	-0.004	0.067	-0.065	0.948	<0.001	0.028	0.026	1.064	0.296	<0.001
1,500 m	0.012	0.066	0.193	0.847	<0.001	0.028	0.025	1.089	0.285	<0.001
1,250 m	0.031	0.063	0.501	0.618	<0.001	0.029	0.024	1.219	0.233	<0.001
1,000 m	0.043	0.061	0.703	0.485	<0.001	0.032	0.022	1.448	0.158	<0.001
750 m	0.036	0.058	0.624	0.535	<0.001	0.036	0.020	1.786	0.085	0.072
500 m	0.059	0.055	1.078	0.286	<0.001	0.038	0.018	2.154	**0.040**	0.115
250 m	0.078	0.053	1.471	0.147	<0.001	-0.015	0.021	-0.714	0.481	<0.001

5.4 DISCUSSION

Some studies have already shown the overall effects of habitat loss on orchid bees (Becker et al. 1991; Brosi 2009; Nemésio 2013; Powell and Powell 1987; Tonhasca Jr et al. 2002; Tonhasca Jr. et al. 2003). Despite our previous expectations, we did not observe any effect of landscape features on the abundances and probability of occurrence in the sampled sites for *El.nigrita*. *Eufriesea auriceps* behaved similarly to *El. nigrita*, once its probability of occurrence was neither negatively (our initial

expectation) or positively affected by the amount of anthropic areas. Nonetheless, this species was positively affected at the scale of the 500 m, in contradiction to our prior expectations that it would be negatively affected by the amount of available anthropic areas.

The matrix habitat formed after habitat loss occur may imply in different permeability and resistances for the species that inhabiting the newly-affected areas. Consequently, the responses of different biological groups vary after a given landscape disturbance (Baum et al. 2004; Fahrig et al. 2011; Kupfer et al. 2006; Metzger and Décamps 1997). Such species' responses to environmental disturbances is generally deeply related to their life-history and ecological traits (body sizes, diet breath, dispersal abilities and others), which directly affect their perception of the surrounding habitats, (Davies et al. 2004; Henle et al. 2004). Therefore, while some orchid bees are associated with forest interiors, protected from edge effects [e.g. *Euglossa sapphirina* or *Eg. Annalis* (Nemésio and Silveira 2006; Tonhasca Jr et al. 2002)], others, (e.g *El. nigrita* and *Ef. auriceps*) may either benefit or not be negatively affected by habitat loss.

From MacArthur & Levins' (1964) perspective, the overall lack of responses of *El. nigrita* and the contradicting response of *Ef. auriceps*, may be related to the way they perceive their surrounding habitats. As large-bodied species, they may perceive their surrounding habitats as fine-grained in contrast to small-bodied ones, for which landscape features may seem coarser. From this stand point, although we did not observe any apparent effect of landscape features on both *El. nigrita* and *Ef. auriceps*, given their high dispersal abilities, landscape features found in broader spatial scales (bigger than 2 Km radii; Jackson and Fahrig 2012) may eventually prove to be important for both of these and other Euglossini bees, and should be tested in future studies. According to Jackson and Fahrig's (2012) suggestions, landscapes shoud

correspond to 4-9 times of the median dispersal distance of the species of interest or 0.3-0.5 of its maximumdispersal distance. Once large-bodied orchid bees may cover daily ranges of 10-20 Km (Janzen 1971; Raw 1989; Wikelski et al. 2010), distances from the focal landscape ranging from 3 to 6 Km may represent good radial distances from focal areas for the habitat types classification that may be used by orchid bees.

Additionally, the occurrence of *El. nigrita* in almost all of our sampling sites may be explained by the inherent features of the Cerrado savanna, where even in pristine areas the vegetation is naturally opened when compared to pristine areas of Atlantic and Amazonian rainforests. Such higher natural amount of open habitats has already been reported to allow increased abundances of *El. nigrita*, especially in the Atlantic forest (Morato 1998; Nemésio and Silveira 2006; Peruquetti et al. 1999; Tonhasca Jr et al. 2002). Although *Ef. auriceps* had considerable smaller abundances in our sampling sites, when compared to *El. nigrita*, it also was not affected by the amount of anthropic areas available. *Eufriesea* species are rarer and seasonal (Ackerman 1983; Dressler 1982; Janzen et al. 1982; Kimsey 1982; Roubik 2001), with abundance peaks occurring during the wet seasons of the year. Therefore, the end of the wet season may explain the abundance differences we observed between *Ef. auriceps* and *El. nigrita*. Some properties and behaviors of the nesting behavior of both species has been described by Zucchi et al.(1969) and both use crevices or pre-existent ground cavities from abandoned termite or ant nests, naturally common in Cerrado (Carrijo et al. 2008), to build their brood cells and nests, what allows these species to maintain the high abundances and higher presence probability.

Large-bodied orchid bees, such as *El. nigrita* and *Ef. auriceps*, have remarkable dispersal abilities, being capable covering great distances in a daily basis (Janzen 1971; Milet-Pinheiro and Schlindwein 2005; Raw 1989; Wikelski et al. 2010).

Consequently, this trait is expected to protect them from negative effects of habitat loss (Cane 1987; Greenleaf et al. 2007). On the other hand, some smaller orchid bees demand habitats with higher quality (e.g. less light, low temperature, higher humidity, high food resources) to maintain viable populations (Morato 1994), what impede them from crossing small opened areas distances (Becker et al. 1991; Powell and Powell 1987). Large forested patches are very important to maintain viable populations and high abundances of these bees, and general orchid bees species richness (Nemésio and Silveira 2010; Nemésio and Silveira 2007a). Nevertheless, since the riparian areas found in Cerrado are naturally narrower than those found in the Amazon or the Atlantic forests, rarely reaching more than 100 m wide (Ribeiro and Walter 1998), border effects acting upon them may impede the survival of orchid bees intolerant to either open areas or border effects (Faria and Silveira 2011). Therefore, we suggest that future studies in Cerrado should invest efforts in testing the same hypotheses with small-bodied orchid bees found in this biome (e.g. species from the *Euglossa* genus), which are expected to show a clearer response to habitat loss in the Cerrado biome than both *El. nigrita* and *Ef. auriceps*.

Considering the results related to *El. nigrita*, its status of indicator species of highly disturbed areas (Morato 1998; Nemésio and Silveira 2006; Peruquetti et al. 1999; Tonhasca Jr et al. 2002) needs to be revised for the Cerrado savanna, despite its effective indicator use for disturbance in Atlantic and Amazonian forests (Morato 1998; Peruquetti et al. 1999; Tonhasca Jr et al. 2002). Especially in the northern region of the Goiás, one of the more preserved Cerrado regions in the state (Sano et al. 2008; DP Silva, pers. comm.), we collected several *El. nigrita* specimens. The same also happened in well-preserved Cerrado areas found in the center of the state (e.g. Silvânia municipality), regions, we sampled new occurrences of the cleptoparasitic orchid-bees,

such as *Aglae caerulea* (Silva et al. 2013) and *Exaerete* (unpublished data). Given their very specialized traits and dependency on other bees to complete their development, cleptoparasitic bees are usually pointed as good indicative of how preserved an area is, once they occupy the apex of bee communities and are one of the first groups to respond to habitat loss (Sheffield et al. 2013).

Even though the abundances of Euglossini bees may show striking variance from one year to another (Ackerman 1983; Janzen et al. 1982; Roubik 2001), *El. nigrita*'s predominance and higher abundances, as also noted in other studies performed within the Cerrado (Alvarenga et al. 2007; Faria and Silveira 2011; Knoll and Penatti 2012; Nemésio 2008; Nemésio and Faria 2004; Pires et al. 2013; Rebêlo and Cabral 1997; Rebêlo and Silva 1999; Viotti et al. 2013), does not necessarily mean these Cerrado areas are disturbed. Therefore, in future studies evaluating orchid bees' responses to habitat loss in Cerrado biome should test, indicator value of *El. nigrita* to human-related disturbances should be addressed. Additionally, we also suggested that further studies evaluating the effects of pristine and disturbed landscapes on orchid bees in other Brazilian biomes (Atlantic and Amazon rainforests) should make use of multivariate analysis, such as INDVAL (Borcard et al. 2011; Dufrêne and Legendre 1997), to assess its association with disturbed and fragmented areas.

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5.7 SUPPLEMENTARY MATERIALS

Table S1 – Logistical regression analysis of the effects of amount of remnant vegetation on the probability of occurrence of *Ef. auriceps*. In all regressions, degrees of freedom were equal to 1.

Spatial scale	Chi-square	p-value
2,000 m	1.861	0.172
1,750 m	1.730	0.188
1,500 m	1.736	0.187
1,250 m	1.820	0.177
1,000 m	2.458	0.116
750 m	2.085	0.148
500 m	1.916	0.166
250 m	2.173	0.140

Table S2 – Regression results of the effects of amount of remnant vegetation on the abundances of both *El. nigrita* and *Ef. auriceps* in multiple spatial scales. Bold values are significant at $\alpha = 0.05$. SE: Standard Error.

	Eulaema nigrita					*Eufriesea auriceps*				
Spatial scale	**B**	**SE of B**	**t-value**	***p*-value**	**R^2**	**B**	**SE of B**	**t-value**	***p*-value**	**R^2**
2,000 m	-0.001	0.005	-0.274	0.784	-	-0.000	0.000	-0.325	0.746	-
1,750 m	-0.000	0.007	-0.069	0.944	-	-0.000	0.000	-0.231	0.817	-
1,500 m	0.001	0.009	0.192	0.848	-	-0.000	0.000	-0.188	0.851	-
1,250 m	-0.001	0.009	-0.193	0.847	-	0.000	0.000	0.225	0.822	-
1,000 m	-0.013	0.019	-0.701	0.486	-	0.000	0.001	0.081	0.935	-
750 m	-0.020	0.032	-0.624	0.535	-0.020	-0.000	0.002	-0.263	0.792	-
500 m	-0.074	0.069	-1.063	0.293	0.0027	-0.003	0.005	-0.685	0.496	-
250 m	-0.250	0.250	-1.010	0.314	0.0006	-0.008	0.020	-0.427	0.671	-

CAPÍTULO VI – Scale effect to landscape structure in harsh and seasonal environments: the cerrado's bees [5]

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ABSTRACT

Landscape structure is an important determinant of the biological fluxes and its properties are important features affecting species responses to landscape structure. Species do not respond equally to landscape features in the same way or spatial extents. Evaluating their "multi-scale" responses to landscape structure in varing spatial scales is an important framework to be considered, allowing insights in the considered groups habitat needs. We evaluated the response of Brazilian Cerrado's bees (whole community vs. eusocial vs. solitary ones) to both the amount and isolation of remnant vegetation in eight nested multiple-local scales. Eusocial species' abundance responded to landscape structure at narrow scales (250 m), while that of solitary ones responded to broader scales (2,000 m). Eusocial species nestedness also responded to landscape features in broader scales (1,500 m). However, the other biological variables did not show any response to the landscape features at any spatial scale considered. Such contrasting responses of the abundances of eusocial vs. solitary species are related to their inherent life-history traits. Their differing requirements on food resources, populational features, and flight abilities may explain such differences. Otherwise, the isolation of habitat patches in the sampled landscapes may be the main determinants of the nestedness patterns of eusocial species at 1,500 m. Although the bees sampled in this study, in general did not respond to landscape features, given their possible resistance to Cerrado's environmental harshness and seasonality, similar analysis considering the multi-scale effects should be considered in future studies.

Keywords: habitat amount, isolation; fragmentation; bees; Cerrado Savanna; spatial extent.

6.1 INTRODUCTION

The matrix surrounding a habitat patch is a complex mosaic of different landcovers and has a very important role regulating the biological fluxes within the landscape (Fischer and Lindenmayer, 2007; Kupfer et al., 2006; Ricketts, 2001). Matrix properties such as its complexity, resistance, and resemblance to the original habitat vegetation directly affect the permeability of biological components (Fahrig et al., 2011; Kupfer et al., 2006; Murphy and Lovett-Doust, 2004), and species' success or failure to cope with such complex mosaics depends on the way they perceive the landscape structure within their surrounding habitats. From a theoretical perspective (MacArthur and Levins, 1964), while specialists may see their habitats as coarse-grains that impede them to effectively disperse through space, generalists may perceive their surrounding habitats as fine-grains, and consequently, disperse more easily from an area to other. Several species' life-history traits (e.g. dispersal ability, home range, diet breath and specialization, nestling sizes etc.) mediate their habitat perception as fine- or coarse-grained, and affect their interactions with the landscapes' configuration (Davies et al., 2004; Henle et al., 2004). Given these different perceptions of their habitat's configuration, the overall effects of landscape structure (habitat amount and its related fragmentation rates) may vary from species to species (Fahrig, 2003).

