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Taxonomy, phylogeography and distribution of the genus *Monastria* (Insects, Blattodea) in the Brazilian Atlantic Forest

Vitor Dias Tarli

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Vitor Dias Tarli

Le 30/01/2018

Taxonomie, phylogéographie et distribution du genre
***Monastria* Saussure 1864 (Insectes, Blattodea) dans la**
forêt atlantique brésilienne

Sous la direction de : **Madame PELLENS Roseli**, Ingénieure de Recherche
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Abstract

The Brazilian Atlantic forest is one of the biodiversity hotspots with the richest species diversity and threat. It is located along the Brazilian Atlantic coast going south til Paraguay and Argentina in the interior of the continent. Due to its longitudinal and altitudinal gradients, complex geology and diversity of soils it harbors an enormous diversity of landscapes and ecosystems that gave rise to its rich biodiversity. However, this biodiversity is extremely threatened because this region is the one with the highest population size and density in south America. So, the Atlantic forest is now limited to less than 5% of its original surface and distributed in scattered fragments. Despite the recognized species richness, much remains to be known about several components of this biodiversity and their origin. Among the groups still poorly known are the insects. In order to contribute to bridge this gap, in this thesis I studied one genus of cockroach endemic from the Atlantic forest, *Monastria* Saussure, 1864 (Blaberidae, Blaberinae). I focused on the taxonomy, phylogeography and on the contribution of the data existing in natural history collections to model the distribution range. The study of the taxonomy consisted in the revision of the genus with the re-description of already known species and description of new ones. Since the known species were described very early, the description (and re-description) comprised the definition of new characters, and consideration paid to genitalia. In addition to that, old nomenclatural problems were solved, a key to species' identification was provided, a key to the identification of nymphs of the genera of Blaberinae endemic to the Atlantic forest were provided. The second study was aimed to understand the diversification and distribution of the genus *Monastria* in the Brazilian Atlantic Forest. This analysis indicates the importance of differential impacts of shifts in temperature between the Southern and Northeastern part of the Atlantic forest in the Last Glacial Maximum for explaining the present pattern of distribution. The third study is an evaluation of the data concerning *Monastria* available in Natural History Collections for estimating its distribution range based on Ecological Niche Models (ENM), and using the data from the field work designed to assess the presence of *Monastria* to validate the results. Here we showed that the dataset is biased in the environmental space. This oversampling in a climate class leads to models with suitable areas much smaller than that of the real distribution of *Monastria*. These biases increase model's specificity and reduced sensitivity. To overcome this problem, we designed two forms of rarefaction and showed deleting points at random in the most biased climate class is very powerful to increase the sensitivity of the ENM.

Keywords: Dictyoptera, Blattaria, taxonomic revision, diversification, distribution, ecological niche models, filters, rarefaction, Maxent.

Résumé

La forêt atlantique brésilienne est des points sensibles de biodiversité avec une richesse spécifique et des risques d'extinction élevés. Cette forêt est située le long de la côte atlantique brésilienne, s'étendant jusqu'au Paraguay vers le Sud et à l'Argentine dans l'intérieur des terres. Du fait des gradients longitudinal et altitudinal, de la géologie complexe et de la diversité des sols, cette forêt comprend une diversité exceptionnelle de paysages et d'écosystèmes qui ont permis à cette riche biodiversité de se développer. Cependant, cette dernière encourt des risques extrêmes d'extinction du fait des densités et des tailles de populations humaines locales les plus élevées en Amérique du Sud. La forêt atlantique est ainsi aujourd'hui réduite à moins de 5% de sa surface originelle, répartie dans des fragments épars. En dépit de cette richesse spécifique reconnue, beaucoup reste à comprendre au sujet de plusieurs composantes de la biodiversité et de leur origine. Parmi les groupes encore mal connus figurent en particulier les insectes. Dans le but de combler cette lacune, j'ai étudié dans cette thèse un genre de blatte endémique de la forêt atlantique, *Monastria* Saussure, 1864 (Blattodea, Blaberinae). Je me suis focalisé sur sa taxonomie, sa phylogéographie et sur la contribution des données de collections d'histoire naturelle à la modélisation de l'aire de distribution. L'étude de la taxonomie a consisté à entreprendre la révision du genre avec la re-description des espèces déjà connues et la description de nouvelles espèces. Les descriptions des espèces connues étaient fort anciennes et la description (et redescription) a donc inclus la définition de nouveaux caractères, ainsi qu'une étude des genitalia. Des problèmes nomenclaturaux anciens ont été également résolus, une clé d'identification des espèces ainsi qu'une clé d'identification des larves des genres de Blaberinae endémiques de la forêt atlantique ont été construites. La deuxième étude concernait l'analyse de la diversification et de la distribution du genre *Monastria* dans la forêt atlantique brésilienne. Cette analyse a indiqué l'importance des impacts différentiels des changements de température durant le dernier maximum glaciaire entre les parties Nord et Sud de la forêt atlantique, ceci résultant dans le patron de distribution présent. La troisième étude est une évaluation de l'intérêt des données disponibles dans les collections d'histoire naturelle concernant *Monastria* pour inférer son aire de répartition en se basant sur des modèles de niches écologiques (ENM), et en utilisant les données issues de l'échantillonnage de terrain ciblé sur *Monastria* pour valider les résultats. Nous montrons ici que le lot de données des collections est biaisé dans l'espace environnemental. Le sur-échantillonnage dans une classe de climat conduit à construire des modèles d'aires favorables plus restreints que ceux de la distribution réelle de *Monastria*. Ces biais augmentent donc la spécificité des modèles et réduisent leur sensibilité. Pour résoudre ce problème, nous avons conçu deux sortes d'analyse de raréfaction et montré que la suppression aléatoire de points dans la classe climatique la plus biaisée augmente de manière très efficace la sensibilité du modèle de niche climatique.

Mots-clés: Dictyoptères, Blattaria, révision taxonomique, diversification, distribution, modèles de niche écologique, filtres, raréfaction, Maxent.

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Introduction à la Thèse
Taxonomie, Phylogéographie et Distribution du
genre *Monastria* Saussure, 1864 (Insectes,
Blattodea) dans la forêt atlantique brésilienne**

Introduction

Taxonomie, Phylogéographie et Distribution du genre *Monastria* Saussure, 1864 (Insectes, Blattodea) dans la forêt atlantique brésilienne

La biodiversité est la résultante d'une longue histoire évolutive (Wilson, 1988), qu'il est indispensable de reconstruire si l'on veut comprendre sa structure et son fonctionnement. Les points sensibles de la biodiversité (Myers et al., 2000) sont des lieux d'étude privilégiés à cet égard. En effet, la richesse et l'endémisme y sont particulièrement importants (Kier et al., 2009) et la résultante de l'histoire évolutive y est donc toujours localement présente et extrêmement diversifiée (Pellens et al., 2016). Cette extraordinaire biodiversité, ayant évolué au moins en grande partie localement, est primordiale pour l'étude de l'origine évolutive de la biodiversité, car elle permet de reconstruire in situ des processus passés dont les détails ne seront pas trop fortement occultés par des événements tels que les extinctions ou les dispersions, comme c'est souvent le cas dans des zones de plus hautes latitudes.

Les points sensibles de la biodiversité sont cependant d'importance et de signification géographiques variées. Certains sont de petites régions ou des systèmes insulaires tandis que d'autres sont de grands bassins forestiers continentaux. Chaque point sensible a donc ses caractéristiques particulières qui permettent de répondre à des questions passablement différentes. Les grands bassins forestiers ont en commun une importance géographique certaine, une visibilité et une taille remarquables, et un contenu

en biodiversité à la fois ancien et très divers. Ils permettent donc d'étudier des problématiques à de larges échelles spatiale, temporelle et taxonomique.

Il en est ainsi de la forêt atlantique du Brésil, un grand massif forestier tropical et subtropical s'étendant sur plus de 3000 km de cote et représentant l'équivalent néotropical d'une deuxième Amazonie (Galindo-Leal & Câmara, 2003), avec laquelle il a d'ailleurs une histoire en partie partagée (Sobral-Souza et al., 2015). Pendant de longues décennies, ce massif forestier est resté infiniment moins étudié que l'Amazonie, si ce n'est à travers les nombreux inventaires réalisés concernant la faune et la flore. Les vingt dernières années ont cependant vu paraître de nombreux travaux approfondis sur l'histoire de la biodiversité de ce massif (par exemple, Costa et al., 2000 ; Cardoso da Silva, 2004 ; Cabanne et al., 2008 ; Carnaval & Moritz, 2008 ; Mello Martins, 2011).

Quelles sont les priorités d'études scientifiques pour ce massif ? En premier lieu, il paraît important de déterminer quelles sont les zones d'endémisme : c'est à dire où sont actuellement les organismes dont les répartitions géographiques sont limitées et s'il y a coïncidence dans les zones d'endémisme pour différents groupes d'organismes. Cette coïncidence déterminera le cas échéant d'éventuels centres de diversité. Il faut aussi comprendre comment et quand ces zones d'endémisme se sont établies, et ce en relation avec l'évolution de l'environnement. L'étude de ces zones d'endémisme en lien avec les paramètres environnementaux doit permettre non seulement de comprendre le déterminisme de leur limitation géographique actuelle mais aussi de comprendre quels ont été les facteurs favorisants ou limitants au cours de l'évolution. Des études récentes ont montré qu'une stabilité locale passée des écosystèmes avait permis le maintien d'une plus grande diversité biologique et il est important de continuer à documenter la situation dans

différents groupes biologiques de manière à montrer si cette tendance reste aussi générale qu'elle semble l'être (Carnaval & Moritz, 2008 ; Mello Martins, 2011).

Les points sensibles sont malheureusement aussi des lieux où les risques actuels d'extinction sont rendus particulièrement élevés du fait des activités humaines (Myers et al., 2000). Il y a donc urgence d'étudier la biodiversité de la forêt atlantique dont subsiste actuellement moins de 5% de la surface originelle du début de l'histoire humaine. Seule une petite partie de ce massif forestier est donc encore existant et disponible à l'étude et à l'échantillonnage (Ribeiro et al., 2009 ; Pellens et al., 2010) (Figure 1). Il est donc important de contribuer à ce sujet à la fois sur la base des inventaires antérieurs et des échantillonnages présents et en étudiant une diversité d'organismes, en particulier des organismes ordinairement considérés comme peu charismatiques et donc souvent moins bien connus que les vertébrés ou certains groupes de plantes.

Il est également important de déterminer à quel point les connaissances taxonomiques ou géographiques que nous avons sur de nombreux groupes d'organismes, aussi fragmentaires et parcellaires soient-elles, peuvent-elles contribuer dans le futur à améliorer notre connaissance générale sur ces zones, bien au-delà de l'étude détaillée de quelques groupes d'organismes particulièrement charismatiques (cf. par exemple, Caesar et al., 2017). De fait, il nous faut trouver le moyen de prendre en compte toute l'information résidente dans les collections, bases de données afférentes et publications taxonomiques. L'étude d'un groupe d'Insectes relativement peu médiatisé nous permettra de traiter cette question et de déterminer les manières dont les données résidentes dans les collections peuvent contribuer aux études sur la biodiversité.