Ongoing ecological processes occurring in different spatial extents may also regulate species' occurrences and incidence probabilities within a given landscape (Hortal et al., 2010), and the spatial extent as perceived by the species also may vary according to landscape structure. For instance, Metzger (2000) showed that plant species with different dispersal syndromes respond to landscape structure and fragmentation in different spatial scales. While barochorous species richness depended more intensely on landscape structure on finer scales (up to 2 km), anemochorous and zoochorus species richness were more responsive to the

landscape structure between (4 to 8 km). In another study, Chust *et al.* (2004) evaluated the responses of homopteran and dipteran species, insect groups with contrasting dispersal features, to landscape structure at several local spatial scales. While homopteran richness was more dependent on landscape configuration finer spatial scales, dipteran richness was more responsive to landscape structure in more coarser spatial scales (Chust et al., 2004). Similar approaches have also been reported for birds (Boscolo and Metzger, 2009), plants (Chust et al., 2006), spiders (Schmidt et al., 2007), butterflies (Cozzi et al., 2007), and soil fauna (Chust et al., 2003). Such "multi-scale effect", usually related to the species' dispersal abilities, represents the scale where biological variables are best predicted by landscape structure (Jackson and Fahrig, 2012). Alternatively from the fixed patch-based perspectives considered in landscape ecology, such multi-scale approach may provide alternative insights to be considered according to the biological features of the species or group of interest (Boscolo and Metzger, 2009; Chust et al., 2004).

The response of pollinating bees to varying landscape structure was also evaluated under such perspective, allowing us to discuss minimum habitat requirements and landscape configuration affecting their survival in fragmented landscapes. For instance, in the local scale at where landscape structure may affect bees' diversity, Steffan-Dewenter *et al.* (2002) showed that while solitary species richness and abundance depend more intensely of the proportion of semi-natural habitats found in small to meso-scales, large-bodied eusocial bees did not respond to any spatial scale. In another study, both the abundance and species richness of solitary bees were mainly determined by the proportion of non-flowering crops in small scales, in larger ones, they were mainly determined by the availability of fields with mixed plant species (Le Féon et al., 2013).

Despite their ecosystemic importance while pollinating and maintaining populations of both wild and crop plant species worldwide (Klein et al., 2007), bees' conservation has been of great public concern lately, once several human-related activities have been reported to affect in their biodiversity (Biesmeijer et al., 2006; Burkle et al., 2013; Cameron et al., 2011; Garibaldi et al., 2013; Ghazoul, 2005; Kearns et al., 1998; Kevan and Phillips, 2001; Williams et al., 2010; Winfree et al., 2009). These organisms have a variety of life-history traits related to feeding habits (generalists/polylectic vs. specialists/oligolectic), nesting places (above-ground vs. below ground nests), and body sizes (large vs. small sized bees). However, by far, their sociality degree is predicted to be an important determinant of their responses to environmental changes (Chapman and Bourke, 2001; Henle et al., 2004). As a general trend with many exceptions, eusocial bees usually prefer natural areas, nesting in cavities commonly found beneath or within mature trees, while solitary species nest in the ground and/or hollow plant stems commonly found in disturbed areas (Michener, 2007; Ricketts et al., 2008). Additionally, both of these groups have contrasting feeding habits: with eusocial bees require floral diversity to complete their development, solitary species have a more specialized diet, which may constrain their development to the blooming periods of determined plants species (Biesmeijer et al., 2006; Müller et al., 2006; Ricketts et al., 2008).

Given this context, our goal in this study was to evaluate the multi-scale effect of landscape structure, represented by habitat amount and patch isolation, on Cerrado's bees diversity (abundances, observed and estimated species richness, and beta diversity) considering them either as a whole community or as separated eusocial and solitary species. We expected that landscape structure at meso-local scales would be the main determinants the whole community biological variables. Nonetheless, we expected contrasting responses of solitary vs. eusocial bees: with the first being affected by landscape structure at broader local

scales, the latter being affected at narrower local scales. Given their overall higher abundances and gregariousness within their nests, we expected that eusocial species would show higher species turnover to landscape structure at narrower local scales, when compared to solitary ones. Additionally, we expected that the eusocial species would show higher nestedness to landscape structure at broader local spatial scales, given their higher dependency on diverse floral resources to complete their development. Given their smaller population sizes when compared to eusocial species, we expected that landscape structure at broader local scales would be the main determinants of solitary bees species turnover to landscape structure at broader scales and a smaller species nestedness to landscape structure at these same spatial scales.

6.2 MATERIAL AND METHODS

6.2.1 Study area and experimental design

The Cerrado is the second largest Brazilian biome and considered as one of the 25 worldwide biodiversity hotspots (Myers et al., 2000). Originally, it covered almost a quarter of the country's political territory (IBGE, 2004), but according to last estimates, 39-55% of its range has been converted from its original vegetation types to soya, maize, and sugar-cane plantations and pastures for extensive cattle-raising enterprises (Carvalho et al., 2009; Klink and Machado, 2005; Klink and Moreira, 2002).

We selected our sampling areas considering both macro- and micro-regional spatial scales. From a land-use classification of the year 2002 for the whole Cerrado biome (Sano et al., 2008), we gridded the state of Goiás, a core Cerrado area, with 25 x 25 km cells. Then, we eliminated all of those with overlapping boundaries with the state political borders (Figure 1A). Later, within all of them, we used the software FRAGSTATS v3.3 (McGarigal and

Marks, 1995) to calculate two different metrics: vegetation remnants isolation (log) and the proportion of vegetation remnants. Subsequently, we evaluated their correlation within the remaining grid cells (Figure 1B). In the third step, we pre-selected twelve landscapes, resembling the observed gradient of remnants isolation vs. proportion of vegetation remnants for the whole state, to be sampled (Figures 1C and 1D).

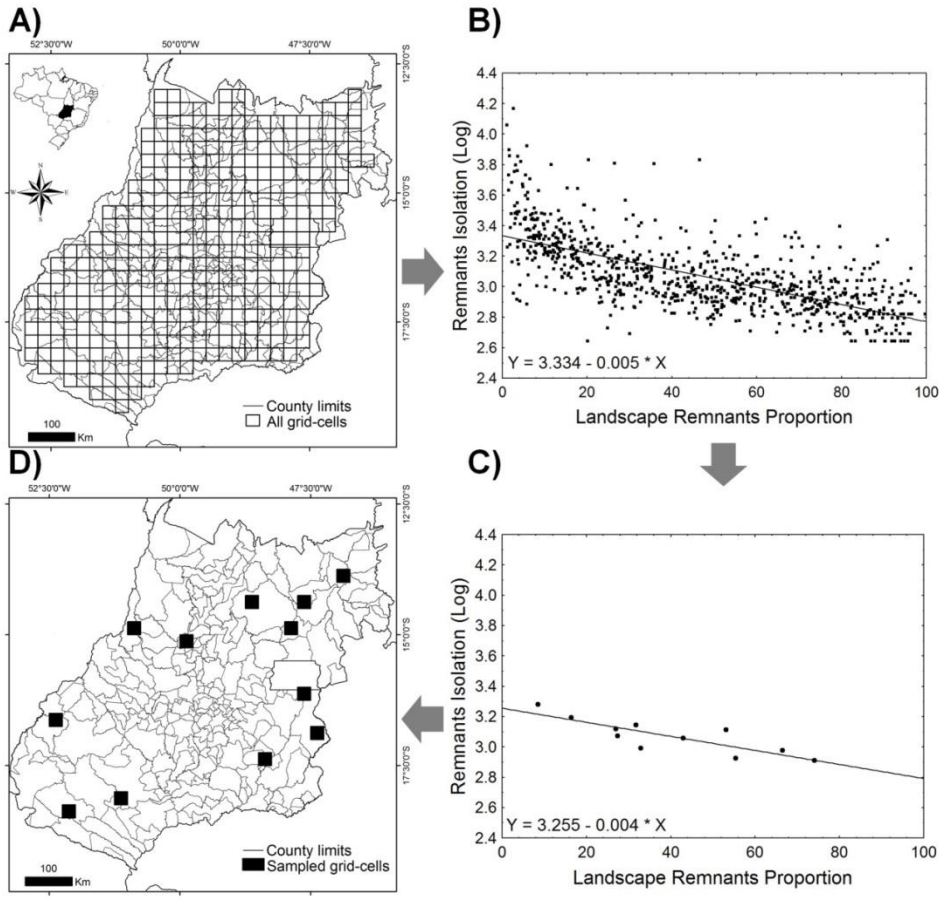

Figure 1 – Visual representation of the process involved with the selection of our sampled landscapes. A) The state of Goiás with all initial 25 km x 25 km grid cells. B) The gradient between landscape remnants proportion and remnants isolation found for the whole state. C) Gradient between landscape remnants proportion and landscape remnants isolation found for the sampled grid cells. D) Spatial distribution of all sampled grid cells within Goiás. The fitted correlations in B) and C) are expressed by inset equations in both steps.

Within each of the selected grid cells, we sampled bees in two locations: one embedded within/near an original vegetation matrix and the other embedded within/near an agriculture matrix. Given logistical and climatic impediments, we only sampled one location within two grid cells, totaling 22 sampling sites. The main components of the agriculture matrix were cattle raising pastures, sugar cane, and soybean plantations.

We obtained Landsat Thematic Mapper (TM hereon) imagery for the year 2010 from the Instituto Nacional de Pesquisas Espaciais (INPE; http://www.inpe.br), composed by up-to seven different spectral bands and a resolution of 30 x 30 m to manually classify the land use around our sampling sites. We georeferenced and registered those TM images to landscape mosaics using the bands TM3, TM4, and TM5 and a 1:25,000 scale. The main classes we used to classify our landscapes were: (1) riparian vegetation, (2) Cerrado vegetation remnants, (3) anthropic areas, and (4) water. Later, the classes (1) and (2) were lumped together and the final classes we used in our analyses were the original Cerrado vegetation, anthropic areas, and water. In each sampling site, as surrogates for the landscape structure, we measured the amount of original vegetation remnants and remnants isolation found within circular buffers with radii of 250 m, 500 m, 750 m, 1,000 m, 1,250 m, 1,500 m, 1,750 m, and 2,000 m from the sampling sites GPS coordinates. These radii buffers are known to be relevant for bee communities as foraging distances (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Steffan-Dewenter et al., 2002; Taki et al., 2007). We used these nested buffers surround each sampling site as the different local scales of our landscapes. All classified sampling sites and their related buffers are found in Figure S1.

The bee samplings took place from February-May 2011 and March-June 2012. Such samplings were composed of a standardized protocol of bee species using pan-traps (Moericke traps). In all sampling areas, we settled a 200m transect, with 20 sampling stations.

Each sampling station was composed of a PVC post with 1.5 m of height and 0.5 inch in diameter (20 mm). In every PVC post, according to the surrounding ground vegetation height, we placed three bowls painted with different ultra-violet colors: UV-white, UV-blue, and UV-yellow, painted with the UV paint Colorgin Luminosa® (Sherwin-Williams do Brasil, São Paulo, Brasil). The transect design we used was based on those previously used in other studies evaluating pan-trapping efficiency while sampling bees (Westphal et al., 2008). We filled each bowl with 240 ml of water and soap. The bowls were made of hard paper and were manufactured by Lidcup Brasil®. In total, the whole transect contained 60 bowls (20 of each color). Every two days (48 h), we retrieved all bee specimens captured in the pan-trap bowls and kept them in alcohol. All transects remained at the field for eight days in each sampled location, with a total sampling period of 96 h, totaling 5,760 trap/hours of sampling effort for each sampling site. We checked each transect daily for painting and/or structural damages, and whenever needed, we replaced them. We refilled each bowl's water daily.

We took the sampled bees to the laboratory, separated, pinned, and identified them to the most specific biological level possible, following genera taxonomic catalogues available for the Brazilian bees (e.g. Michener, 2007; Silveira et al., 2002). We separated specimens from the same genus into morphospecies, which generally yields good coverage of the real species level (Oliver and Beattie, 1996). Whenever possible, we sent some specimens to bee specialists for further species identification. After the identification process was finished, we also sent the data on the sampled bee species to specialists and also consulted specialized publications on bee ecology (e.g. Michener, 2007; Silveira et al., 2002) to separate which taxa represented either social or solitary species. Cleptoparasitic taxa (e.g. *Acanthopus*, *Nomada*, *Sphecodes*), as well as those not exihibiting true eusociality, but only degrees of this behavior

(e.g. parasocial or communal species, as *Eulaema* and *Exomalopsis*, respectively), were lumped under the solitary bees group.