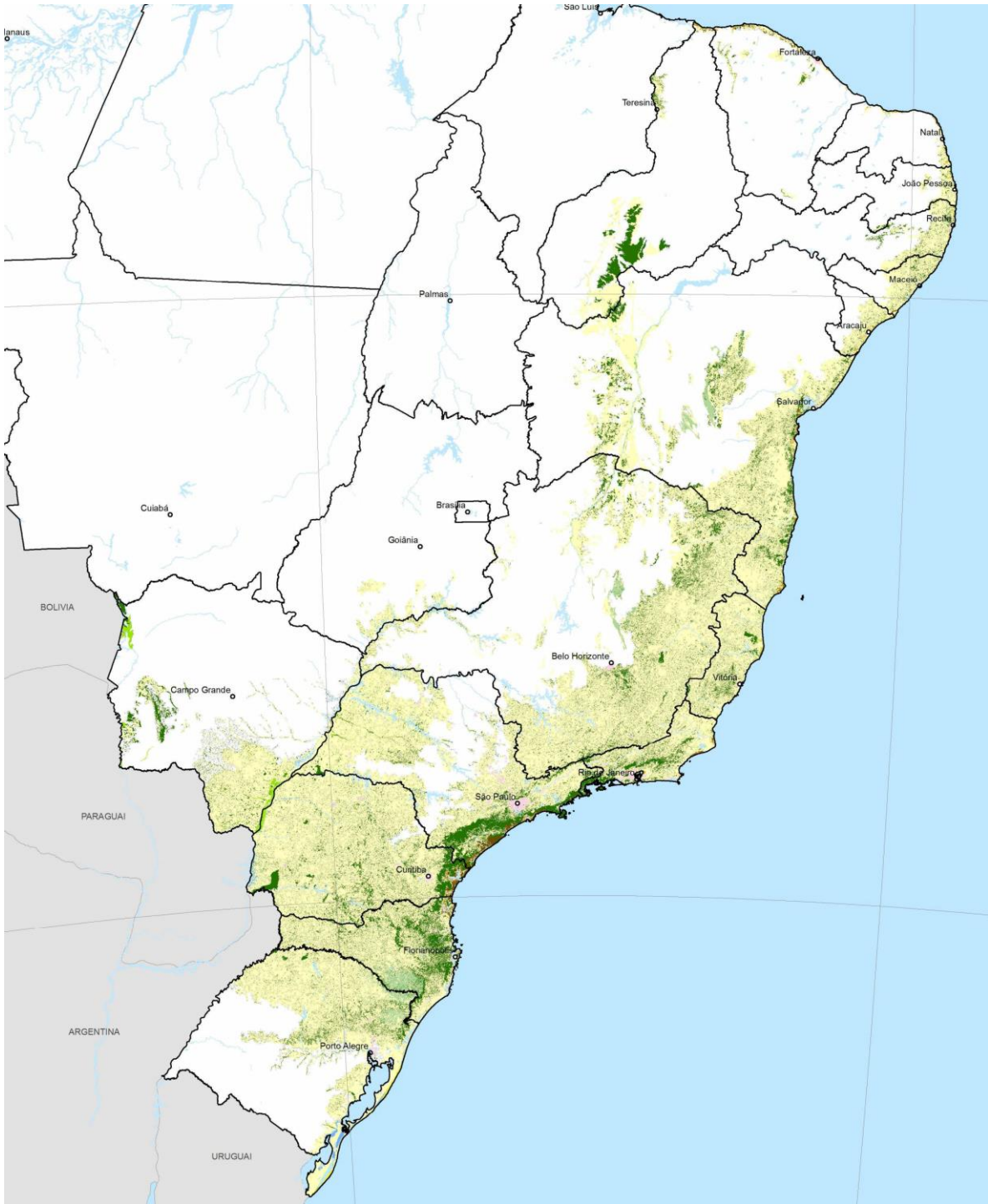


Figure 1. Distribution actuelle de la forêt atlantique. (Source: SOS Mata Atlantica, Inpe, 2017)

Notre étude se focalise ainsi sur les Insectes Dictyoptères (blattes, mantes, termites ; Legendre et al., 2015), un groupe fortement diversifié dans les milieux forestiers au Brésil et comportant des genres endémiques de l'ensemble de la forêt atlantique (Grandcolas & Pellens, 2012). Plusieurs de ces genres ont en outre fait l'objet d'études écologiques détaillées, qui permettent de bien saisir leur insertion dans les écosystèmes locaux (Pellens et al., 2002, 2007 ; Pellens & Grandcolas, 2003, 2007).

Nous nous sommes intéressés au genre *Monastria* Saussure, 1864 qui est endémique de la forêt atlantique. Ce genre comprend des espèces d'assez grande taille, susceptibles d'être capturées par des collecteurs occasionnels et comportant donc potentiellement des informations intéressantes dans des collections d'histoire naturelle. Leur écologie strictement forestière est assez bien connue (Pellens & Grandcolas, 2003, 2007) et doit permettre d'interpréter des résultats géographiques obtenus à large échelle. Il n'en reste pas moins que leur degré tout relatif de connaissance nécessite des missions de terrain pour approfondir l'état de leur taxonomie et de leur répartition. Nous avons donc conduit la révision taxonomique du genre et construit une phylogénie moléculaire qui ont eu pour but de se nourrir mutuellement. L'histoire évolutive ainsi retracée du genre doit permettre de contribuer à l'histoire de la forêt atlantique par comparaison avec les études réalisées sur d'autres organismes. Enfin, la comparaison des informations résidentes dans les collections d'histoire naturelle avec celles acquises durant quelques années d'échantillonnage de terrain doit nous permettre aussi de statuer généralement sur l'intérêt des informations disponibles dans les collections et sur les manières dont il est possible de les utiliser malgré le caractère non dirigé de leur obtention.

La forêt atlantique brésilienne

La forêt atlantique est l'un des biomes les plus menacés au monde, étant considérée comme l'un des 34 hotspots de la biodiversité dans le monde (Myers et al., 2000, Mittermeier et al., 2004, 2011). On estime qu'elle contient de 1 à 8% des espèces vivantes du monde, dont plus de 20 000 espèces végétales, 680 espèces d'oiseaux, 261 espèces de mammifères, 280 espèces d'amphibiens, 200 espèces de reptiles et 8 567 espèces de faune et de flore endémique à cette forêt (Myers et al., 2000, Silva & Casteleti, 2003). Le fort endémisme et la grande diversité sont principalement liés aux gradients latitudinaux, affectant fortement la distribution géographique des organismes (Willig et al., 2003, Canello et al., 2014). Les différences d'altitude, qui varie du niveau de la mer à 2700m dans deux chaînes de montagnes, la Serra do Mar et la Serra da Mantiqueira, favorisent l'existence de gradients altitudinaux importants, avec des forêts qui diffèrent selon la distance de la côte atlantique (Silva & Casteleti, 2003; Joly et al., 2014).

Avec une surface originale estimée à 1,36 million de km², ce biome recouvrait 17% du territoire total brésilien. Distribué depuis le Nord-Est de l'Argentine, l'Est du Paraguay, il atteint la côte atlantique du Brésil où il s'étend sur 28 degrés (plus de 3300 km) (Joly et al., 2014). Dans le Centre-Ouest et le Sud-Est, la forêt atlantique est en contact avec le Cerrado et dans le Nord-Est avec la Caatinga (toutes deux étant des formations végétales sèches et moins forestières), étant limité par ce que l'on appelle la diagonale sèche (Ab'Saber 1977) (Figure. 2). Elle s'étend sur 17 États brésiliens, où se trouve plus de 70% de la population brésilienne (SOS Mata Atlantica, 2017) (Figure 2).

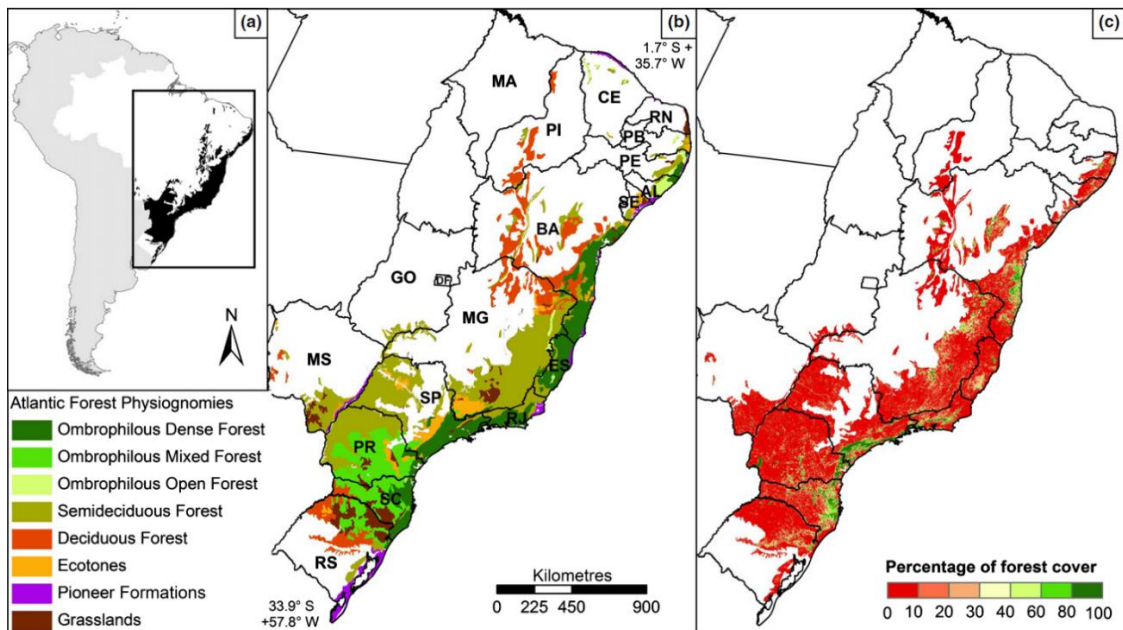


Figure 2. Distribution de du biome forêt atlantique dans l’Amérique du Sud (a) ses différentes formations végétales (b) et la couverture végétale actuelle (Source: Joly et al., 2014).

La forêt atlantique est composée d'un continuum de formations végétales différenciées - forêts ombrophiles denses, forêts ombrophiles ouvertes, forêts ombrophiles mixtes (forêts d'*Araucaria*), forêts semi-décidues et forêts décidues (Oliveira Filho & Fontes, 2000) (Figure 2b). La répartition des pluies est le principal facteur de différenciation entre les forêts ombrophiles, semi-décidues et décidues. Les forêts ombrophiles sont distribuées dans des endroits sans saison sèche, avec seulement deux mois de faible humidité et les températures moyennes varient entre 22 et 25°C. Les forêts semi-décidues et décidues se rencontrent dans les régions présentant les mêmes variations de température, mais avec deux à cinq mois de saison sèche. Des forêts ombrophiles mixtes, connues comme forêts d'*Araucaria*, distribués dans le Sud et le Sud-Est du Brésil, dans un climat subtropical, avec des températures comprises entre 12 et 22°C (Colombo & Joly, 2010). Les différences entre les forêts du Nord et du Sud sont directement liées aux combinaisons de température et de

précipitations (Scudeller et al., 2001). La différence entre l'Est et l'Ouest est liée aux précipitations saisonnières, augmentant avec la distance à l'océan (Joly et al., 2014).

La plupart des sols où la forêt atlantique s'est développée est formée par le dépôt de sédiments marins et de coulées de lave. Le relief des régions Sud et Sud-Est est formé en raison des failles tectoniques et des centres volcaniques de nature alcaline pendant la période crétacée (86Ma). Toute cette activité tectonique a donné lieu aux montagnes de la Serra do Mar et de la Mantiqueira (Vieira & Gramani, 2015). Ces montagnes sont caractérisées par la diversité des formes avec des altitudes allant de 800 à 1300m et des pics qui dépassent 2700m. Contrairement au sud, dans le nord-est, le dépôt de sédiments marins du Cénozoïque a joué un rôle important dans la formation des sols et les plateaux côtiers, appelés « Tabuleiros » (Alkimim, 2015). C'est sur ce sol sédimentaire qui se sont développées les forêts de plaine, connues comme la forêt de « Tabuleiros », distribuées dès nord de l'état du Espírito Santo jusqu'au Rio Grande do Norte (Silva & Casteleti, 2003).