6.2.2 Statistical analyses

For each site, considering the whole bee community, as well as both eusocial and solitary groups, we obtained the 1) observed and 2) estimated species richness, 3) species abundances, and 4) beta diversity parameters using R (R Development Core Team, 2013). We estimated species richness using Jackknife to correct for its intrinsic bias (Coddington et al., 1991; Colwell and Coddington, 1994; Heltshe and Forrester, 1983). Jackknife is a resampling statistical process that provides an estimate for the species richness and its 95% confidence interval. We used a pairwise dissimilarity partitioning approach (Baselga, 2010) to decompose beta diversity into nestedness and turnover components. Under this approach, we portioned the total pairwise dissimilarity (Sørensen dissimilarity; β_{sor}) into a spatial turnover component (Simpson dissimilarity; β_{sim}) and a nestedness dissimilarity component caused by species richness differences among sites (Almeida-Neto et al., 2012; Baselga, 2012, 2010). We used the function *beta.pair* available in the *betapart* package (Baselga et al., 2013) to perform our analyses.

We considered multiple linear regressions to test for the multi-scale effect of both predictor variables vegetation remnant isolation and amount of remnant areas on the observed abundances, observed species richness, and estimated species richness of all bee groups (whole community vs. eusocial species vs. solitary species). All data was tested for normality and homogeneity of variances, and it was transformed whenever these assumptions were not meet (Zar, 2010). We assessed each model's goodness-of-fit by retaining the R^2 values for the whole model and *p*-values both for the whole models and for each predictor variable.

Regarding the beta-diversity components, we analyzed the multi-scale effect of our predictor variables on the three dissimilarities components from Baselga's (2010) beta diversity partitioning (β_{nes}, β_{sim}, and β_{sor}), using a distance-based Redundancy Analysis (db-RDA; Legendre and Anderson, 1999). At first, we performed a principal coordinate analysis (PCoA) for each dissimilarity matrix, adding a constant to control the formation of negative eigenvalues. Later, we ran an analysis of redundancy (RDA) with the resultant PCoA axes only keeping those with non-negative eigenvalues (Borcard et al., 2011). Finally, we extracted the db-RDA R^2c to assess the main effects of our predictors and their interaction on our response variables for each local spatial scale at each local spatial scale. We used the functions *cmdscale* and *rda*, from *stats* (R Development Core Team, 2013) and *vegan* (Oksanen et al., 2013) packages to respectively calculate both PCoA and db-RDA. We based the models' overall significance with 999 ANOVA-like randomizations tests.

In addition, we assessed the partial contribution of each predictor with a multivariate regression analysis of distance matrices (Zapala and Schork, 2006). Under this approach, the distance matrices are sequentially regressed against each environmental predictor, without the use of an ordination transformation, what produces an unbiased partial-R^2. Later, the statistical significance of this process is assessed with a permutation of original matrix by the *pseud*-F statistics, appropriated for non-metric dissimilarities (Zapala and Schork, 2006). We performed this analysis using the function *adonis* from the *vegan* package (Oksanen et al., 2013), testing the results using 999 permutations. We assessed each model's goodness-of-fit by retaining the db-RDA squared canonical correlation coefficient (R^2c), and *p*-values for both of our predictor variables, as well as for the whole model at each one of the different spatial scales considered.

6.3 RESULTS

6.3.1 Communities description

In total, we collected 2,819 bees from 158 taxa in the 22 sampling sites (Table S1). In total, 667 bees were eusocial, 2,139 were solitary, and only 13 individuals were unidentified. The most abundant species were *Exomalopsis auropilosa* (*n*=433), *Melissodes* sp. (*n*=206), *Trigona* sp.1 (*n*=179), and *Apis mellifera* (*n*=152), being the first two solitary species and the two latter, eusocial ones. On the other hand, 83 taxa were represented by only three or less individuals, what shows the relative rarity of the sampled bee species as previously observed before (Silveira and Campos, 1995; Silveira and Cure, 1993; Williams et al., 2001). The taxa with the broader distribution were exotic *A. mellifera*, and *Augochlora* sp.1, which occurred in 19 sampling sites, followed by *Trigona* sp.1, and, the also exotic species, *Lithurgus huberi*, occurring in 18 and 17 sites, respectively. One hundred and three taxa were observed in only three or less sites (Table S1), reflecting a restricted distribution pattern for the majority of the species we sampled.

Of all bee taxa, only 22 species were eusocial, while 127 were solitary ones. For nine unidentified taxa, we did not find their sociality degree in the literature and disregarded them in the analyses with separated bee groups. The overall mean species richness, eusocial species richness, and solitary species richness was 27.87$\pm$7.68 (mean$\pm$SD), 5.45$\pm$2.48, and 22.18$\pm$6.63 per site, respectively. The most specious Apidae subfamily was Apinae, with 117 sampled taxa, followed by Halictinae (18 taxa), Megachilinae (17 taxa), Andreninae (three taxa), and Colletinae (one taxa). In general, the pattern observed for solitary bee species was very similar to that observed for the whole bee community, but when eusocial species responded to any spatial scale, it differed from the pattern observed for both the solitary bee species, as well as that for the whole community (Figure 2; Tables S2-S19).

6.3.2 Multi-scale effect analyses

As expected, the abundance of eusocial species showed higher responses to narrower spatial scales, at 250 m (R^2 = 0.55; Figure 2A; Table S3), while solitary species showed higher coefficients at broader spatial scales, at 2,000 m (R^2 = 0.373; Figure 2A; Table S4). The abundance of the whole community did not respond to the landscape structure at any scale (Figure 2A; Table S2). The amount of remnant vegetation negatively affected the abundances of whole bee community, as well as that of solitary bees at both 1,000 m and 1,250 m scales (Table S2 and S4). On the other hand, remnants isolation positively affected the abundance of eusocial species at the 250 m scale, while their interaction negatively affected their abundances (Table S3).

The overall model of the observed and the estimated richness of all groups did not respond to the landscape features at any of the spatial scales (Figure 2B and C; Tables S5-S10). Nonetheless, the isolation of remnant vegetation positively affected the observed and estimated species richness of the whole community, as well as solitary bees at the 750 m scale (Tables S5, S7, S8, and S10). The interaction between our predictors negatively affected the observed and the estimated species richness of the whole community and the solitary bees also at the 750 m scale (Tables S5, S7, S8, and S10). The isolation of remnant vegetation patches negatively affected estimated eusocial species richness at the 1,000 m scale, while the interaction between the variables had a positive effect on this variable at the 1,250 m (Table S9).

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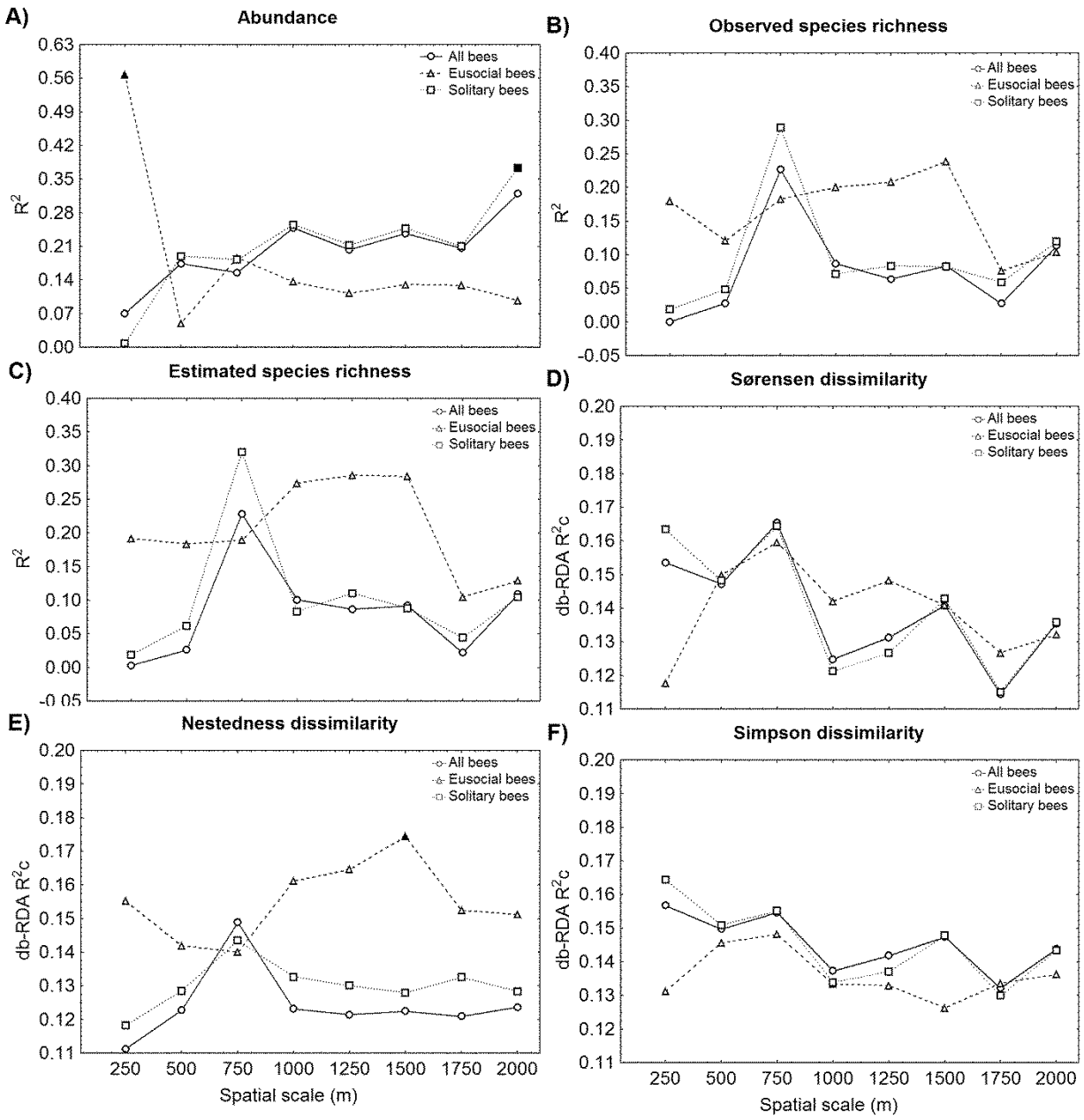

2 **Figure 2** – Global determination coefficients (R^2) and db-RDA squared canonical correlation
3 coefficient (R^2c) for each bee groups considering A) abundances; B)observed species
4 richness; C) estimated species richness; D) Sørensen dissimilarity; E) Nestedness
5 dissimilarity; F) Simpson dissmilarity. The closed symbols correspond to significant R^2 and
6 db-R^2c values.

Independently of the considered group, the overall Sørensen dissimilarity (β_{sor}) did not respond to the landscape structure found at our sampling site in any of the considered local multi-scales (Figure 2D; Tables S11-S13). Individually, the effect of the amount of remnant area on the β_{sor} estimates for the whole community and for the solitary bees at the 250 m scale was not explained by random effects, but reached a low effect-size and low amount of explained proportion (partial-R^2 = 0.079, p = 0.042 and partial-R^2 = 0.086, p = 0.036, respectively). The overall nestedness component (β_{nes}) for the whole bee community, as well as the solitary species group were not affected by landscape structure at any of the considered scales (Tables S14 and S16; Figure 2E). Individually, the interaction between both predictor variables affected the nestedness for the whole community at the 750 m scale. The landscape structure affected the nestedness component of the eusocial species at the 1,500 m scale (db-RDA R^2c = 0.174, P < 0.05; Figure 2E), mainly due to the positive effects of remnants isolation (partial-R^2 = 0.167, p = 0.020; Tables S15). The overall landscape structure did not affect the bee taxa spatial turnover (β_{sim}) in any of the considered spatial scales (Figure 2F; Tables S17-S19). However, the amount of remnant area had positive effects on this variable for the whole community at both 250 m and 500 m scale (partial-R^2 = 0.099, p = 0.008 and partial-R^2 = 0.083, p = 0.049, respectively; Table S17), as well as for the solitary community at 250 m (partial-R^2 = 0.107, p = 0.009; Table S19).

6.4 DISCUSSION

Here, we observed that the abundance of both eusocial and solitary bees from the Brazilian Cerrado savanna show contrasting responses to landscape structure: while the abundance of eusocial ones responded to narrower-scales, the abundance of solitary ones was more dependent on features found at broader spatial scales. Additionally, according to our

previous expectations, eusocial species showed an increased response of species nestedness in meso- to broad- spatial scales. Nonetheless, although both the amount of remnant vegetation and the remnant vegetation isolation individually affected one or other of our biological variable for the whole community, the eusocial, and the solitary groups, the overall models for the observed and estimated taxa richness, spatial species turnover did not respond to any of our multi-scales considered here.

The main explanation to the observed differences between eusocial and solitary bees regarding their abundance's response to landscape features lay upon their life-history differences. Despite both groups are central place foragers, the gregariousness of eusocial species is much more prominent than the species we considered as solitaries. Eusocial bees, specially *Apis mellifera* and stingless bees (tribe Meliponini), usually show high recruitment rates towards their food sources (Nieh, 2004; von Frisch, 1967; Wilson, 1971), even though they may also have long foraging bouts if needed (more than 1,000 m; Araújo et al., 2004; Kuhn-Neto et al., 2009). Thus, the occurrence resources near our sampling sites are certainly the main determinants of eusocial abundances at narrower scales. Additionally, bees' flight ability, assessed by body sizes such as the intertegular span (Cane, 1987; Greenleaf et al., 2007), may also explain these results. Considering that our pool of eusocial bee taxa was mainly composed of small-bodied Meliponini bees [except for *Apis mellifera* and a few bumblebees (*Bombus* genus), as medium- and large-bodied eusocial bees)], the nests of the small-sized eusocial bees were expected in the areas surrounding where they were pan-trapped.

On the other hand, solitary species abundance response to broader scales contradicts the results found by previous studies from temperate regions (in France; Le Féon et al., 2013; in Germany; Steffan-Dewenter et al., 2002), on which solitary bees were much more dependent

on landscape structure found at finer scales. Such discrepancy may be explained by solitary bees inherent dietary specialization on determined plant species (Biesmeijer et al., 2006; Müller et al., 2006; Ricketts et al., 2008), in a biome which is a natural mosaic of contrasting phytophysiognomies, with both horizontal and vertical complexity, as the Cerrado. Given such habitat complexity, solitary species' specialized food resources may be more scattered within their habitats, what may explain their higher response to landscape features found at broader scales. The occurrence of large-bodied solitary bees, such as those from *Xylocopa*, and both tribes Centridini and Euglossini, may also explain the observed results. These bees have high dispersal abilities that may reach from 2-6 Km for *Xylocopa* (Pasquet et al., 2008) up to 10-20 Km among some orchid-bees (Janzen, 1971; Wikelski et al., 2010), what allows them to search for resources in wider home ranges than that for small-bodied species.

The nestedness compostion of the eusocial species at the 1,500 m scale, mainly caused by patch isolation, reflects the difference in the eusocial bee richness caused by no random loss of species in our sampling sites. Even though eusocial species richness did not respond to our predictors, differential eusocial species' sensitivity to remnants amount and isolation, or even differences in species dispersal abilities may have contributed to the observed nestedness pattern (Hill et al., 2011). For the isolated fragments, local extinction is expected to be the most important process generating a community nestedness pattern (Wright et al., 1998), while isolation negatively affects species' immigration rates in fragments far from colonizer source (Kadmon, 1995). On the other hand, beta diversity reflects species spatial turnover among areas especially in the presence of rare species constituting the regional pool heterogeneously distributed along our areas and their sensitivity to environmental gradients (Baselga, 2010), specifically remnants isolation for bees in this study. For solitary bees, however, a common cause of the spatial turnover was related to remnant's area. Therefore, it

is possible that the high quality habitat requirements that some eusocial species need to occur in a given area had a bigger influence in the observed results than their rarity. For instance, the tiny Meliponini bees from the *Paratrigona*, *Frieseomelitta*, *Trigonisca*, and *Leurotrigona* genera, with poorer flight ability, are certainly more affected by landscape structure in small scales than larger Meliponini bees, such as *Trigona*, and *Apis mellifera*.

The overall small effect of the bee-related biological variables to the landscape structure on this multi-scale framework raise the question whether sociality alone is an effective trait mediating their responses to a changing landscape structure, although each group responded to one or the other predictor variable in some spatial scales. Once species are a combination of different life-history traits, their interaction may maintain the species in disturbed areas, even though that trait alone may affect the species' occurrence by mediating negative responses to landscape structure (Davies et al., 2004; Henle et al., 2004; McKinney, 1997). Previous studies already showed non-random extinctions towards parasites (Sheffield et al., 2013), specialists, cavity-nesters (Williams et al., 2010), eusocial species (Ricketts et al., 2008; Williams et al., 2010), and those involved in weak plant-pollinators interactions (Aizen et al., 2012; Burkle et al., 2013), after changes in landscape structure caused by habitat loss. Another possible caveat is that we lumped different species together and treated all of them as single biological components (whole community vs. eusocial vs. solitary species). Even though such categories are biologically valid, different species-specific contrasting set of life-history traits may show contrasting responses to the same landscape features (Boscolo and Metzger, 2009; Schmidt et al., 2007). Therefore, in the next steps, in case we consider the individual responses of the most abundant species along our sampling sites we may obtain better individual responses of the species to the landscape structure than that we obtained we considering them as uniform biological groups. Previous approaches evaluating the multi-

scale effects already found differing species-specific responses to landscape structure at different spatial scales (Boscolo and Metzger, 2009; Cozzi et al., 2007; Schmidt et al., 2007). Other approaches also include the use of functional/phylogenectic diversity may reveal more precisely bees relationships to changing environments, even though they demand higher sampling sizes and bigger biological information.

From another standpoint, the lack of species responses to the landscape structure at our sampled sites may also be related to Cerrado's inherent environmental features. First of all, this Brazilian biome is naturally heterogeneous and several of its vegetation physiognomies are characterized by open-habitats areas composing a natural landscape mosaic (Klink and Moreira, 2002; Pivello et al., 1999). Therefore, the (bee) species inhabiting these environments are adapted to these relatively sunny, dry areas, which would usually be considered as edge habitats in fragmented landscapes of closed vegetation formations, such as the Amazon and Atlantic rainforests (Faria and Silveira, 2011). Additionally, this biome is marked by a striking seasonality (Batalha and Mantovani, 2000; Batalha and Martins, 2004), with unquestionable and strong reflexes upon its inhabiting entomofauna (Pinheiro et al., 2002). Under this perspective, the bees we sampled would constitute a pool of species well-adapted to the harsh environmental seasonality found in this biome, as also observed for drosophilids community from Cerrado's preserved vs. conserved savannas (Da Mata and Tidon, 2013) and dung-beetles along a Cerrado-Forest gradient (Durães et al., 2005). Nonetheless, this does not mean that landscape structure from Cerrado areas do not exert any effects on its insects biodiversity. Although bees, beetles, and drosophilids may cope better with all the different natural mosaics available in Cerrado's phytophysiognomies because of their flight abilities, landscape structure changes was already shown to be important for less vagile insects, such as ants, at least in their non-winged forms (Brandão et al., 2011). These

contrasting responses of Cerrado's biodiversity components to landscape structure are certainly mediated by the different perceptions of their surrounding habitats.

Given abundance peaks from Cerrado's hymenopterans twice a year (wet season: November-December - dry season: June-July; Pinheiro et al., 2002), the pool of species we sampled through February-June 2011 and 2012 may only represent those with more resistance to the environmental harshness and opened habitats microclimatic conditions while the most sensitive species remained undetected due to the inherent biome seasonality. Additionally, bees' abundances are naturally seasonal, showing great amount of variation from time to time (Roubik, 2001; Williams et al., 2001). Therefore, future studies evaluating Cerrado bees' responses to landscape structure should consider long-term samplings (as proposed by Lebuhn et al., 2013), in both abundance peaks from the wet and dry seasons to properly check whether these communities are indeed affected by landscape structure.

Even though the multi-scale approach we used did not improve our models' ability to capture the species' responses to changing landscape structures, to consider biological components constrained to only one single spatial scale may not properly described their complex interactions with their environments (Boscolo and Metzger, 2009). Such approach is even more important when we consider that related species performing similar ecosystem functions may have different environmental requirements, which vary with scale and consequently elicit contrasting responses within the same landscape features. Therefore, we suggest that future studies should continue to evaluate the multi-scalar responses of different biological groups to landscape features also consider more life-history traits to evaluate species' response to landscape features.

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6.7 SUPPLEMENTARY MATERIAL

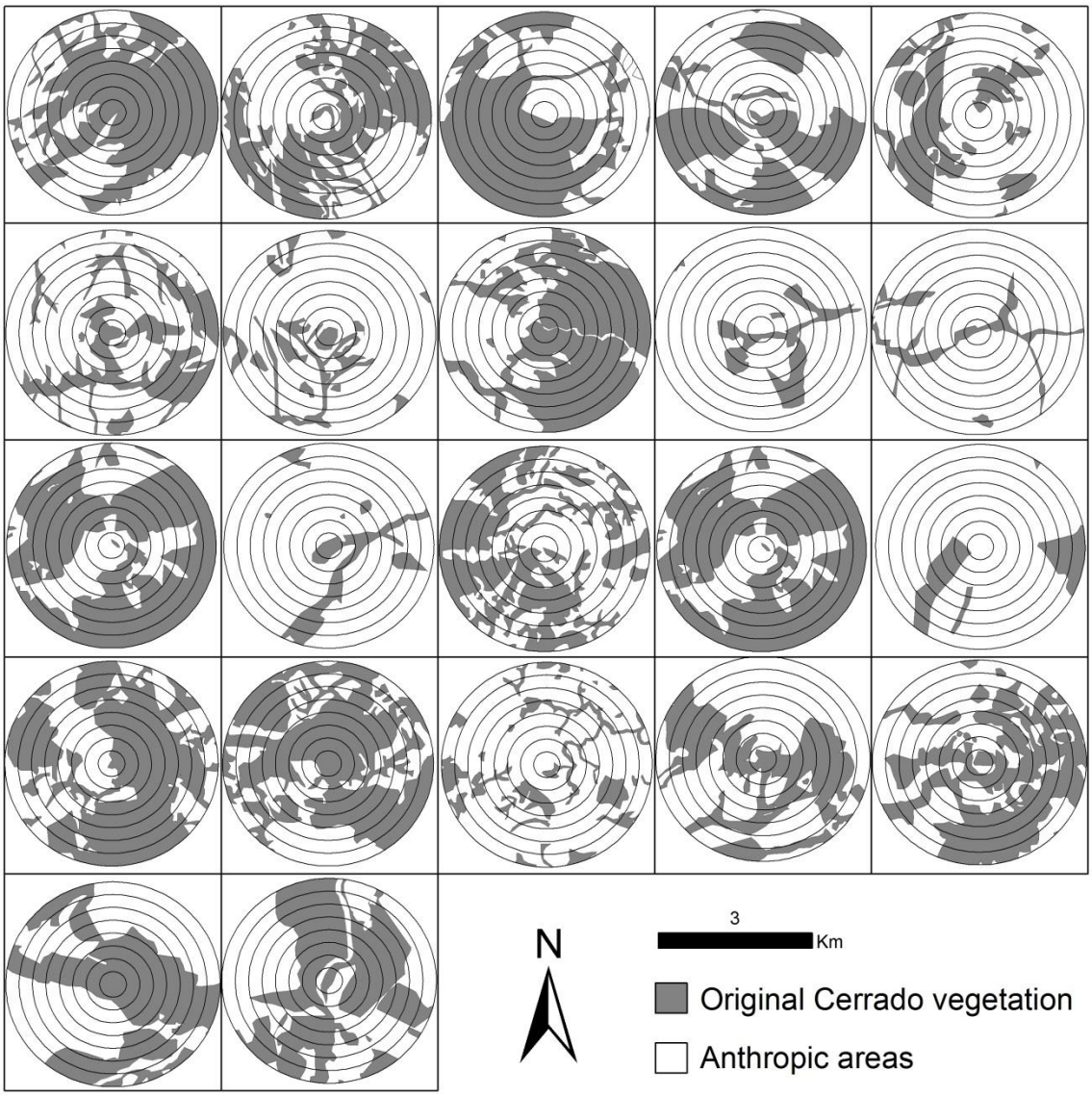

Figure S1 – The 22 study sites where bees were sampled in the Brazilian Cerrado savanna, and the eight different surrounding buffers we used to quantify the landscape metrics. Shaded areas indicate original vegetation remnants while with areas represent anthropic areas.

Table S1 – Taxa sampled in the study, their abundance, occupancy and sociality degree.
Abd= Abundance; Occ= Occupancy; Soc = Sociaty; S=Solitary, E=Eusocial, U=Unknown.