Malgré de nombreuses controverses, la forêt atlantique est considérée comme la plus ancienne forêt brésilienne. Elle consiste en un assemblage d'espèces qui ont évolué à partir des forêts originelles datant de 100 millions d'années, lorsque l'Amérique du Sud était connectée au continent africain (Colombo & Joly, 2010). Les espèces les plus récentes sont le résultat d'événements évolutifs liés à plusieurs facteurs, tels que les expansions et les rétractions de la forêt, les refuges, et la stabilité du climat au Quaternaire (Behling & Pillar, 2007; Ledru et al., 2007; Carnaval et al., 2009, Carnaval et al., 2014). Pendant les fluctuations du Pléistocène (environ 120 000 ans) plusieurs événements importants ont eu lieu. La modélisation des zones forestières stables suggère des rétractions forestières dans le Sud et le Sud-Est et des refuges à Bahia et Pernambuco (Carnaval et Moritz 2008, Carnaval et al., 2009, Carnaval et al., 2014, Mello Martins 2001). Pendant la dernière période glaciaire (~21

kybp), l'impact des phases de climat plus sec était plus important au Sud qu'au Nord (Por, 1992). Le plus grand impact du climat sur le Sud a déclenché les rétractions de la forêt et a permis au Cerrado de s'établir (Behling, 2002). En conséquence, les forêts d'*Araucaria* se sont déplacées à 400 km au Nord de la distribution actuelle dans des forêts semi-décidues (Behling et al., 2004). Mais cette situation s'est inversée lorsque la température a augmenté dans la période postglaciaire et que les forêts d'*Araucaria* ont été remplacées par des forêts semi-décidues (Ledru et al., 2009). Le nouveau climat dans le Sud a permis la réinstallation des forêts mixtes à la place du Cerrado jusqu'à ce que la configuration soit semblable à celle d'aujourd'hui (Behling et al., 2004). Un autre scénario à considérer pour expliquer toute la diversité concerne l'expansion de la forêt sur le plateau continental dans la période qui va de la dernière période interglaciaire jusqu'à la dernière période glaciaire (soit de -120 000 a - 22000 ans) (Caruso et al., 2000; Leite et al., 2016). Pendant la dernière période glaciaire, le niveau maximum de la mer a diminué de 150 m (Rabineau et al., 2006). Ceci a amené à une expansion de centaines de kilomètres de la côte au Sud et Sud-Est du Brésil, exposant le plateau continental brésilien ce qui a été interprété comme le facteur qui a permis l'expansion des forêts dans vastes zones (Leite et al., 2016). Des registres polliniques confirment que cette expansion des forêts est trouvée aussi pendant la dernière période interglaciaire (Ledru et al. 2009). Une grande partie de cette dynamique d'expansion de la forêt a permis une connexion des îles au continent et a ainsi joué un rôle important dans l'évolution des habitats côtiers et dans les îles.

**B) Chapitre II –
Taxonomic revision of the genus *Monastria* Saussure,
1864 (Blattodea: Blaberidae, Blaberinae)**

Taxonomic revision of the genus *Monastria* Saussure, 1864 (Blattodea: Blaberidae, Blaberinae)

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Abstract

The genus *Monastria* Saussure, 1864 includes medium to large sized (40–55 mm) dark brown cockroaches found in the understory of the Neotropical Atlantic Forest. The genus shows evident sexual dimorphism: males are elongated and have long elongated wings extending beyond the apex of cerci and females are oval and brachypterous. We revised the genus with redescription of the three species already known *Monastria biguttata* (Thunberg, 1826), *Monastria similis* (Serville, 1838) and *Monastria angulata* Saussure, 1864, and description of five new species, *Monastria itubera* **sp. n.** and *Monastria itabuna* **sp. n.** from state of Bahia, *Monastria cabocla* **sp. n.** from state of Sergipe, *Monastria kaingangue* **sp. n.** from state of São Paulo and *Monastria sagittata* **sp. n.** from state of Minas Gerais. We provide a determination key for distinguishing the genus *Monastria* Saussure, 1864 from other Atlantic genera of Blaberinae and detailed morphological descriptions and diagnoses for the genus and for all species; for the first time the male genitalia are described. The juvenile stages of this genus are characterized and compared to other genera of Blaberinae of the Atlantic forest. A distribution map and an identification key for all species are also provided.

Key Words: Atlantic forest, *Monastria*, endemic cockroach, male genitalia, juvenile stages, distribution range.

Resumo

O gênero *Monastria* Saussure, 1864 inclui baratas de coloração negra com tamanho médio a grande (40 - 55 mm) que ocorrem no sub-bosque da floresta Atlântica neotropical. Com evidente dimorfismo sexual, os machos são alongados e possuem asas longas que se estendem além do ápice dos cercos enquanto as fêmeas são braquípteras e ovais. Este estudo é uma revisão do gênero com re-descrição das três espécies conhecidas *Monastria biguttata* (Thunberg, 1826), *Monastria similis* (Serville, 1838) e *Monastria angulata* Saussure, 1864 e descrição de cinco novas espécies: *Monastria itubera* **sp. n.** e *Monastria itabuna* **sp. n.** do estado da Bahia, *Monastria cabocla* **sp. n.** do estado de Sergipe, *Monastria kaingangue* **sp. n.** do estado de São Paulo e *Monastria sagittata* **sp. n.** do estado de Minas Gerais. Nós descrevemos detalhadamente a morfologia do gênero e de todas as espécies e pela primeira vez, as genitálias masculinas foram descritas. Também pela primeira vez o estágio juvenil deste gênero é caracterizado e comparado com os de outros gêneros da radiação de Blaberinae da Mata Atlântica. Um mapa de distribuição e uma chave de identificação para todas as espécies também são fornecidos.

Introduction

Cockroaches have evolved with diverse continental radiations. One of the most conspicuous corresponds to the subfamily Blaberinae distributed in the Neotropical region (Grandcolas 1993a,b, 1998b; Pellens & Grandcolas, 2007; Pellens *et al.* 2007a,b; Grandcolas & Pellens, 2012; Legendre *et al.*, 2015). This early-recognized group (McKittrick, 1964; Roth, 1970, 2003) has been the subject of several behavioral and ecological studies (Grandcolas, 1998). Despite this early recognition, some of its components have been poorly studied, such as the genera endemic from the Atlantic forest in Brazil, namely *Monastria* Saussure, 1864, *Monachoda* Burmeister, 1838, *Petasodes* Saussure, 1864, *Hiereoblatta* Rehn, 1937, and *Minablatta* Rehn, 1940 (Grandcolas 1993a,b, 1998; Pellens *et al.* 2007a,b; Grandcolas & Pellens, 2012). The genus *Monastria* Saussure, 1864 is certainly the best known amongst them (Pellens & Grandcolas, 2003, 2007). Nevertheless, its taxonomy needs a complete revision.

The genus *Monastria* was established by Saussure, 1864 in which he included the species *Monastria biguttata* (Thunberg, 1826), *Monastria similis* (Serville, 1838) and described two new species *Monastria angulata* and *Monastria semialata*. Walker (1868)

included the known species of *Monastria* in his catalogue, but described a new genus *Tarraga guttiventris* and a new species *Blabera nigripennis* of cockroaches that were posteriorly brought back into *Monastria*. Kirby (1904) recognized that *Monastria semialata* (Saussure, 1864) was a synonym of *Monastria cassidea* (Eschscholtz, 1822), *Blabera nigripennis* (Walker, 1868) was a synonym of *M. biguttata*, *Monachoda granosa* Brunner von Wattenwyl, 1865 was a synonym of *Monastria papillosa*. He also incorrectly synonymised *Tarraga guttiventris* to *Blaberus giganteus* (Linnaeus, 1758). Shelford (1907) in his study on the species published by Thunberg incorrectly synonymized *Monastria semialata* (Saussure, 1864), *Monachoda granosa* Brunner von Wattenwyl, 1865 and *Phoraspis cassidea* (Dalman, 1823) to *Monastria papillosa* (Thunberg, 1826). In the same study *Blabera monstrosa* Stål, 1855 was considered a synonym of *Monastria biguttata* (Thunberg, 1826). Kirby (1910) published a correction in which *Blatta papillosa* Thunberg, 1826 was synonymized to *Monastria cassidea* (Eschscholtz, 1822). Rehn (1937) described the genus *Hiereoblatta* and accepted *Monastria semialata* (Saussure, 1864) as the only synonym of *Hiereoblatta cassidea* (Eschscholtz, 1822). Princis (1946) described *Monastria flavomarginata*, but in 1951 he stated that it was a synonym of *Monastria similis* (Serville, 1838). Princis (1949) maintained *Blatta papillosa* Thunberg, 1826 as a synonym of *Monastria papillosa* (Thunberg, 1826). In 1958, Princis synonymized *Tarraga guttiventris* Walker, 1868 to *M. biguttata* (Thunberg, 1826). In the catalogue published in 1963, Princis included four valid species to the genus: *Monastria angulata* Saussure, 1864; *Monastria biguttata* (Thunberg, 1826); *Monastria papillosa* (Thunberg, 1826); *Monastria similis* (Serville, 1838).

In the present study, we provide a determination key to distinguish the genus *Monastria* Saussure, 1864 from other Blaberinae genera of the Atlantic forest, we revise the genus *Monastria* Saussure, 1864, redescribe three known species, describe five new ones, and provide an identification key for all of them. We did not include *Monastria papillosa* (Thunberg, 1826) because it is a non-valid synonym (see Princis, 1949) of *Hiereoblatta cassidea* (Eschscholtz, 1822), incorrectly attributed to *Monastria*. For the first time the male genitalia of specimens of this genus are described and the juvenile stages are characterized and compared to juveniles of the other genera endemic from the Atlantic forest. The records of occurrence of the specimens analyzed here indicate that the distribution range of the genus is much broader than previously known, and confirms the initial hypothesis of an endemism to the Neotropical Atlantic forest.

Material and Methods

Specimens were measured with a digital caliper and stereoscopic microscope Leica MZ12. This microscope is equipped with an eyepiece micrometer scale that allows for observations and measurements of interocular and interantennal distance, and of genitalia as well. Genitalia were observed after dissection of re-hydrated specimens and treated in cold 10% KOH to remove remains of soft tissue and rinsed with water. They were kept in glass vials with glycerin and pinned under specimens. Sclerites in male genitalia were named according to Grandcolas (1996), modified from Grandcolas (1991, 1993b) and abbreviations used here are: L1, L2d, R2, R3d, N, R3v, Lb (Lateral Branch), Cs (Crown of spines), Notch (Subapical incision) and Clf (Cleft).

Digital images of habitus, pronotum, head, supra-anal plate and juvenile stages were taken with a camera Cannon 6D. The genital sclerites were photographed with a stereomicroscope Nikon attached to a camera Cannon 6D in MNHN's scanning digitization laboratory. Images of external morphology and genitalia were combined with the Helicon Focus 6.7.1 software and edited in Adobe Photoshop Elements 11. The cuticle of juvenile stages of five specimens were critical point dried, coated with gold-palladium and digitally photographed using a HITACHI SU3500 scanning electron microscope in MNHN's electron microscopy and microanalysis technical platform.

The holotypes were deposited in the collection of the Museum of Zoology of the University of São Paulo (MZUSP). The material examined are part of the collections of the following institutions: Muséum National d'Histoire Naturelle in Paris (MNHN), Muséum d'Histoire Naturelle de la Ville de Genève (MHNG), Natural History Museum London (NHM), Museu de Zoologia Universidade de São Paulo (MZUSP), Museu Nacional do Rio de Janeiro (MNRJ) and Uppsala University Museum of Evolution, Uppsala in Sweden.