Subfamily	Species	Author	Abd	Occ	Soc type
Andreninae	*Acamptopoeum priini*	Holmberg, 1884	1	1	S
	Oxaea austera	Gerstaecker, 1867	1	1	S
	Oxaea flavescens	Klug, 1807	9	5	S
Apinae	*Tapinotaspoides* sp.1	Moure, 1944	1	1	S
	Apis mellifera	Linnaeus, 1758	152	19	E
	Bombus morio	(Swederus, 1787)	8	6	E
	Bombus sp.2	Latreille, 1802	2	2	E
	Centris (Centris) aenea	Lepeletier, 1841	2	1	S
	Centris (Hemisiella) tarsata	Smith, 1874	2	2	S
	Centris (Melacentris) collaris	Lepeletier, 1841	3	3	S
	Centris (Ptilotopus) atra	Friese, 1899	9	2	S
	Centris (Trachina) sp.1	Klug, 1807	5	5	S
	Centris (Trachina) sp.2	Klug, 1807	1	1	S
	Centris (Xanthemisia) lutea	Friese, 1899	1	1	S
	Epicharis (Epicharitides) iheringi	Friese, 1899	1	1	S
	Epicharis (Epicharitides) sp.2	Moure, 1945	1	1	S
	Epicharis (Epicharitides) sp.3	Moure, 1945	1	1	S
	Epicharis (Hoplepicharis) affinis	Smith, 1874	1	1	S
	Epicharis (Hoplepicharis) sp.1	Moure, 1945	6	3	S
	Epicharis (Triepicharis) sp.1	Moure, 1945	8	2	S
	Epicharis (Triepicharis) sp.2	Moure, 1945	3	1	S
	Ancyloscelis sp.1	Lattreille, 1829	8	6	S
	Ancyloscelis sp.2	Lattreille, 1829	43	9	S
	Diadasina sp.1	Moure, 1950	9	6	S
	Emphorini sp.		1	1	U
	Melitoma sp.1	Lepeletier & Serville, 1828	135	16	S
	Melitoma sp.2	Lepeletier & Serville, 1828	68	16	S
	Melitomella sp.1	Roig-Alsina, 1999	1	1	S
	Mesoplia sp.1	Lepeletier, 1841	2	2	S
	Mesoplia sp.2	Lepeletier, 1841	1	1	S
	Ptilothrix sp.1	Smith, 1853	16	9	S
	Ptilothrix sp.2	Smith, 1853	5	1	S
	Rhogepeolus sp.1	Moure, 1955	1	1	S
	Acanthopus sp.1	Klug, 1807	3	3	S
	Dasyhalonia sp.1	Michener & Moure, 1955	1	1	U
	Dasyhalonia sp.2	Michener & Moure, 1955	1	1	U

Table S1 continued

Subfamily	Species	Author	Abd	Occ	Soc type
Apinae	*Florilegus (Euflorilegus)* sp.1	Oglobin, 1955	5	4	S
	Florilegus (Euflorilegus) sp.2	Oglobin, 1955	1	1	S
	Florilegus (Florilegus) sp.1	Robertson, 1902	6	3	S
	Florilegus (Florilegus) sp.2	Robertson, 1902	1	1	S
	Melissodes sp.	Latreille, 1829	206	9	S
	Melissoptila sp.1	Holmberg, 1884	9	4	S
	Melissoptila sp.2	Holmberg, 1884	1	1	S
	Eufriesea aff. auriceps	(Friese, 1899)	6	4	S
	Eufriesea sp.2	Cockerell, 1907	1	1	S
	Eufriesea sp.3	Cockerell, 1907	8	5	S
	Euglossa carolina	(Linnaeus, 1758)	1	1	S
	Euglossa cordata	(Linnaeus, 1758)	2	2	S
	Euglossa fimbriata	Moure, 1968	1	1	S
	Euglossa hemichlora	Cockerell, 1917	1	1	S
	Euglossa imperialis	Cockerell, 1922	3	2	S
	Euglossa melanotricha	Moure, 1967	3	3	S
	Euglossa securigera	Dressler, 1982	1	1	S
	Euglossa sp.	Latreille, 1802	7	6	S
	Eulaema nigrita	Lepeletier, 1841	9	5	S
	Exomalopsis auropilosa	Spinola, 1853	433	12	S
	Exomalopsis sp.1	Spinola, 1853	150	11	S
	Exomalopsis sp.2	Spinola, 1853	13	7	S
	Exomalopsis sp.3	Spinola, 1853	18	6	S
	Exomalopsis sp.5	Spinola, 1853	31	8	S
	Exomalopsis sp.6	Spinola, 1853	15	7	S
	Exomalopsis sp.7	Spinola, 1853	70	6	S
	Exomalopsis sp.8	Spinola, 1853	1	1	S
	Exomalopsis sp.9	Spinola, 1853	13	5	S
	Frieseomelitta sp.1	Ihering, 1912	19	7	E
	Frieseomelitta sp.2	Ihering, 1912	12	4	E
	Geotrigona sp.1	Moure, 1943	8	5	E
	Leurotrigona sp.1	Moure, 1950	1	1	E
	Melipona sp.1	Illiger, 1806	1	1	E
	Melipona sp.2	Illiger, 1806	2	2	E
	Oxytrigona sp.	Cockerell, 1917	2	1	E
	Paratrigona sp.1	Schwarz, 1938	62	15	E
	Paratrigona sp.2	Schwarz, 1938	17	7	E
	Partamona sp.1	Schwarz, 1939	10	4	E
	Scaptotrigona sp.1	Moure, 1942	36	8	E
	Scaptotrigona sp.2	Moure, 1942	3	3	E
	Trigona sp.1	Jurine, 1807	179	18	E
	Tetragona clavipes	Fabricius, 1804	79	6	E
	Trigona sp.2	Jurine, 1807	52	2	E

	Trigona sp.3	Jurine, 1807	1	1	E

Table S1 continued

Subfamily	Species	Author	Abd	Occ	Soc type
Apinae	*Trigona* sp.5	Jurine, 1807	12	2	E
	Trigona sp.6	Jurine, 1807	1	1	E
	Trigonisca sp.1	Moure, 1950	8	5	E
	Nomada sp.1	Scopoli, 1770	6	6	S
	Nomada sp.2	Scopoli, 1770	2	1	S
	Nomada sp.3	Scopoli, 1770	2	1	S
	Monoeca sp.1	Lepeletier & Serville, 1828	1	1	S
	Monoeca sp.2	Lepeletier & Serville, 1828	1	1	S
	Paratetrapedia (Lophopedia) sp.1	Moure, 1941	3	1	S
	Paratetrapedia (Lophopedia) sp.2	Moure, 1941	1	1	S
	Tetrapedia sp.1	Klug, 1810	31	9	S
	Tetrapedia sp.2	Klug, 1810	2	2	S
	Ceratina (Ceratinula) sp.1	Moure, 1941	1	1	S
	Ceratina sp.1	Latreille, 1802	30	10	S
	Ceratina sp.2	Latreille, 1802	45	13	S
	Ceratina sp.3	Latreille, 1802	3	3	S
	Ceratina sp.4	Latreille, 1802	6	5	S
	Ceratina sp.5	Latreille, 1802	19	7	S
	Ceratina sp.6	Latreille, 1802	10	4	S
	Ceratina sp.7	Latreille, 1802	15	5	S
	Ceratina sp.8	Latreille, 1802	7	5	S
	Ceratina sp.9	Latreille, 1802	22	4	S
	Ceratina sp.10	Latreille, 1802	10	6	S
	Ceratina sp.11	Latreille, 1802	6	2	S
	Ceratina sp.12	Latreille, 1802	4	1	S
	Ceratina sp.13	Latreille, 1802	1	1	S
	Ceratina sp.14	Latreille, 1802	7	1	S
	Ceratina sp.15	Latreille, 1802	9	2	S
	Ceratina sp.16	Latreille, 1802	1	1	S
	Ceratina sp.17	Latreille, 1802	1	1	S
	Xylocopa (Cirroxylocopa) vestita	Smith, 1879	1	1	S
	Xylocopa (Monoxylocopa) abbreviata	Hurd & Moure, 1963	4	4	S
	Xylocopa (Neoxylocopa) sp.1	Michener, 1954	1	1	S
	Xylocopa (Neoxylocopa) sp.2	Michener, 1954	15	7	S
	Xylocopa (Neoxylocopa) sp.3	Michener, 1954	2	2	S
	Xylocopa (Neoxylocopa) sp.4	Michener, 1954	1	1	S
	Apidae sp.14		1	1	U
	Apidae sp.15		4	3	U
	Apidae sp.16		1	1	U
	Apidae sp.17		3	3	U
	Apidae sp.18		2	2	U

	Apidae sp.19		1	1	U
Colletinae	*Ptiloglossa* sp.1	Smith, 1853	28	15	S
Halictinae	*Ceratalictus* sp.1	Moure, 1943	2	1	U

Table S1 continued

Subfamily	Species	Author	Abd	Occ	Soc type
Halictinae	*Megalopta aegis*	(Vachal, 1904)	3	2	S
	Megalopta amoena	(Spinola, 1853)	4	2	S
	Megalopta guimaresi	Santos & Silveira, 2009	3	3	S
	Thectochlora alaris	(Vachal, 1904)	7	3	S
	Augochlora sp.1	Smith, 1853	122	19	S
	Augochlora sp.2	Smith, 1853	2	1	S
	Augochlora sp.3	Smith, 1853	70	10	S
	Augochlora sp.4	Smith, 1853	9	4	S
	Augochlora sp.5	Smith, 1853	2	2	S
	Augochlora sp.6	Smith, 1853	1	1	S
	Augochlorini sp.2		2	1	S
	Augochloropsis sp.2	Cockerell, 1897	17	6	S
	Augochloropsis sp.3	Cockerell, 1897	6	2	S
	Dialictus sp.1	Robertson, 1902	47	13	S
	Dialictus sp.2	Robertson, 1902	18	6	S
	Dialictus sp.3	Robertson, 1902	26	4	S
	Dialictus sp.4	Robertson, 1902	1	1	S
Megachilinae	*Sphecodes* sp.1	Latreille, 1804	4	4	S
	Hypanthidium sp.1	Cockerell, 1904	16	2	S
	Larocanthidium bilobatum	Urban, 1997	1	1	S
	Lithurgus huberi	Ducke, 1907	85	17	S
	Coelioxys sp.1	Latreille, 1809	1	1	S
	Megachile (Acentron) sp.1	Mitchell, 1943	2	2	S
	Megachile (Chrysosarus) sp.1	Mitchell, 1943	6	6	S
Megachilinae	*Megachile (Chrysosarus)* sp.2	Mitchell, 1943	4	3	S
	Megachile (Chrysosarus) sp.3	Mitchell, 1943	1	1	S
	Megachile (Grafella) sp.1	Mitchel, 1980	1	1	S
	Megachile (Leptorachina) sp.1	Mitchel, 1980	1	1	S
	Megachile (Leptorachis) sp.1	Mitchel, 1934	1	1	S
	Megachile (Pseudocentron) sp.1	Mitchel, 1934	2	2	S
	Megachile (Pseudocentron) sp.2	Mitchel, 1934	2	2	S
	Megachile (Pseudocentron) sp.3	Mitchel, 1934	4	4	S
	Megachile (Trichurochile) sp.1	Mitchell, 1980	1	1	S
	Megachile sp.	Latreille, 1802	1	1	S

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Table S2 – Multiple regression results for the abundance of all bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.319	Amount	-0.236	0.116	-2.028	0.058
	Isolation	-0.276	0.16	-1.728	0.101
	Interaction	0.000	0.001	0.098	0.923
1,750 m R^2= 0.206	Amount	-0.207	0.191	-1.083	0.293
	Isolation	-0.208	0.218	-0.951	0.354
	Interaction	0.000	0.002	-0.122	0.904
1,500 m R^2= 0.237	Amount	-0.337	0.193	-1.746	0.098
	Isolation	-0.316	0.201	-1.577	0.132
	Interaction	0.000	0.001	0.27	0.790
1,250 m R^2= 0.203	Amount	-0.480	0.228	-2.106	**0.050**
	Isolation	-0.334	0.194	-1.721	0.102
	Interaction	0.002	0.001	1.058	0.304
1,000 m R^2= 0.248	Amount	-0.678	0.316	-2.145	**0.046**
	Isolation	-0.547	0.276	-1.985	0.063
	Interaction	0.002	0.002	0.694	0.497
750 m R^2= 0.155	Amount	-0.120	0.510	-0.236	0.816
	Isolation	0.324	0.304	1.066	0.300
	Interaction	-0.007	0.005	-1.538	0.141
500 m R^2= 0.174	Amount	-1.150	0.906	-1.269	0.220
	Isolation	-0.499	0.403	-1.239	0.231
	Interaction	0.005	0.012	0.433	0.670
250 m R^2= 0.07	Amount	0.010	0.598	0.017	0.987
	Isolation	0.939	1.265	0.742	0.468
	Interaction	-0.009	0.028	-0.314	0.757

Table S3 – Multiple regression results for the abundance of eusocial bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.097	Amount	-0.042	0.045	-0.940	0.360
	Isolation	-0.081	0.062	-1.305	0.208
	Interaction	0.000	0.000	0.654	0.522
1,750 m R^2= 0.128	Amount	-0.02	0.067	-0.303	0.766
	Isolation	-0.066	0.077	-0.86	0.401
	Interaction	0.000	0.001	-0.249	0.806
1,500 m R^2= 0.130	Amount	-0.025	0.069	-0.354	0.727
	Isolation	-0.073	0.072	-1.018	0.322
	Interaction	0.000	0.001	-0.275	0.786
1,250 m R^2= 0.112	Amount	-0.077	0.081	-0.952	0.354
	Isolation	-0.096	0.069	-1.387	0.182
	Interaction	0.001	0.001	1.255	0.226
1,000 m R^2= 0.136	Amount	-0.048	0.114	-0.425	0.676
	Isolation	-0.109	0.1	-1.097	0.287
	Interaction	0.000	0.001	-0.058	0.954
750 m R^2= 0.186	Amount	0.011	0.168	0.062	0.951
	Isolation	-0.022	0.100	-0.216	0.831
	Interaction	-0.001	0.002	-0.928	0.366
500 m R^2= 0.050	Amount	0.060	0.327	0.183	0.857
	Isolation	-0.070	0.145	-0.480	0.637
	Interaction	0.000	0.004	0.098	0.923
250 m R^2= 0.567	Amount	0.208	0.137	1.511	0.148
	Isolation	1.081	0.291	3.718	**0.002**
	Interaction	-0.014	0.006	-2.131	**0.047**

Table S4 – Multiple regression results for the abundance of solitary bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.373	Amount	-0.192	0.094	-2.046	0.056
	Isolation	-0.199	0.129	-1.539	0.141
	Interaction	0.000	0.001	-0.262	0.796
1,750 m R^2= 0.210	Amount	-0.184	0.161	-1.148	0.266
	Isolation	-0.145	0.184	-0.79	0.440
	Interaction	0.000	0.001	-0.063	0.951
1,500 m R^2= 0.247	Amount	-0.305	0.161	-1.889	0.075
	Isolation	-0.247	0.168	-1.473	0.158
	Interaction	0.000	0.001	0.354	0.727
1,250 m R^2= 0.212	Amount	-0.403	0.191	-2.109	**0.049**
	Isolation	-0.248	0.162	-1.529	0.144
	Interaction	0.001	0.001	0.732	0.473
1,000 m R^2= 0.255	Amount	-0.627	0.265	-2.363	**0.030**
	Isolation	-0.451	0.231	-1.949	0.067
	Interaction	0.002	0.002	0.876	0.393
750 m R^2= 0.182	Amount	-0.095	0.423	-0.226	0.824
	Isolation	0.356	0.252	1.413	0.175
	Interaction	-0.006	0.004	-1.541	0.141
500 m R^2= 0.189	Amount	-1.152	0.756	-1.523	0.145
	Isolation	-0.441	0.336	-1.313	0.206
	Interaction	0.005	0.01	0.528	0.604
250 m R^2= 0.008	Amount	-0.151	0.521	-0.291	0.775
	Isolation	-0.180	1.102	-0.163	0.872
	Interaction	0.006	0.024	0.249	0.806

Table S5 – Multiple regression results for the observed species richness of all bees in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.109	Amount	-0.011	0.013	-0.860	0.401
	Isolation	-0.013	0.017	-0.729	0.475
	Interaction	0.000	0.000	-0.201	0.843
1,750 m R^2= 0.022	Amount	-0.004	0.020	-0.191	0.851
	Isolation	0.001	0.023	0.055	0.957
	Interaction	0.000	0.000	-0.154	0.879
1,500 m R^2= 0.092	Amount	-0.018	0.020	-0.872	0.395
	Isolation	-0.018	0.021	-0.866	0.398
	Interaction	0.000	0.000	0.076	0.940
1,250 m R^2= 0.086	Amount	-0.024	0.024	-1.035	0.314
	Isolation	-0.019	0.020	-0.933	0.363
	Interaction	0.000	0.000	0.428	0.673
1,000 m R^2= 0.100	Amount	-0.029	0.033	-0.868	0.397
	Isolation	-0.026	0.029	-0.888	0.386
	Interaction	0.000	0.000	-0.017	0.987
750 m R^2= 0.228	Amount	0.041	0.047	0.875	0.393
	Isolation	0.054	0.028	1.929	0.070
	Interaction	-0.001	0.000	-2.292	**0.034**
500 m R^2= 0.026	Amount	-0.030	0.094	-0.325	0.749
	Isolation	-0.028	0.042	-0.678	0.506
	Interaction	0.001	0.001	0.712	0.486
250 m R^2= 0.003	Amount	0.005	0.059	0.092	0.928
	Isolation	-0.001	0.125	-0.006	0.995
	Interaction	0.000	0.003	-0.003	0.998

Table S6 – Multiple regression results for the observed species richness of eusocial bees in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.103	Amount	-0.001	0.004	-0.310	0.760
	Isolation	-0.005	0.006	-0.936	0.362
	Interaction	0.000	0.000	0.132	0.896
1,750 m R^2= 0.075	Amount	0.001	0.006	0.143	0.888
	Isolation	-0.003	0.007	-0.462	0.649
	Interaction	0.000	0.000	-0.141	0.889
1,500 m R^2= 0.238	Amount	0.001	0.006	0.161	0.874
	Isolation	-0.007	0.006	-1.106	0.283
	Interaction	0.000	0.000	-0.627	0.539
1,250 m R^2= 0.208	Amount	-0.005	0.007	-0.705	0.490
	Isolation	-0.010	0.006	-1.594	0.128
	Interaction	0.000	0.000	1.797	0.089
1,000 m R^2= 0.200	Amount	-0.003	0.010	-0.343	0.736
	Isolation	-0.015	0.009	-1.671	0.112
	Interaction	0.000	0.000	0.830	0.417
750 m R^2= 0.182	Amount	0.010	0.015	0.657	0.520
	Isolation	-0.004	0.009	-0.459	0.652
	Interaction	0.000	0.000	-0.389	0.702
500 m R^2= 0.13	Amount	0.039	0.029	1.352	0.193
	Isolation	-0.001	0.013	-0.064	0.950
	Interaction	0.000	0.000	0.021	0.983
250 m R^2= 0.179	Amount	0.028	0.017	1.588	0.130
	Isolation	0.037	0.037	1.011	0.325
	Interaction	0.000	0.001	-0.509	0.617

Table S7 – Multiple regression results for the observed species richness of solitary bees in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.119	Amount	-0.009	0.011	-0.850	0.406
	Isolation	-0.008	0.015	-0.508	0.618
	Interaction	0.000	0.000	-0.287	0.777
1,750 m R^2= 0.059	Amount	-0.005	0.017	-0.274	0.787
	Isolation	0.004	0.020	0.182	0.857
	Interaction	0.000	0.000	-0.133	0.895
1,500 m R^2= 0.082	Amount	-0.018	0.017	-1.05	0.308
	Isolation	-0.012	0.018	-0.675	0.508
	Interaction	0.000	0.000	0.301	0.767
1,250 m R^2= 0.083	Amount	-0.020	0.020	-0.971	0.344
	Isolation	-0.011	0.017	-0.614	0.547
	Interaction	0.000	0.000	-0.099	0.922
1,000 m R^2= 0.071	Amount	-0.024	0.029	-0.837	0.414
	Isolation	-0.011	0.025	-0.442	0.664
	Interaction	0.000	0.000	-0.267	0.793
750 m R^2= 0.289	Amount	0.033	0.039	0.843	0.410
	Isolation	0.057	0.023	2.476	**0.023**
	Interaction	-0.001	0.000	-2.523	**0.021**
500 m R^2= 0.048	Amount	-0.060	0.080	-0.750	0.463
	Isolation	-0.024	0.036	-0.669	0.512
	Interaction	0.001	0.001	0.791	0.439
250 m R^2= 0.018	Amount	-0.019	0.051	-0.381	0.708
	Isolation	-0.042	0.107	-0.395	0.698
	Interaction	0.001	0.002	0.227	0.823

Table S8 – Multiple regression results for the estimated species richness of all bees in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.109	Amount	-0.017	0.018	-0.943	0.358
	Isolation	-0.023	0.025	-0.941	0.359
	Interaction	0.000	0.000	0.002	0.998
1,750 m R^2= 0.002	Amount	-0.004	0.029	-0.141	0.889
	Isolation	-0.001	0.033	-0.029	0.977
	Interaction	0.000	0.000	-0.218	0.830
1,500 m R^2= 0.092	Amount	-0.03	0.029	-1.053	0.306
	Isolation	-0.033	0.030	-1.124	0.276
	Interaction	0.000	0.000	0.357	0.725
1,250 m R^2= 0.086	Amount	-0.038	0.033	-1.138	0.270
	Isolation	-0.034	0.028	-1.187	0.251
	Interaction	0.000	0.000	0.484	0.635
1,000 m R^2= 0.100	Amount	-0.039	0.047	-0.835	0.415
	Isolation	-0.038	0.041	-0.926	0.367
	Interaction	0.000	0.000	-0.095	0.925
750 m R^2= 0.228	Amount	0.075	0.066	1.126	0.275
	Isolation	0.083	0.04	2.097	**0.050**
	Interaction	-0.001	0.001	-2.274	**0.035**
500 m R^2= 0.026	Amount	-0.014	0.134	-0.107	0.916
	Isolation	-0.027	0.059	-0.461	0.651
	Interaction	0.001	0.002	0.654	0.522
250 m R^2= 0.003	Amount	0.013	0.084	0.154	0.879
	Isolation	-0.022	0.178	-0.123	0.903
	Interaction	0.000	0.004	0.123	0.904

Table S9– Multiple regression results for the estimated species richness of eusocial bees in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.129	Amount	-0.001	0.006	-0.160	0.875
	Isolation	-0.007	0.008	-0.910	0.375
	Interaction	0.000	0.000	0.014	0.989
1,750 m R^2= 0.104	Amount	0.004	0.009	0.437	0.667
	Isolation	-0.003	0.010	-0.287	0.777
	Interaction	0.000	0.000	-0.419	0.680
1,500 m R^2= 0.284	Amount	0.001	0.008	0.136	0.894
	Isolation	-0.012	0.009	-1.315	0.205
	Interaction	0.000	0.000	-0.598	0.557
1,250 m R^2= 0.286	Amount	-0.008	0.010	-0.844	0.410
	Isolation	-0.016	0.008	-1.892	0.075
	Interaction	0.000	0.000	2.268	**0.036**
1,000 m R^2= 0.274	Amount	-0.007	0.014	-0.492	0.629
	Isolation	-0.026	0.012	-2.125	**0.048**
	Interaction	0.000	0.000	1.231	0.234
750 m R^2= 0.189	Amount	0.017	0.023	0.745	0.466
	Isolation	-0.010	0.013	-0.752	0.462
	Interaction	0.000	0.000	0.101	0.921
500 m R^2= 0.183	Amount	0.074	0.041	1.816	0.086
	Isolation	0.003	0.018	0.168	0.868
	Interaction	0.000	0.001	-0.262	0.796
250 m R^2= 0.191	Amount	0.049	0.025	1.941	0.068
	Isolation	0.045	0.053	0.851	0.406
	Interaction	-0.001	0.001	-0.53	0.602

Table S10 – Multiple regression results for the estimated species richness of solitary bees in the multiple spatial scales considered in this study. Bold values are significant at α=0.05.