Results

Key to the genera of the subfamily *Blaberinae* endemic from the Neotropical Atlantic forest

Adults

- 1 Pronotum with lateral margin rounded, without notch or spine.....2
- Pronotum with lateral margin angular, most often with a notch or a spine.....3

- 2 Pronotal cuticle smooth; dark brown with two yellow spots; males brachypterous (Fig. 1C).....***Minablatta Rehn, 1940***
- Pronotum strongly gibbous; yellow darker in the middle; males brachypterous (Fig. 1D)..... ***Hiereoblatta Rehn, 1937***
- 3 Pronotum unicolored (tawny beige); fore margin very abruptly curved upward; central part inside which the head is ventrally inserted strongly protruding (Fig.1B).....***Petasodes Saussure, 1864***
- Pronotum with a more complex coloration; roughly triangular; lateral margin angular most often with a notch or a spine.....4
- 4 Pronotum smooth, with a very light prominence above the head and a black complex spot in the postero-central part and reaching the posterior margin (Fig. 1E)..... ***Monachoda Burmeister, 1838***
- Pronotum gibbose, with a complex dark and brightly-colored pattern in the middle (Fig. 1A)..... ***Monastria Saussure, 1864***

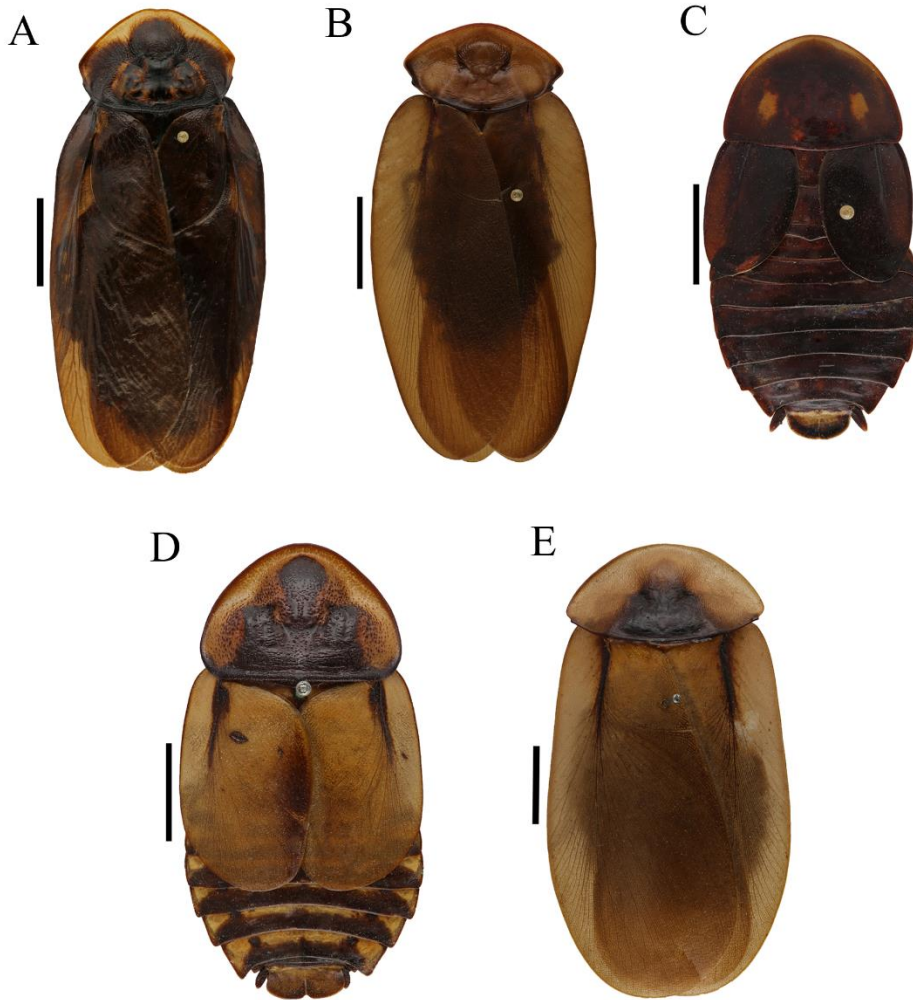


Figure 1. Five genera of Blaberinae endemic from the Neotropical Atlantic forest in dorsal view. A) *Monastria*; B) *Petasodes*; C) *Minablatta*; D) *Hiereoblatta*; E) *Monachoda*. Scales: Habitus=1cm.

Juvenile stages

- 1 Pronotum hind margin nearly straight..... 2
- Pronotum hind margin not straight..... 3
- 2 Dorsal surface totally covered by very abundant long thorn-like spines (including pronotum) with a row of larger spines at hind margins; supra anal plate bilobed with a deep incision; each lobe forming straight angles; hind region wider (Fig. 2E, 3E).....*Monachoda* Burmeister, 1838
- Dorsal surface covered by microsculptures formed by triangular spines, except pronotum; supra-anal plate bilobed with a very small median incision; fore region wider (Fig. 2C, 3C)...
.....*Minablatta* Rehn, 1940

3 Ratio between total body length and width $\approx 2:1$; pronotum strongly gibbous; yellow, darker in the middle; dorsal microsculptures very short ending with a seta (Fig. 2D, 3D).....***Hiereoblatta* Rehn, 1937**

- Ratio between total body length and width $\approx 1,7:1$; pronotum hind margin forming 120° angle.....4

4 Very flat, smooth, specially dorsally, with dark spots very visible in the dorsal surface from the pronotum to the fore region of the supra-anal plate, dorsal microsculptures very slender, making like a row of columns along the hind margins of pronotum and tergites (Fig. 2B, 3B).....***Petasodes* Saussure, 1864**

4 Not very flat, dorsal surface of pronotum and tergites very rough covered by thorn-like cuticular microsculptures much more abundant near the hind margins (Fig. 2A, 3A).....***Monastria* Saussure, 1864**

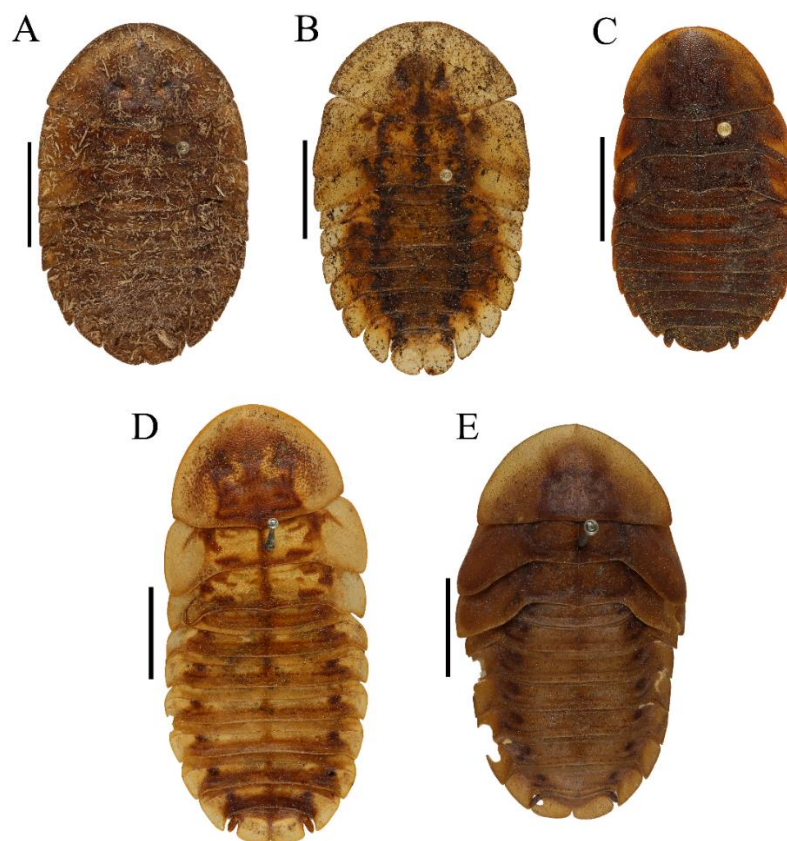


Figure 2. Juveniles stages of five genera of Blaberinae endemic to the Neotropical Atlantic forest in dorsal view. A) *Monastria*; B) *Petasodes*; C) *Minablatta*; D) *Hiereoblatta*; E) *Monachoda*. Scales: Habitus=1cm.

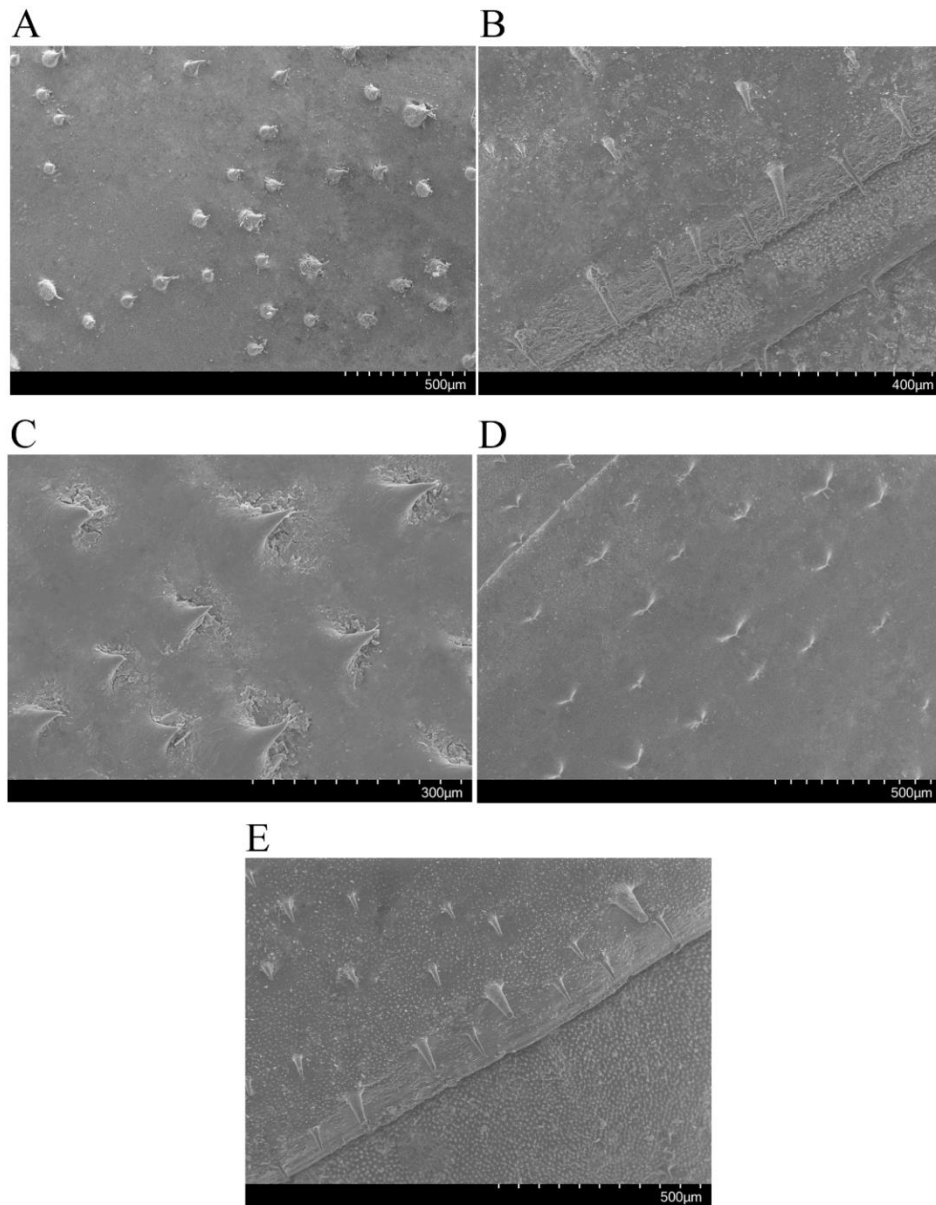


Figure 3. Scanning electron photographs showing the cuticular microsculptures on the dorso of juveniles stages. A) *Monastria*; B) *Petasodes*; C) *Minablatta*; D) *Hiereoblatta*; E) *Monachoda*. Note that the scale differs from among pictures.

***Monastria* Saussure, 1864**

Monastria Saussure, 1864a: 255, 1864b: 348; Kirby, 1904: 161; Princis, 1958: 75, Princis, 1963: 141.

Tarraga Walker, 1868: 16; Princis, 1963: 141 (as syn. of *M. biguttata*).

Type Species. *Monastria biguttata* (Thunberg, 1826) = *Blatta biguttata* Thunberg, 1826 (Fig. 4).



Figure 4. *Monastria biguttata*, female holotype. Not to scale.

Diagnosis. Dark brown to black or shiny black cockroaches with pronotum having orange or ochre spots in the middle. Evident sexual dimorphism with males having long wings extending beyond the cerci apex and elongated shape and females brachypterous and oval. Male pronotum with a characteristic pentagonal transverse shape, lateral margins with sharp angles and a conspicuous small notch. Female pronotum subtriangular with a depression near the margins, and lateral margins with conspicuous small notch or spine. Coxae covered by setae in males, antero-ventral femora margins with spines of equal size. Apical and genicular spines absent. First meta tarsomere of hind leg short and without spines, claws symmetrical and simple, small arolia. Apex of sclerite L1 solidly strongly attached to the rest of the sclerite without any membrane separating them; almost entirely covered by crown of small, closely packed spines, and extending below the apex of posterior margin of sclerite L1.

Generic description. Male (Fig. 5). Medium size (40–55 mm). Head subtriangular; eyes extending antero-laterally beyond the antennal socket; interocular space narrow at its closest distance and smaller than the one between the antennal sockets (0.8–1.8 mm) (Fig. 5C). Antennae not surpassing the apex of the tegmina, filiform and setose from the eighth flagellar segment. First flagellar segment larger than the pedicel. Maxillary palps with the fifth segment more dilated and very tomentose. Pronotum pentagonal with fore margin strongly arcuate, hind margin nearly very weakly arcuate, and a specific black coloration pattern in the central region (Fig. 5B). Tegmina developed, extending beyond the apex of cerci; marginal field short and slightly concave; scapular field tapering toward apex; mid-field discoidal, extended apically, slightly angular along veins; subcostal vein with a carina on its ventral surface, anal veins reaching the posterior border (Fig. 5A). Wing marginal field narrow, subcostal vein reaching basal third of scapular field; cubital vein with numerous complete and few incomplete veins; apical triangle absent. Setae in the dorsal region of the three thoracic segments and in the first abdominal segment. Fore-femora ventro-anterior margins with 16 spines of the same size, the last one directed outward near the apex, ventro-posterior margins with 3 spines, the last one near the apex. Middle legs ventro-anterior margins of with 3 or 4 spines, the last one close to the apex. Tarsomeres 1-4 with pulvilli, the pulvillus of the first metatarsomere very long, covering more than half of the length of metatarsomere; tarsal claws simple and symmetrical; small arolium present. First abdominal tergite unspecialized. Supra-anal plate with an invagination in the median portion. Cerci short, cylindrical, with different coloration in the last segments. Subgenital plate slightly asymmetric. Internally, attached to this plate, a membranous pouch with genital sclerites L1 (Figs. 5G, H), L2d (Figs. 5F, I) and R (right phallomere) (Figs. 5D, E). Sclerite L1 long and thin with the apical part distinct, quite sclerotized and the left branch tooth-shaped; central portion with a small projection and a branch on the right side pointing upwards; apical region on a crown of sclerotized spines. Sclerite L2d hook-shaped, like in most species of Ectobiidae and Blaberidae. Distal area elongated with subapical notch. Hook membranous tube with a sclerotized left lateral area. Sclerite R (right phallomere) formed by sclerotized regions R2, R3d, R3v and N. Sclerite R2 (“cleft”) curved, deep and directed upward. Sclerite R3d wide and elongated longitudinally with a dorsal part reduced and a large ventral one in the distal region. Sclerite R3v with a flattened shape in ventral view, rounded laterodistal apex, and short caudal branch.

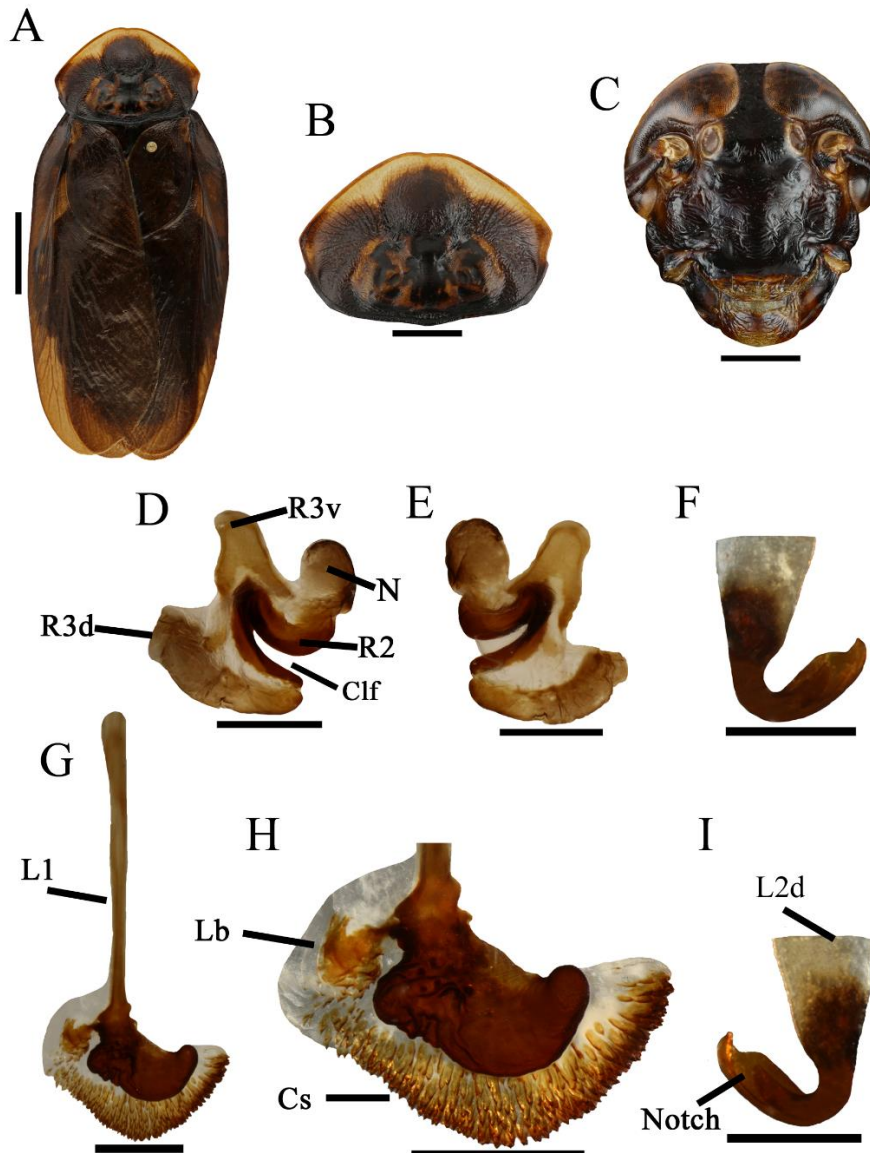


Figure 5. *Monastria biguttata*, ♂: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Head, ventral view; **D)** Right phallomere, dorsal view; **E)** Right phallomere, ventral view; **F)** Left phallomere (L2d), ventral view; **G)** Median sclerite (L1), dorsal view; **H)** Median sclerite (L1), detail; **I)** Left phallomere (L2d), dorsal view. Scales: Habitus=1cm, Pronotum=5mm, Head=2 mm, all others =1 mm.

Female (Figs. 4, 6A–D). Species of medium size (30–45 mm). Head rounded, with wide interocular space measuring 1/2 the distance between the antennal sockets (2.0–3.1 mm). Eyes reniform with straight interocular margin. Antennae reaching the apex of the tegmina, filiform and setose from the eighth flagellar segment. Ocelli developed and deflected. Front broad and frontal suture with a cuticular invagination (Fig. 6D). Pronotum subtriangular with

anterior region rounded and slightly concave near the margins, dorsal region rough with striae, lateral angles rounded ending in a corner, posterior margin slightly curved in the median region (Fig. 6B). Brachypterous. Tegmina truncated with a marked curvature towards the interior and not extending further than the second abdominal tergite; wings much shorter and undeveloped (Fig. 6A). Legs short and robust. Fore femora ventro-anterior margins with 13 spines of the same size, the last one close to the apex; ventro-posterior margins with 4 spines, the last one close to the apex. Middle legs ventro-anterior margins with 4 spines, the last one close to the apex. Supra-anal plate bilobed with a small median incision, each lobe with slightly rounded lateral and straight posterior margin (Fig. 6C). Tergite with slightly rounded lateral angles (Fig. 6A).

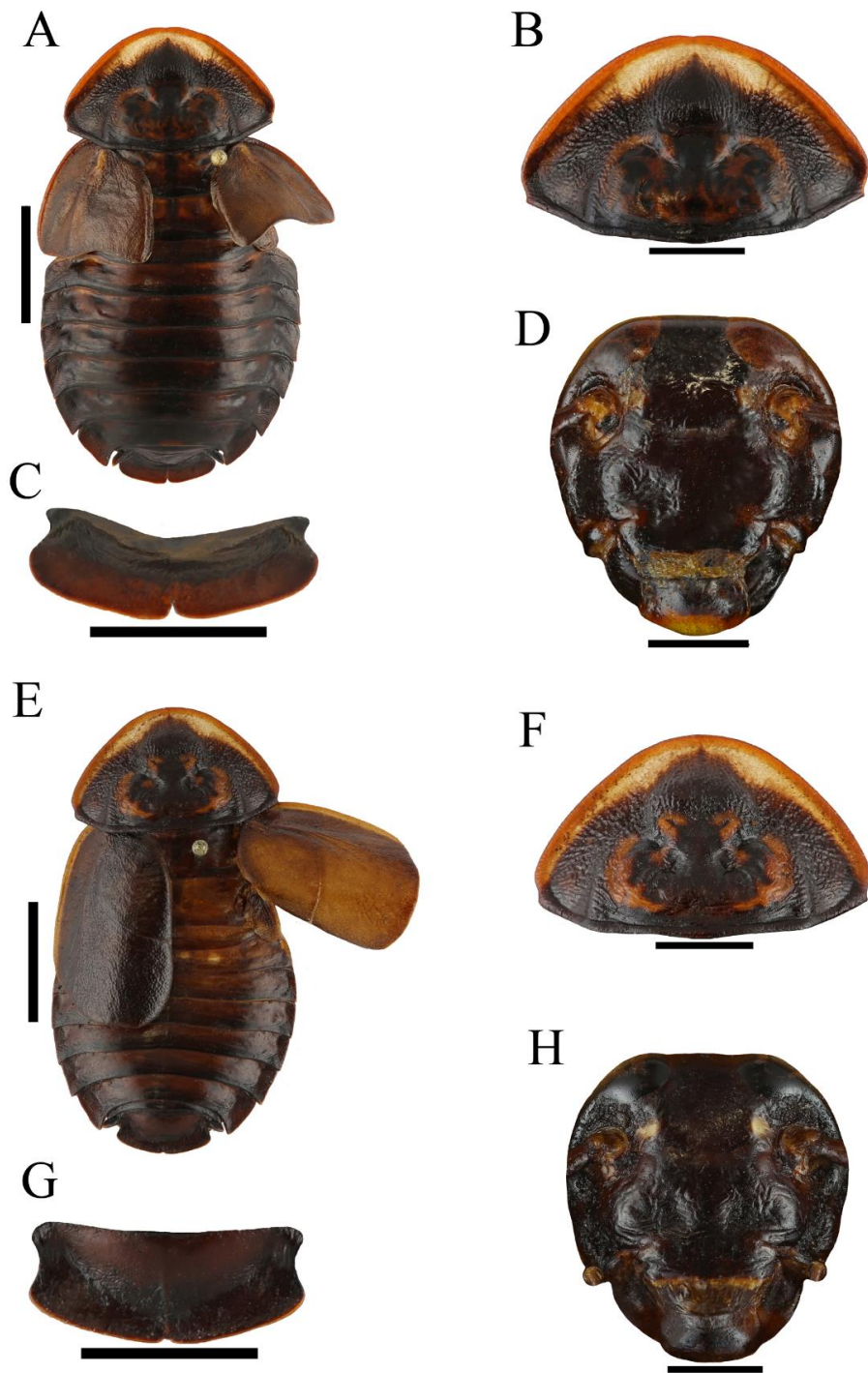


Figure 6. Figs. **A-D**, *Monastria biguttata*, ♀: **A**) Habitus, dorsal view; **B**) Pronotum, dorsal view; **C**) Supra-anal plate, dorsal view; **D**) Head, ventral view. Figs. **E-H**, *Monastria similis*, ♀: **E**) Habitus, dorsal view; **F**) Pronotum, dorsal view; **G**) Supra-anal plate, dorsal view; **H**) Head, ventral view. Scales: Habitus=1cm, Pronotum=5mm, Supra-anal plate=5mm, Head=2 mm.