Spatial scale	Variable	Beta coeff.	SD error	t	*p* value
2,000 m R^2= 0.104	Amount	-0.016	0.016	-0.980	0.340
	Isolation	-0.017	0.022	-0.749	0.463
	Interaction	0.000	0.000	-0.020	0.984
1,750 m R^2= 0.044	Amount	-0.008	0.025	-0.308	0.761
	Isolation	0.001	0.029	0.022	0.983
	Interaction	0.000	0.000	-0.119	0.906
1,500 m R^2= 0.088	Amount	-0.031	0.025	-1.235	0.233
	Isolation	-0.024	0.026	-0.912	0.374
	Interaction	0.000	0.000	0.591	0.562
1,250 m R^2= 0.110	Amount	-0.030	0.029	-1.049	0.308
	Isolation	-0.021	0.025	-0.838	0.413
	Interaction	0.000	0.000	-0.181	0.859
1,000 m R^2= 0.083	Amount	-0.032	0.042	-0.769	0.452
	Isolation	-0.014	0.037	-0.378	0.71
	Interaction	0.000	0.000	-0.45	0.658
750 m R^2= 0.320	Amount	0.060	0.055	1.080	0.294
	Isolation	0.091	0.033	2.764	**0.013**
	Interaction	-0.001	0.001	-2.658	**0.016**
500 m R^2= 0.061	Amount	-0.073	0.117	-0.628	0.538
	Isolation	-0.024	0.052	-0.472	0.642
	Interaction	0.001	0.002	0.806	0.431
250 m R^2= 0.018	Amount	-0.031	0.074	-0.422	0.678
	Isolation	-0.077	0.157	-0.491	0.629
	Interaction	0.001	0.003	0.396	0.696

Table S11 – Multivariate regression analysis of distance matrices results for the Sørensen dissimilarity (β_{sor}) of all bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.135	Amount	0.131	0.131	0.585	0.028	0.906
	Isolation	0.241	0.241	1.074	0.052	0.383
	Interaction	0.250	0.250	1.115	0.054	0.317
1,750 m db-RDA R^2c=0.114	Amount	0.140	0.140	0.607	0.030	0.913
	Isolation	0.152	0.152	0.659	0.033	0.879
	Interaction	0.208	0.208	0.899	0.045	0.570
1,500 m db-RDA R^2c=0.141	Amount	0.156	0.156	0.703	0.034	0.820
	Isolation	0.250	0.250	1.125	0.054	0.298
	Interaction	0.246	0.246	1.106	0.053	0.320
1250 m db-RDA R^2c=0.131	Amount	0.169	0.169	0.747	0.036	0.780
	Isolation	0.133	0.133	0.591	0.029	0.947
	Interaction	0.297	0.297	1.317	0.064	0.143
1,000 m db-RDA R^2c=0.125	Amount	0.188	0.188	0.827	0.040	0.654
	Isolation	0.224	0.224	0.984	0.048	0.456
	Interaction	0.151	0.151	0.666	0.033	0.847
750 m db-RDA R^2c=0.165	Amount	0.225	0.225	1.050	0.048	0.410
	Isolation	0.250	0.250	1.164	0.054	0.283
	Interaction	0.323	0.323	1.505	0.069	0.077
500 m db-RDA R^2c=0.147	Amount	0.313	0.313	1.418	0.067	0.114
	Isolation	0.141	0.141	0.640	0.030	0.880
	Interaction	0.238	0.238	1.078	0.051	0.375
250 m db-RDA R^2c=0.154	Amount	0.369	0.369	1.691	0.079	**0.042**
	Isolation	0.223	0.223	1.021	0.048	0.414
	Interaction	0.138	0.138	0.634	0.030	0.913

Table S12 – Multivariate regression analysis of distance matrices results for the Sørensen dissimilarity (β_{sor}) of eusocial bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m	Amount	0.193	0.193	1.07	0.053	0.395
db-RDA	Isolation	0.168	0.168	0.93	0.046	0.507
R^2c=0.132	Interaction	0.083	0.083	0.46	0.023	0.823
1,750 m	Amount	0.212	0.212	1.18	0.058	0.327
db-RDA	Isolation	0.057	0.057	0.31	0.015	0.908
R^2c=0.127	Interaction	0.161	0.161	0.89	0.044	0.492
1,500 m	Amount	0.241	0.241	1.37	0.066	0.254
db-RDA	Isolation	0.151	0.151	0.85	0.041	0.501
R^2c=0.141	Interaction	0.115	0.115	0.65	0.031	0.700
1250 m	Amount	0.258	0.258	1.49	0.070	0.171
db-RDA	Isolation	0.052	0.052	0.29	0.014	0.920
R^2c=0.148	Interaction	0.256	0.256	1.48	0.070	0.190
1,000 m	Amount	0.257	0.257	1.46	0.070	0.190
db-RDA	Isolation	0.137	0.137	0.77	0.037	0.603
R^2c=0.142	Interaction	0.113	0.113	0.64	0.031	0.708
750 m	Amount	0.235	0.235	1.39	0.064	0.240
db-RDA	Isolation	0.128	0.128	0.76	0.035	0.595
R^2c=0.160	Interaction	0.275	0.275	1.63	0.075	0.144
500 m	Amount	0.208	0.208	1.20	0.057	0.339
db-RDA	Isolation	0.203	0.203	1.17	0.055	0.335
R^2c=0.150	Interaction	0.144	0.144	0.83	0.039	0.583
250 m	Amount	0.156	0.156	0.83	0.042	0.560
db-RDA	Isolation	0.103	0.103	0.55	0.028	0.765
R^2c=0.118	Interaction	0.065	0.065	0.34	0.018	0.897

Table S13 – Multivariate regression analysis of distance matrices results for the Sørensen dissimilarity (β_{sor}) of solitary bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.136	Amount	0.139	0.139	0.576	0.028	0.908
	Isolation	0.241	0.241	0.997	0.048	0.458
	Interaction	0.291	0.291	1.205	0.058	0.251
1,750 m db-RDA R^2c=0.115	Amount	0.147	0.147	0.589	0.029	0.881
	Isolation	0.162	0.162	0.652	0.032	0.874
	Interaction	0.229	0.229	0.917	0.046	0.590
1,500 m db-RDA R^2c=0.143	Amount	0.160	0.160	0.667	0.032	0.798
	Isolation	0.255	0.255	1.066	0.051	0.358
	Interaction	0.302	0.302	1.261	0.060	0.196
1250 m db-RDA R^2c=0.127	Amount	0.167	0.167	0.683	0.033	0.821
	Isolation	0.151	0.151	0.616	0.030	0.922
	Interaction	0.296	0.296	1.210	0.059	0.222
1,000 m db-RDA R^2c=0.121	Amount	0.189	0.189	0.764	0.038	0.737
	Isolation	0.237	0.237	0.958	0.047	0.505
	Interaction	0.157	0.157	0.635	0.031	0.862
750 m db-RDA R^2c=0.164	Amount	0.237	0.237	1.025	0.047	0.455
	Isolation	0.272	0.272	1.174	0.054	0.288
	Interaction	0.352	0.352	1.520	0.070	0.083
500 m db-RDA R^2c=0.148	Amount	0.352	0.352	1.485	0.070	0.094
	Isolation	0.129	0.129	0.543	0.026	0.919
	Interaction	0.272	0.272	1.147	0.054	0.304
250 m db-RDA R^2c=0.163	Amount	0.430	0.430	1.858	0.086	**0.036**
	Isolation	0.246	0.246	1.063	0.049	0.371
	Interaction	0.179	0.179	0.771	0.036	0.727

Table S14 – Multivariate regression analysis of distance matrices results for the nestedness component (β_{nes}) of all bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.124	Amount	0.030	0.030	0.880	0.045	0.462
	Isolation	0.023	0.023	0.660	0.034	0.598
	Interaction	0.002	0.002	0.055	0.003	0.906
1,750 m db-RDA R^2c=0.121	Amount	0.028	0.028	0.794	0.041	0.471
	Isolation	0.019	0.019	0.559	0.029	0.637
	Interaction	0.002	0.002	0.071	0.004	0.918
1,500 m db-RDA R^2c=0.122	Amount	0.026	0.026	0.749	0.038	0.521
	Isolation	0.018	0.018	0.525	0.027	0.667
	Interaction	0.010	0.010	0.303	0.015	0.766
1250 m db-RDA R^2c=0.121	Amount	0.023	0.023	0.658	0.034	0.586
	Isolation	0.025	0.025	0.720	0.037	0.536
	Interaction	0.003	0.003	0.092	0.005	0.923
1,000 m db-RDA R^2c=0.123	Amount	0.013	0.013	0.363	0.019	0.746
	Isolation	0.019	0.019	0.562	0.029	0.633
	Interaction	0.022	0.022	0.633	0.032	0.549
750 m db-RDA R^2c=0.149	Amount	0.002	0.002	0.064	0.003	0.909
	Isolation	0.006	0.006	0.189	0.009	0.859
	Interaction	0.100	0.100	3.166	0.148	**0.048**
500 m db-RDA R^2c=0.123	Amount	-0.014	-0.014	-0.402	-0.020	0.992
	Isolation	0.060	0.060	1.766	0.089	0.190
	Interaction	0.015	0.015	0.452	0.023	0.695
250 m db-RDA R^2c=0.111	Amount	-0.021	-0.021	-0.591	-0.031	0.999
	Isolation	0.012	0.012	0.324	0.017	0.775
	Interaction	0.044	0.044	1.242	0.065	0.297

Table S15 – Multivariate regression analysis of distance matrices results for the nestedness component (β_{nes}) of eusocial bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.151	Amount	0.143	0.143	1.565	0.070	0.242
	Isolation	0.150	0.150	1.641	0.074	0.217
	Interaction	0.102	0.102	1.113	0.050	0.365
1,750 m db-RDA R^2c=0.152	Amount	0.160	0.160	1.779	0.079	0.200
	Isolation	0.224	0.224	2.480	0.109	0.111
	Interaction	0.036	0.036	0.401	0.018	0.722
1,500 m db-RDA R^2c=0.174	Amount	0.173	0.173	2.334	0.085	0.126
	Isolation	0.341	0.341	4.594	0.167	**0.020**
	Interaction	0.191	0.191	2.576	0.094	0.091
1250 m db-RDA R^2c=0.165	Amount	0.168	0.168	2.065	0.082	0.161
	Isolation	0.162	0.162	1.983	0.079	0.155
	Interaction	0.247	0.247	3.028	0.121	0.072
1,000 m db-RDA R^2c=0.161	Amount	0.181	0.181	2.163	0.089	0.153
	Isolation	0.233	0.233	2.784	0.114	0.090
	Interaction	0.121	0.121	1.438	0.059	0.280
750 m db-RDA R^2c=0.140	Amount	0.190	0.190	1.919	0.093	0.189
	Isolation	0.135	0.135	1.364	0.066	0.279
	Interaction	-0.065	-0.065	-0.656	-0.032	0.981
500 m db-RDA R^2c=0.142	Amount	0.206	0.206	2.098	0.101	0.142
	Isolation	0.043	0.043	0.437	0.021	0.677
	Interaction	0.031	0.031	0.317	0.015	0.742
250 m db-RDA R^2c=0.155	Amount	0.155	0.155	1.754	0.076	0.221
	Isolation	0.221	0.221	2.493	0.108	0.107
	Interaction	0.075	0.075	0.846	0.037	0.431

Table S16 – Multivariate regression analysis of distance matrices results for the nestedness component (β_{nes}) of solitary bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.128	Amount	0.043	0.043	1.193	0.061	0.337
	Isolation	0.018	0.018	0.492	0.025	0.686
	Interaction	-0.001	-0.001	-0.035	-0.002	0.926
1,750 m db-RDA R^2c=0.133	Amount	0.040	0.040	1.126	0.056	0.357
	Isolation	0.019	0.019	0.537	0.027	0.668
	Interaction	0.011	0.011	0.304	0.015	0.790
1,500 m db-RDA R^2c=0.128	Amount	0.040	0.040	1.099	0.056	0.390
	Isolation	0.006	0.006	0.165	0.008	0.884
	Interaction	0.014	0.014	0.375	0.019	0.767
1250 m db-RDA R^2c=0.130	Amount	0.036	0.036	0.999	0.050	0.406
	Isolation	0.023	0.023	0.626	0.032	0.620
	Interaction	0.008	0.008	0.211	0.011	0.829
1,000 m db-RDA R^2c=0.133	Amount	0.022	0.022	0.611	0.031	0.636
	Isolation	0.016	0.016	0.446	0.022	0.716
	Interaction	0.030	0.030	0.841	0.042	0.493
750 m db-RDA R^2c=0.144	Amount	0.008	0.008	0.228	0.011	0.826
	Isolation	0.013	0.013	0.396	0.019	0.757
	Interaction	0.080	0.080	2.367	0.113	0.088
500 m db-RDA R^2c=0.129	Amount	-0.013	-0.013	-0.348	-0.018	0.976
	Isolation	0.057	0.057	1.574	0.080	0.215
	Interaction	0.016	0.016	0.436	0.022	0.716
250 m db-RDA R^2c=0.118	Amount	-0.024	-0.024	-0.640	-0.034	0.998
	Isolation	0.020	0.020	0.527	0.028	0.656
	Interaction	0.029	0.029	0.745	0.040	0.524

Table S17 – Multivariate regression analysis of distance matrices results for the turnover component (β_{sim}) of all bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.144	Amount	0.108	0.108	0.593	0.028	0.834
	Isolation	0.205	0.205	1.125	0.053	0.365
	Interaction	0.241	0.241	1.322	0.063	0.225
1,750 m db-RDA R^2c=0.132	Amount	0.120	0.120	0.638	0.031	0.788
	Isolation	0.132	0.132	0.700	0.034	0.772
	Interaction	0.202	0.202	1.071	0.052	0.385
1,500 m db-RDA R^2c=0.147	Amount	0.138	0.138	0.762	0.036	0.723
	Isolation	0.218	0.218	1.205	0.057	0.278
	Interaction	0.231	0.231	1.276	0.060	0.245
1250 m db-RDA R^2c=0.142	Amount	0.152	0.152	0.826	0.039	0.623
	Isolation	0.105	0.105	0.570	0.027	0.909
	Interaction	0.284	0.284	1.551	0.074	0.090
1,000 m db-RDA R^2c=0.137	Amount	0.180	0.180	0.971	0.047	0.529
	Isolation	0.190	0.190	1.026	0.049	0.472
	Interaction	0.138	0.138	0.745	0.036	0.715
750 m db-RDA R^2c=0.155	Amount	0.224	0.224	1.265	0.058	0.241
	Isolation	0.241	0.241	1.365	0.063	0.191
	Interaction	0.195	0.195	1.103	0.051	0.382
500 m db-RDA R^2c=0.150	Amount	0.320	0.320	1.781	0.083	**0.049**
	Isolation	0.073	0.073	0.408	0.019	0.943
	Interaction	0.217	0.217	1.210	0.057	0.276
250 m db-RDA R^2c=0.157	Amount	0.379	0.379	2.158	0.099	**0.008**
	Isolation	0.214	0.214	1.218	0.056	0.295
	Interaction	0.086	0.086	0.491	0.022	0.908