Juvenile stages. Juveniles of both sexes are oval, almost rectangular with a body length and width ratio $\approx 1,7:1$. Beige to light brown, uniformly colored, the dorsal surface of pronotum and tergites is very rough (Fig. 7), covered by thorn-like cuticular microsculptures, often more abundant at their hind margins. (Fig. 3A). Head, eyes, antennae, legs, supra-anal and subgenital plate very similar to those in adults (Fig. 7E).

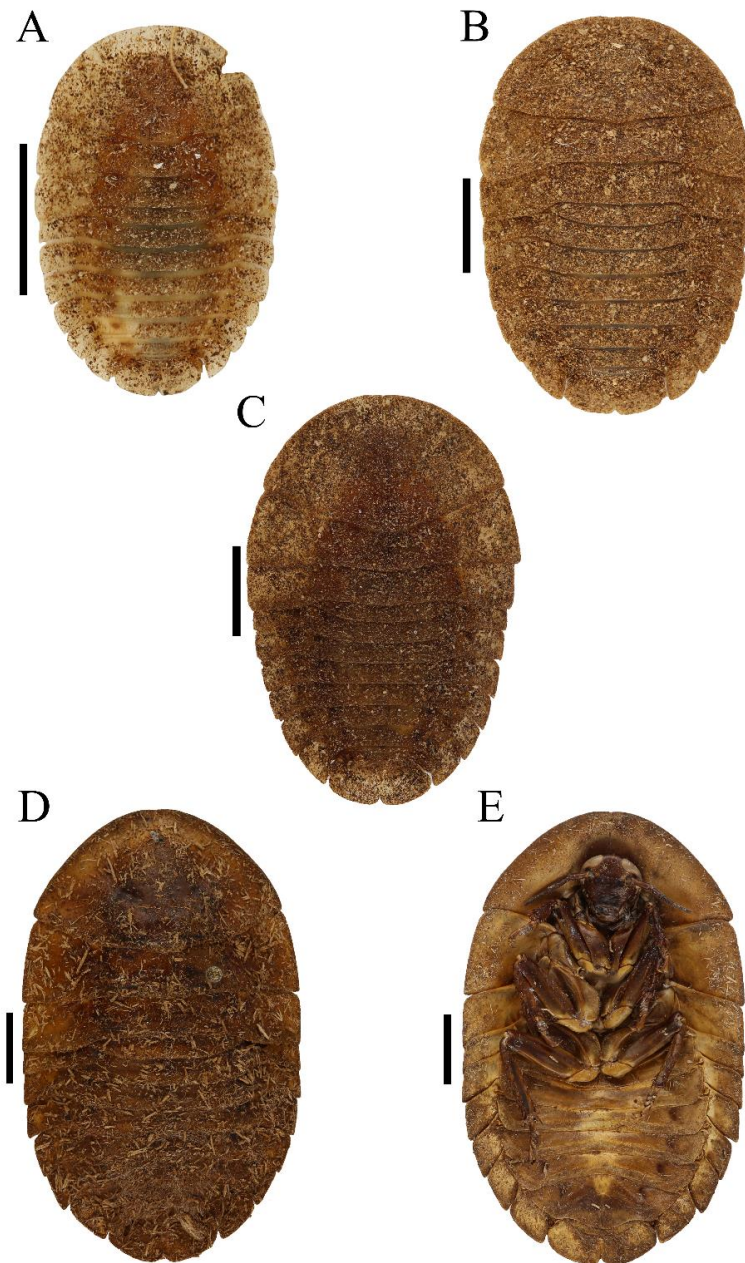


Figure 7. Male juveniles of *Monastria* in different stages of development. Scales: Habitus=5mm. Note the rough surface covered by particles in all stages.

Habitat and Behavior. Specimens of *Monastria* were observed in a large array of forest ecosystems, ranging from semi-deciduous forests at the Northeast to the humid montane forests in the central region and the *Araucaria* forests in the South. All specimens were observed and collected in the forest understory on the underside of dead trunks of various sizes, as it was described in details for *M. biguttata* (Pellens & Grandcolas, 2003). Most of them were found grasping on the underside of the bark or the wood of dead trunks, immediately freezing when disturbed. The body of the juveniles are covered by fine particles of the substrate where they are found, which are attached to the tegument structures (Fig. 7). Adult males have never been seen flying, even if they look able to do so with their large and mobile wings. As any blaberid species, they are ovoviviparous, the females retract the large oothecae in the brood sac. Juvenile stages are often observed in groups that remain near each other until adulthood.

Key to the species of the genus *Monastria*

- 1 Female pronotum with arcuate lateral angles; absence of notch or spines (Fig. 9A, B).....***M. angulata* Saussure, 1864**
- Male and Female pronotum with sharp or rounded lateral angles; with notch or spines..... 2
- 2 Female tegmina long, reaching the fifth abdominal tergite; hind margins curved and rounded. Male with L1 sclerite with lateral branch curved, rounded and with some small spines.....3
- Female tegmina short, not extending further than the fourth abdominal tergite; hind margin truncated or with a curvature. Male with L1 sclerite with lateral branch slightly curved forward, with the aspect of a big sharp tooth.....4
- 3 L1 sclerite with lateral branch curved, rounded and smooth with some small spines; R3d sclerite with a clear prominence like a tooth in ventral view (Fig. 14).....***M. kaingangue* sp. n.**
- L1 sclerite with lateral branch curved and rounded with large spines directed downwards; R2 sclerite near the N shorter and forming a straight angle (Fig. 8)..***M. similis* (Serville, 1838)**
- 4 Male L1 sclerite with a big lateral dilatation and an edge in the median region. Female supra-anal plate with straight posterolateral angles (Fig. 10).....***M. cabocla* sp. n.**
- Male L1 sclerite without a big lateral dilatation and an edge in the median region. Female supra-anal plate with rounded posterolateral angles.....5
- 5 L1 sclerite slightly concave region with irregular distal margins with grooves. Female frons with a prominence (Fig. 11).....***M. itubera* sp. n.**

- L1 sclerite without slightly concave region and irregular distal margins with grooves. Female frons flat.....6
- 6 L1 sclerite with lateral branch slightly curved with some spines reaching the crown of spines at the posterior region (Fig. 13).....***M. itabuna* sp. n.**
- L1 sclerite without lateral branch with some spines reaching the crown of spines in the posterior region.....7
- 7 L1 sclerite with a sharp dorsal protuberance and with a projection in the right side turned forward; L2d sclerite, hook with internal ventral margin concave (Fig. 5)..... ***M. biguttata* (Thunberg 1826)**
- L1 sclerite with a roughly triangular spear-shaped apical region, hind margin with a large non-sclerotized projection. L2d sclerite, hook with internal ventral margin strongly convex (Fig. 16).....***M. sagittata* sp.n**

Species

***Monastria biguttata* (Thunberg, 1826)**

Male – Figure 5.

Female – Figures 4; 6A–D.

Blatta biguttata Thunberg, 1826: 276; Scudder, 1868: 13.

Blaberus biguttata Serville, 1831.

Monachoda biguttata Burmeister, 1838: 514; Brunner v. W, 1865: 365; Finot, 1897: 207

Blabera biguttata Serville, 1839: 80.

Monastria biguttata Saussure, 1864a: 256; Saussure, 1864b: 348; Walker, 1868: 11; Saussure, 1870: 120; Kirby, 1904: 161; Shelford, 1907-1908: 469; Rehn, 1911: 248, Rehn, 1913: 282, Rehn, 1915: 275, Rehn, 1920: 217; Hebard, 1921: 246; Princis, 1949: 66; Princis, 1958: 75, Princis, 1963: 141.

Blabera nigripennis Walker, 1868: 6; Finot, 1897: 210; Princis, 1963: 142 (as syn. of *M. biguttata*).

Tarraga guttiventris Walker, 1868: 16; Finot, 1897: 213; Princis, 1963: 142 (as syn. of *M. biguttata*).

Blabera monstrosa Stål, 1855: 351; Kirby, 1904: 165; Princis, 1963: 142 (as syn. of *M. biguttata*).

Blabera mostruosa Sjostedt, 1933: 10; Princis, 1963: 142 (as syn. of *M. biguttata*, lapsus calami).

Examined material. Brazil – Rio de Janeiro: 7♂, 3♀ Niterói. “Parque da Cidade”, 225m, 22°55’42”S, 43°05’10”W, 500m de la plage du saco de São Francisco, Forêt semp. humide, 21 IX 2009, R. Pellens & P. Grandcolas rec. (MNHN). 1♂ Angra dos Reis, Ilha Grande, “Sentier Abraão/Enseada das Palmas”, 50m, 23°08’34”S, 44°08’91”W, 21km E Angra Dos Reis, Forêt semp. humide, 07 VIII 2007, R. Pellens & P. Grandcolas rec. (MNHN). 1♂, 1♀ Visconde de Mauá, “Apa da Serrinha do Alambari”, 528m, 22°23’16.4”S, 44°29’58.1”W, 26 XI 2010, R. Pellens & P. Grandcolas rec. (MNHN). 1♂ Montagnes des Orgues, Prov. de Rio de Janeiro, Environs de la Tijuca, E. R. Wagner - 1902 (MNHN). 1♂ Floresta da Tijuca, V 1966, M. Alvarenga col. (MZUSP). 1♀ “Tejuca”, I 1857, coll. H. Clark (NHM). **Espirito Santo:** 2♂, 3♀ Res de Linhares, “CVRD”, 19°09’10.2”S, 40°11’07.8”W, 19 X 1999, 40km NNE Linhares, Forêt semi-décidue, “Mata Alta”, R. Pellens & P. Grandcolas rec. (MNHN). 1♂ Linhares, Fragment “Sitio São Pedro”, 19°09’14.2”S, 40°11’34.3”W, 11 VII 2005, 40km NNE Linhares, Forêt semi-décidue, R. Pellens & P. Grandcolas rec. (MNHN). Santa Teresa, Est. Biol. Santa Lucia, 810m, 19°58’18.5”S, 40°32’07.6”W, 6-9 IV 2001, Malaise, ponto 3 trilha, C. O. Azevedo & equipe col. (MZUSP). **Without locality:** 3♀ (America Meridionale) (MHNG). 2♂, 6♀ (NHM).

Diagnosis. This species is characterized by the presence of two additional cuticular depressions in the frons near the clypeus. L1 sclerite with lateral branch slightly curved forward, with the aspect of a big sharp tooth, and with spines in the ventral region near the crown of spines; a pointy medial region with a projection in the right side turned forward. R2 sclerite cleft very sclerotized, rounded at the side of N sclerite. N sclerite tiny in the dorsal region, and large and globular in the ventral one. R3d slightly curved dorsally and wider and straight in ventral view. R3v sclerite with a wide and rounded latero-distal region and a short and slightly narrow caudal branch.

Redescription. Male. Head subtriangular, with interocular space measuring approximately 1/5 of the distance between the antennal sockets. Ocelli developed and slightly deflected. Frontal suture with a cuticular invagination. Two additional cuticular depressions in the frons near the clypeus (Fig. 5C). Pronotum transverse, pentagonal, dorsal surface rough with striae, fore margin rounded, lateral margins with sharp angles and round ends, hind margin nearly

straight (Fig. 5B). Legs short and robust. Fore-femora ventro-anterior margins with 16 spines of the same size; ventro-posterior margins with 3 spines. Middle-legs ventro-anterior margins with 3 or 4 spines. Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed with a strong invagination in the median portion. Subgenital plate asymmetrical with long styles, funneled in the apical region.

L1 sclerite with apical region with two distinct parts: a lateral branch slightly curved forward, with the aspect of a big sharp tooth, and with spines in the ventral region near the crown of spines at the posterior region; another region with a pointy medial protuberance and a projection turned forward in the right side (Fig. 5G, H). L2d sclerite hook with a subconical and slightly narrow anterior region, a short apical region, and a wide space connecting them. Apex internal cavity concave, short lateral-external margin and with a typical sub-apical notch (Fig. 5F, I). R2 sclerite cleft very sclerotized, curved inward with the apex directed upward. Region at the side of sclerite N rounded (Fig. 5D). Sclerite N tiny in the dorsal region, and large and globular in the ventral one. R3d slightly curved dorsally and wider and straight in ventral view. R3v sclerite with a wide and rounded latero-distal region and a short and slightly narrow caudal branch (Fig. 5D, E).

Female. Head rounded, with wide interocular space measuring $1/2$ the distance between the antennal sockets. Eyes with straight interocular margin. Ocelli developed and deflected. Front broad and frontal suture with a cuticular invagination (Fig. 6D). Pronotum subtriangular with anterior region rounded and slightly concave near the margins, dorsal region rough with striae, lateral angles rounded ending in a corner, hind margin slightly curved in the median region (Fig. 6B). Tegmina with anterior margin slightly triangular; hind margin truncated with a marked curvature inside; very short and not extending further than the second abdominal tergite (Fig. 6A). Legs short and robust. Fore femora ventro-anterior margins with 13 spines of the same size, ventro-posterior margin with 4 spines. Middle legs ventro-anterior margins with 4 spines. Supra-anal plate bilobed with a small median incision, each lobe with a slightly rounded lateral margin and a straight posterior margin (Fig. 6C). Tergites with slightly rounded lateral angles (Fig. 6A).

Measurements (mm). ♂: Body length 51.70; pronotum length 12.36×17.35 maximum width; tegmen length 42.55×15.90 width; interocular width 1.0; interantennal width between sockets 5.5

♀: Body length 38.50 ; pronotum length 11.20 × 17.55 maximum width ; tegmen length 10.00 × 11.25 width; interocular width 2.3; interantennal width between sockets 5.0.

Coloration. ♂: General coloration brown (Fig. 5A). Pronotum dark brown with a anterior margin buff brown; central disk pale brown with scattered black marks (Fig. 5B). Head dark brown-black; clypeus and labrum amber. Antennae with basal segments brown pigmented and apical segments pale brown. Ocelli pale brown (Fig. 5C). Legs and spines dark brown; tarsal claws, pulvilli and arolia amber. Tegmina and abdomen following general coloration of body but with dark brown tergite and sternites hind margins (Fig. 5A).

Distribution. Brazil (Rio de Janeiro, Espirito Santo). See Fig. 17 for details.

Monastria similis (Serville, 1838)

Male – Figure 8.

Female – Figure 6E–H.

Blabera similis Serville, 1839: 81.

Monastria similis Saussure, 1864a: 256; Walker, 1868: 11; Scudder, 1868: 54; Kirby, 1904: 161; Princis, 1958: 75, Princis, 1963: 142.

Monachoda similis Brunner v. W, 1865: 367; Finot, 1897: 207.

Monastria flavomarginata Princis, 1946: 162, Princis, 1963: 142 (as syn. of *M. similis*).

Examined material. Brazil – Paraná: 1♀ Aurora do Iguaçu, “Fazenda Dona Iolanda”, 260m, 25°23’047”S, 54°07’048”W, 20km NE São Miguel do Iguaçu, Fragment=60ha, Forêt semp. Humide, 18 XI 2008, Jour, coll. R. Pellens & P. Grandcolas (MNHN). 2♂, 1♀ Foz do Iguaçu, “Fazenda John Keller”, 220 m, 25°34’9.14”S, 54°26’7.41”W, 1km Parc National do Iguaçu, Forêt semp. humide, 20 XI 2008, R. Pellens & P. Grandcolas rec. (MNHN). Santa Catarina: 1♂ Blumenau, VI 1919, coll. Luderm? (MZUSP). 3♂, 2♀ Campo Alegre, “Ilha, Fazenda Sr. Egon”, 830m, 26°10’29”S, 49°16’22”W, 1km Campo Alegre, 14 VIII 2007, Forêt d’*Araucaria*, R. Pellens & P. Grandcolas rec. (MNHN). 1♀ Campo Alegre, “Fazenda Sr. Gilson”, 853m, 26°12’6.61”S, 49°18’4.58”W, 5km W Campo Alegre, Forêt d’*Araucaria*, 15 VIII 2007, R. Pellens & P. Grandcolas rec. (MNHN). 1♀ Florianopolis, “Chemin Mirante. route Lagoa da Conceição”, 295m, 27°35’5.05”S, 48°28’6.08”W, Forêt semp. humide, 01 XII 2008, R. Pellens & P. Grandcolas rec. (MNHN). 2♀ Joinville, “Alto da Serra Dona

Francisca”, 755m, 26°11’882” S, 49°03’144” W, 35km NW Joinville, Forêt semp. humide, III 2007, R. Pellens & P. Grandcolas rec. (MNHN). 1♂ 4♀ Lages, Brunner d. w. (MHNG). 1♂ 1♀ Rio Capivary, 1888, H. Fruhstorfer (MHNG). Rio Grande do Sul: 2♂ Lhering, (MHNG). São Paulo: 1♂ Poa, 13 IV 1963, Rabello col. (MZUSP). 1♂ Salesópolis, “Estação biológica de Boracéia, Trilha do poço verde”, 23°38’56.9”S, 45°52’50”W, Malaise, pt1, 17-28 IV 2003, coll. A.P. Aguiar & F.M. Rodrigues (MZUSP). 1♂ Salesópolis, “Est. biológica de Boracéia”, 850m, (MZUSP). **Paraguay**: 1♀ Asunción, sept.1922–apl.1923, E.G.Kent, B.M. 1925 – 262 (NHM). 1♂, Carlos Pfanni (MHNG) **Without locality**: 1♂ Brésilien, H. Fruhstorfer, 1903 – 321(NHM). 2♀ (NHM). 1♂ (America Meridionale/Colombie?), D. Ruhl (MHNG). 1♂ coll. Pantel, co-type (MNHN).

Diagnosis. This species is characterized by having male L1 sclerite with short, rounded lateral branch turned downwards, with strong spines near the crown of spines of the posterior region; a wide region slightly concave with a slight curvature ending in a small projection towards the front on the right. L2d sclerite hook with internal cavity strongly concave, external lateral margin very near the very narrow sub-apical notch. R2 sclerite cleft with lateral at the side of R3 shorter and forming a straight angle. R3 sclerite reduced in the dorsal region and a wide and globular ventral surface. R3v small, triangular, with a short and slightly quadrangular latero-distal region; caudal branch short with a finger shaped apex.

Redescription. Male. Head subtriangular, with interocular space measuring nearly 1/3 of the distance between the antennal sockets. Ocelli developed and slightly deflected. Frontal suture with a slight cuticular invagination (Fig. 8C). Pronotum transverse, pentagonal, dorsal surface rough with deep striae, anterior margin rounded, lateral margins with sharp angles and round ends, hind margin nearly straight (Fig. 8B). Tegmina with orange lateral margins in the first half of its length (Fig. 8A). Legs short and robust. Fore-femora ventro-anterior margins with 21 or 22 spines decreasing in size from basal to apical; ventro-posterior margins with 3 long and 2 slightly smaller spines. Middle legs ventro-anterior margins with 10 spines. Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed with a invagination in the median portion. Subgenital plate asymmetrical with long styles, funneled in the apical region. L1 sclerite with apical region with two distinct parts: a short, rounded lateral branch turned downwards, with strong spines near the crown of spines of the posterior region; a wide region slightly concave with a slight curvature ending in a small projection towards the front on the right (Fig. 8H, I). L2d sclerite hook with anterior

region subconical and slightly wide and a short apical region; internal cavity strongly concave, external lateral margin very near the very narrow sub-apical notch (Fig. 8F, G). R2 sclerite cleft curved inwards with the apex very sclerotized and directed upwards, lateral region at the side of N shorter and forming a straight angle (Fig. 8D). Sclerite N dorsal region reduced, ventral surface wide and globular. R3d slightly curved dorsally and wider and straight in ventral view. R3v small, triangular, with a short and slightly quadrangular latero-distal region; caudal branch short with a finger shaped apex (Fig. 8D, E).

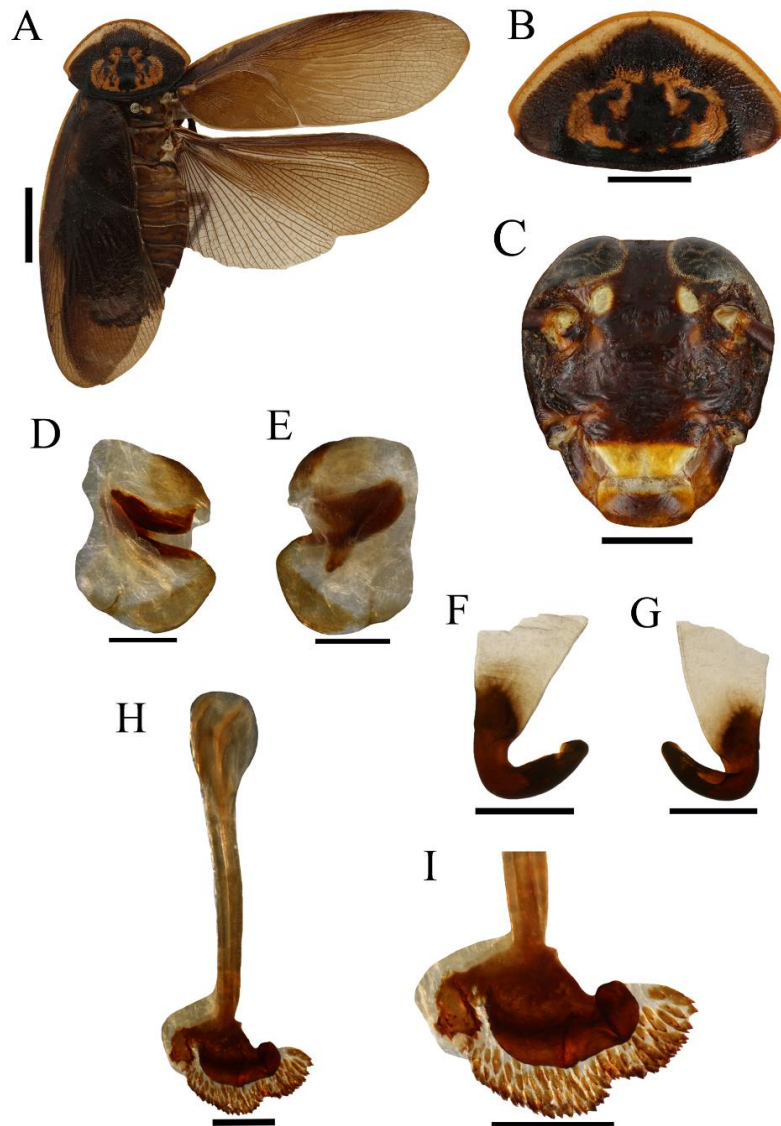


Figure 8. *Monastria similis*, ♂: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Head, ventral view; **D)** Right phallomere, dorsal view; **E)** Right phallomere, ventral view; **F)** Left phallomere (L2d), ventral view; **G)** Left phallomere (L2d), dorsal view; **H)** Median sclerite (L1), dorsal view; **I)** Median sclerite (L1), detail (see Fig. 5 for abbreviations). Scales: Habitus=1 cm, Pronotum=5 mm, Head=2 mm, all other figures=1 mm.