Table S18 – Multivariate regression analysis of distance matrices results for the turnover component (β_{sim}) of eusocial bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.136	Amount	0.088	0.088	0.797	0.041	0.539
	Isolation	0.070	0.070	0.635	0.033	0.603
	Interaction	0.005	0.005	0.044	0.002	0.797
1,750 m db-RDA R^2c=0.134	Amount	0.092	0.092	0.858	0.043	0.511
	Isolation	-0.024	-0.024	-	-0.011	0.881
	Interaction	0.152	0.152	1.422	0.071	0.311
1,500 m db-RDA R^2c=0.126	Amount	0.102	0.102	0.895	0.048	0.496
	Isolation	-0.031	-0.031	-	-0.014	0.908
	Interaction	0.018	0.018	0.156	0.008	0.769
1250 m db-RDA R^2c=0.133	Amount	0.113	0.113	1.048	0.053	0.477
	Isolation	0.021	0.021	0.191	0.010	0.791
	Interaction	0.076	0.076	0.710	0.036	0.550
1,000 m db-RDA R^2c=0.133	Amount	0.099	0.099	0.890	0.046	0.516
	Isolation	-0.022	-0.022	-	-0.010	0.869
	Interaction	0.075	0.075	0.674	0.035	0.585
750 m db-RDA R^2c=0.148	Amount	0.075	0.075	0.783	0.035	0.546
	Isolation	0.008	0.008	0.085	0.004	0.774
	Interaction	0.342	0.342	3.571	0.159	0.057
500 m db-RDA R^2c=0.146	Amount	0.053	0.053	0.534	0.025	0.649
	Isolation	0.179	0.179	1.809	0.083	0.230
	Interaction	0.134	0.134	1.356	0.062	0.332
250 m db-RDA R^2c=0.131	Amount	0.038	0.038	0.320	0.018	0.705
	Isolation	-0.062	-0.062	-	-0.029	0.904
	Interaction	0.030	0.030	0.250	0.014	0.741

Table S19 – Multivariate regression analysis of distance matrices results for the turnover component (β_{sim}) of solitary bee species in the multiple spatial scales considered in this study. Bold values are significant at α=0.05. db-RDA R^2c: Distance-based RDA squared canonical correlation coefficient. SS: Sums of squares. MS: Mean squares.

Spatial scale	Variable	SS	MS	F	Partial R^2	*p* value
2,000 m db-RDA R^2c=0.143	Amount	0.100	0.100	0.506	0.024	0.867
	Isolation	0.213	0.213	1.080	0.051	0.379
	Interaction	0.279	0.279	1.414	0.067	0.174
1,750 m db-RDA R^2c=0.130	Amount	0.110	0.110	0.538	0.027	0.848
	Isolation	0.141	0.141	0.690	0.034	0.749
	Interaction	0.210	0.210	1.024	0.051	0.401
1,500 m db-RDA R^2c=0.148	Amount	0.123	0.123	0.631	0.030	0.775
	Isolation	0.240	0.240	1.227	0.058	0.250
	Interaction	0.270	0.270	1.380	0.065	0.188
1250 m db-RDA R^2c=0.137	Amount	0.135	0.135	0.671	0.032	0.741
	Isolation	0.125	0.125	0.624	0.030	0.830
	Interaction	0.272	0.272	1.354	0.066	0.198
1,000 m db-RDA R^2c=0.134	Amount	0.169	0.169	0.838	0.041	0.578
	Isolation	0.214	0.214	1.062	0.052	0.410
	Interaction	0.134	0.134	0.663	0.032	0.735
750 m db-RDA R^2c=0.155	Amount	0.228	0.228	1.198	0.055	0.326
	Isolation	0.250	0.250	1.312	0.060	0.219
	Interaction	0.240	0.240	1.261	0.058	0.252
500 m db-RDA R^2c=0.151	Amount	0.356	0.356	1.843	0.086	0.072
	Isolation	0.066	0.066	0.343	0.016	0.944
	Interaction	0.247	0.247	1.281	0.060	0.239
250 m db-RDA R^2c=0.164	Amount	0.444	0.444	2.401	0.107	**0.009**
	Isolation	0.237	0.237	1.281	0.057	0.229
	Interaction	0.138	0.138	0.747	0.033	0.692

CONCLUSÕES GERAIS

Nesta tese, observamos que como quaisquer outros dados relacionados à diversidade de espécies, os dados distribucionais das abelhas cortadeiras (Apidae: *Megachile*) e sem-ferrão (Apidae: Meliponini) estão enviesados. Qualitativamente, tal viés ocorreu em direção a áreas ao longo da costa leste brasileira, nos estados onde há mais cidades, e consequentemente, maior atividade de pesquisadores envolvidos com a taxonomia, biologia e ecologia de abelhas. Quantitativamente, para muitos grupos tais coletas se deram mais próximo à cidades e grandes centros de pesquisas de abelhas do que quando comparados à distribuições de pontos aleatorizados no espaço. Entretanto, para alguns grupos de abelhas Meliponini, é evidente a atuação de exímios melitólogos e apidólogos (p.ex. Pe. Jesus Santiago Moure e Prof. Dr. João Maria Camargo), que coletaram e descreveram várias espécies de abelhas longe de seus centros de atuação (Curitiba e Ribeirão Preto, respectivamente). Da mesma forma, também observamos a ocorrência de outros importantes vícios amostrais relativos à densidade de rios e riachos, que, principalmente em locais ermos, são os principais meios de deslocamento de pesquisadores desvelando a biodiversidade de abelhas (e outros grupos biológicos) brasileiras.

De forma adicional aos vícios amostrais, outros vícios relacionados ao processo de curadoria, identificação, impedimento taxonômico (i.e. falta de chaves ou revisões taxonômicas) e disponibilização de dados biológicos digitalizados efetivamente afetam a quantidade de dados biológicos disponíveis para se avaliar o *status* de conservação de espécies, principalmente em áreas amplamente diversas. Apesar destes

impedimentos, fomos capazes de avaliar em escalas macroecológicas, a real situação de dados digitalizados disponíveis para ambos os grupos de abelhas.

Tentando enfrentar os problemas descritos no primeiro terço desta tese, com dados de distribuição de duas espécies coletadas no Cerrado goiano [*Aglae caerulea* (Apidae: Euglossini); *Lithurgus huberi* (Apidae: Lithurgini)], utilizando-se de modelos de distribuição potencial de espécies, nos apresentamos as distribuições potenciais destas espécies na América do Sul, discutindo e tentando otimizar áreas para novas coletas no continente. Em especial, para *L. huberi*, uma espécies exótica na América do Sul, utilizando-se de informações relativas à sua ecologia, tentamos delimitar melhor locais para novas coletas. De maneira geral, para ambas espécies, novas coletas na região central do Brasil são indicadas, apesar de que, grandes extensões de terra possuem as condições mínimas para a ocorrência de ambas as espécies no continente Sulamericano.

Por fim, na última parte da tese, utilizando-se as abelhas *Eulaema nigrita* e *Eufriesea auriceps* (Apidae: Euglossini), bem como análises considerando-se toda a comunidade de abelhas coletadas no Cerrado goiano, avaliamos a resposta destes insetos quanto à estrutura da paisagem em diferentes escalas locais. Como conclusão, acreditamos que as duas espécies de abelhas-das-orquídeas não são bons indicadores de perda de habitat e fragmentação para o Cerrado, apesar de que este fato é bem provável para outros biomas brasileiros, principalmente a Mata Atlântica e Amazônia. Apesar de também não termos observado grandes respostas das comunidades de abelhas à características da paisagem, acreditamos que isso se deva ao fato de que, por viverem em um bioma mais variável quanto ao clima e naturalmente mais aberto, as espécies do Cerrado sejam mais protegidas à variações da paisagem.

Futuros trabalhos, tanto em escalas macroecológicas, quanto em escalas mais regionais são de extrema importância para que a biodiversidade de abelhas brasileiras continue a ser descrita e os efeitos das atividades antrópicas sejam devidamente contabilizados. Neste sentido, o incentivo contínuo à coleções biológicas para que disponibilizem seus dados em grandes bancos de dados de ocorrência é vital para a melhor descrição da biodiversidade. Adicionalmente, tais dados, após serem meticulosamente filtrados e padronizados, compõem uma informação biológica de extrema importância para dar suporte a ações práticas voltada à conservação destes grupos de organismos.

ANEXOS

Artigos publicados no período do doutorado (exceto Capítulos III e IV)

Journal of Pollination Ecology, 11(4), 2013, pp 27-32

— Novel Ideas and Pilot Projects —

EFFICIENCY IN POLLEN FORAGING BY HONEY BEES: TIME, MOTION, AND POLLEN DEPLETION ON FLOWERS OF *SISYRINCHIUM PALMIFOLIUM* (ASPARAGALES: IRIDACEAE)

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Current and historical climate signatures to deconstructed tree species richness pattern in South America

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ABSTRACT. The purpose of this study was to investigate the importance of present and historical climate as determinants of current species richness pattern of forestry trees in South America. The study predicted the distribution of 217 tree species using Maxent models, and calculated the potential species richness pattern, which was further deconstructed based on range sizes and modeled against current and historical climates predictors using Geographically Weighted Regressions (GWR) analyses. The current climate explains more of the wide-ranging species richness patterns than that of the narrow-ranging species, while the historical climate explained an equally small amount of variance for both narrow-and-wide ranging tree species richness patterns. The richness deconstruction based on range size revealed that the influences of current and historical climate hypotheses underlying patterns in South American tree species richness differ from those found in the Northern Hemisphere. Notably, the historical climate appears to be an important determinant of richness only in regions with marked climate changes and proved Pleistocenic refuges, while the current climate predicts the species richness across those Neotropical regions, with non-evident refuges in the Last Glacial Maximum. Thus, this study's analyses show that these climate hypotheses are complementary to explain the South American tree species richness.

Keywords: climate changes, glacial refuges, water-energy availability, GWR analysis, spatial non-stationarity.

Field Biology of *Edessa rufomarginata* (Hemiptera: Pentatomidae): Phenology, Behavior, and Patterns of Host Plant Use

DANIEL P. SILVA[1,2] AND PAULO S. OLIVEIRA[3]

Environ. Entomol. 39(6): 1903–1910 (2010); DOI: 10.1603/EN10129

ABSTRACT Pentatomids may cause direct and indirect damage to important crop plants. Biological and ecological features of phytophagous stink bugs in natural environments, however, remain poorly documented. Here, we provide an ecological account of *Edessa rufomarginata* De Geer on *Caryocar brasiliense* (Caryocaraceae) in the Brazilian savanna. The phenology of *E. rufomarginata* matched that of its host plant, with immatures developing in the wet season simultaneously with the production of vegetative and reproductive plant tissue. Females do not exhibit parental care and lay eggs more frequently on larger plants. Oviposition frequency, however, does not differ between plants with and without flowers/fruits. Nymphs and adults usually feed on stem parts and more rarely on flower buds and fruits. First- and second-instar nymphs remain aggregated, but disperse as third-instar nymphs. Adults and nymphs were more abundant on mature stems of *C. brasiliense* compared with other plant

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Adult odonate abundance and community assemblage measures as indicators of stream ecological integrity: A case study

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ABSTRACT

Water resources demand constant conservation actions due to several problems (e.g. riparian vegetation cut-off, construction of dams, acidification, sewage and pesticide spills) that degrade the aquatic systems worldwide and affect its physicochemical parameters and habitat characteristics. Odonata is a potential group of organisms that could indicate these habitat alterations once they have aquatic and terrestrial life forms. In this study, we tested the use of adult odonate individual species and community assemblage measures to evaluate the effect of riparian vegetation cut-off and sewage discharges. The study was performed at Turvo Sujo River, in Viçosa, Southern Brazil. We selected twelve sites, six of them

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Goiânia, 06 de dezembro de 2013.

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