Female. Head rounded, with wide interocular space measuring 1/2 of the distance between the antennal sockets. Eyes with straight interocular margin. Ocelli small and located on the area slightly deflected above the antennal socket. Frons broad and flattened, frontal suture with a small cuticular depression. Clypeus distal half larger and yellow transparent (Fig. 6H). Pronotum subtriangular with anterior region rounded and slightly concave near the margins, dorsal region rough with deep striae, lateral angles rounded ending in a corner, hind margin slightly curved in the median region (Fig. 6F).

Tegmina with a rounded anterior margin, orange lateral margin, and rounded and curved hind margin. Long, reaching the fifth abdominal tergite (Fig. 6E). Legs short and robust. Fore-femora ventro-anterior margins with 21 or 19 long spines of the same size, ventro-posterior margins with 5 spines. Middle legs ventro-anterior margins with 5 spines. Supra-anal plate bilobed with a small median notch, each lobe with a slightly rounded lateral and a straight hind margin (Fig. 6G). Tergites with rounded lateral angles (Fig. 6E).

Measurements (mm). ♂: Body length 49.35; pronotum length 10.95 × 16.80 maximum width; tegmen length 39.75 × 15.45 width; interocular width 1.6; interantennal width between sockets 4.6.

♀: Body length 36.65; pronotum length 11.35 × 16.90 maximum width; tegmen length 16.50 × 11.00 width; interocular width 2.6; interantennal width between sockets 5.6.

Coloration. ♂: General coloration brown (Fig. 8A). Pronotum dark brown with anterior margin buff brown; central disk orange with large dark brown mark (Fig. 8B). Head dark burnt umber; clypeus amber and labrum orange. Antennae with basal segments brown pigmented and apical segments pale brown. Ocelli white (Fig. 8C). Legs brown and spines with brown base and dark brown apex; pulvilli yellowish white; tarsal claws and arolia amber. Tegmina with orange lateral margins (Fig. 8A). Abdomen following general coloration of body but with brown tergites and sternites hind margins.

Distribution. Brazil (São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Paraguay (Asunción). See Fig. 17 for details.

***Monastria angulata* Saussure, 1864**

Figure 9A–D.

Monastria angulata Saussure, 1864a: 257; Walker, 1868: 11; Kirby, 1904: 161; Princis, 1963: 142.

Monachoda Finot, 1897: 207.

Examined material. Syntype ♀. Brazil, Bahia. (MHNG)

Diagnosis. Pronotum triangular, with rounded anterior region slightly concave near the margins, inconspicuous dorsal roughness and striae. Lateral angles pointy, without corners, hind margin slightly curved in the median region. Tegmina anterior angle nearly square, hind margin truncated with a marked curvature towards the medial margin. CuP vein ending at the half of the hind margin. Supra-anal plate bilobed, lateral margins of each lobe very rounded.

Redescription. Female. Head subtriangular, with wide interocular space measuring 1/2 of the distance between the antennal sockets. Eyes with straight interocular margin. Ocelli developed and deflected. Front broad and frontal suture with a small cuticular invagination (Fig. 9D). Pronotum triangular, with anterior region rounded and slightly concave near the margins; dorsal roughness and striae inconspicuous. Lateral angles pointy, without corners, hind margin slightly curved in the median region (Fig. 9B). Tegmina very short and not extending further than the second abdominal tergite; anterior angle nearly square, hind margin truncated with a marked curvature towards the medial region. CuP vein ending at the half of the hind margin (Fig. 9A). Legs short and robust. Fore-femora ventro-anterior margins with 16 or 17 spines of the same size, ventro-posterior margins with 4 spines. Middle legs ventro-anterior margins with 4 spines. Supra-anal plate bilobed with a small median notch, each lobe with a very rounded lateral margin and a slightly straight hind margin (Fig. 9C). Tergites with quadrangular lateral angles (Fig. 9A).

Male. Unknown

Measurements (mm). Syntype ♀: Body length 30.70; pronotum length 10.00 × 17.57 maximum width ; tegmen length 9.80 × 12.20 width; interocular width 2.6; interantennal width between sockets 5.6.

Coloration. Syntype ♀: General coloration burnt umber (Fig. 9A). Pronotum burnt umber with a anterior margin ochre; central disk yellowish brown with scattered dark brown marks (Fig. 9B). Head burnt umber and clypeus and labrum dark brown (Fig. 9D). Antennae with segments yellowish brown. Ocelli ochre. Legs and spines dark brown; tarsal claws, pulvilli and arolia yellowish brown. Tegmina with anal field burnt umber and marginal field brown; abdomen following general coloration of body but with tergites and sternites hind margins dark brown (Fig. 9A). Supra-anal plate burnt umber (Fig. 9C).

Distribution. Brazil (Bahia).

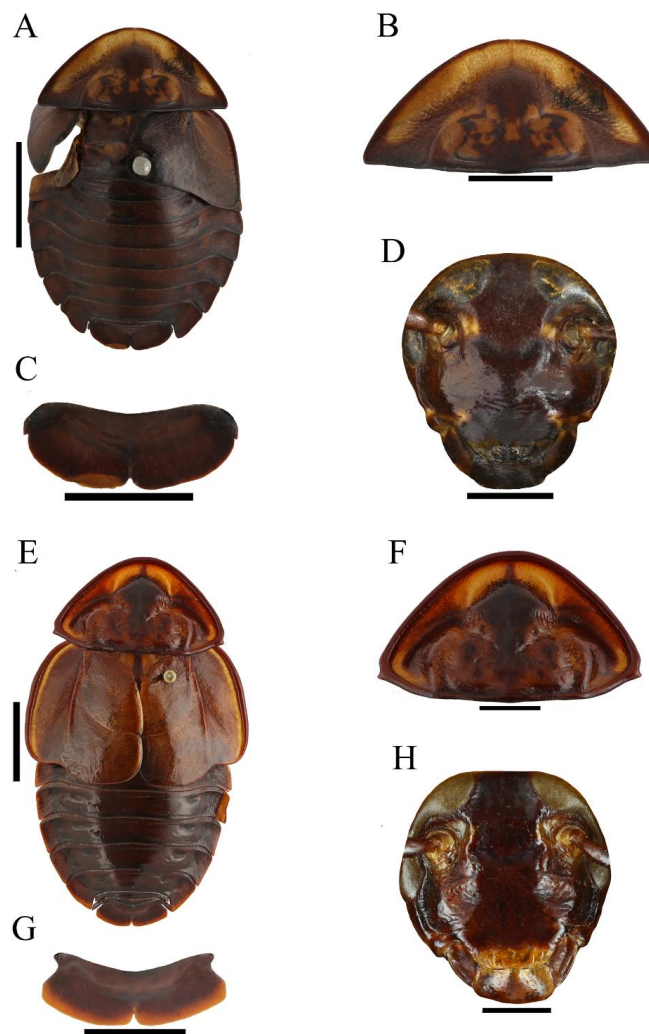


Figure 9. Figs. **A-D**, *Monastria angulata*, Syntype ♀: **A**) Habitus, dorsal view; **B**) Pronotum, dorsal view; **C**) Supra-anal plate, dorsal view; **D**) Head, ventral view. Figs. **E-H**, *Monastria cabocla* sp. n. Paratype ♀: **E**) Habitus, dorsal view; **F**) Pronotum, dorsal view; **G**) Supra-anal plate, dorsal view; **H**) Head, ventral view. Scales: Habitus=1cm, Pronotum=5mm, Supra-anal plate=5mm, Head=2 mm.

***Monastria cabocla* Tarli, Grandcolas & Pellens sp. n.**

Male – Figure 10.

Female – Figure 9E–H.

Type material. Holotype ♂ Brazil, Sergipe, Santo Amaro das Brotas, “Gravata” 13 I 1979 (MZUSP). Paratypes: 1♂, 3♀, same data as holotype (MZUSP). 1♀ Sergipe, Santo Amaro das Brotas, “871” (MNRJ).

Diagnosis. This species is characterized by having frons depressed below the antennal sockets and prominent above the ocelli. Ocelli positioned laterally. Pronotum dorsal surface slightly rough and striated, with two quite evident lobes with plain surface, and a wider central lobe covering the head. Short lateral margins with sharp angle and a conspicuous small spine. Legs longer and less robust. L1 sclerite with a lateral branch little sclerotized slightly curved downwards, smooth and with only a small spine and a region with a big lateral dilatation and an edge in the median region ending in a projection turned forward. Crown with a smaller number of sclerotized spines in the posterior region. L2d sclerite, hook with subconical and very wide anterior region. Sclerite N triangular on the dorsal region. R3d with a slight depression in the dorsal median region, straight.

Description. Male. Head subtriangular, with interocular space measuring 1/4 of the distance between the antennal sockets. Frons with a depression below the antennal sockets and prominent above the ocelli. Frontal suture localized in a deep cuticular invagination, ocelli developed and positioned laterally (Fig. 10C). Pronotum transverse, pentagonal, dorsal surface slightly rough and striated, with two quite evident lobes with plain surface and a wider central lobe covering the head, anterior margin rounded, short lateral margins with sharp angle and a conspicuous small spine, hind margin nearly straight (Fig. 10B). Legs longer than in other species and less robust. Fore-femora ventro-anterior margins with 24 or 22 spines slightly decreasing in size from basal to apical; ventro-posterior margins with 5 spines. Middle legs ventro-anterior margins with 5 spines. Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed, lobes very narrow and with a strong invagination in the median portion. Subgenital plate asymmetrical with long styles, funneled in the apical region. L1 sclerite apical region with two distinct parts: a lateral branch little sclerotized slightly curved downwards, smooth and with only a small spine, and a

region with a big lateral dilatation and an edge in the median region ending in a projection turned forward. Crown with a smaller number of sclerotized spines in the posterior region (Fig. 10G, H). L2d sclerite hook with subconical and very wide anterior region, a median apical region, and a narrow space connecting them. Apex internal cavity concave with short lateral external margin and narrow subapical notch (Fig. 10F, I). R2 sclerite cleft sclerotized, curved inward with a conic opening at its base and an apex directed upwards. Sclerite N triangular on the dorsal region and with a small surface in the ventral one (Fig. 10D). R3d with a slight depression in the dorsal median region, straight and narrow in ventral view. R3v sclerite with a long, rectangular and slightly wide latero-distal region, and quadrangular caudal branch very near R3d (Fig. 10D, E).



Figure 10. *Monastria cabocla* sp. n., Holotype ♂: **A**) Habitus, dorsal view; **B**) Pronotum, dorsal view; **C**) Head, ventral view; **D**) Right phallomere, dorsal view; **E**) Right phallomere, ventral view; **F**) Left phallomere (L2d), ventral view; **G**) Median sclerite (L1), dorsal view; **H**) Median sclerite (L1), detail; **I**) Left phallomere (L2d), dorsal view (see Fig. 5 for abbreviations). Scales: Habitus=1cm, Pronotum=5mm, Head=2 mm, all other figures=1 mm.

Female (Paratype). Head rounded, with wide interocular space measuring 1/2 of the distance between the antennal sockets. Eyes with curved interocular margin. Ocelli developed and deflected. Frons broad, frontal suture with a large cuticular invagination (Fig. 9H). Pronotum subtriangular, dorsal surface slightly rough and striated, with two quite evident lobes with plain surface, and a wider central lobe covering the head; anterior margin rounded, lateral margins short with sharp angle and a conspicuous small spine, hind margin nearly straight (Fig. 9F). Tegmina latero-anterior angle nearly straight; lateral margin wider, and hind margin with a strong curvature near the radial vein; extends further than the third abdominal tergite. CuP vein very marked (Fig. 9E). Legs short and robust. Fore-femora ventro-anterior margins with 19 small spines of the same size, ventro-posterior margins with 4 spines. Middle legs ventro-anterior margins with 9 spines. Supra-anal plate bilobed with a median incision, and each lobe with straight posterolateral angles (Fig. 9G).

Measurements (mm). Holotype ♂: Body length 42.95; pronotum length 9.85 × 15.70 maximum width; tegmen length 35.25 × 13.45 width; interocular width 0.9; interantennal width between sockets 3.6.

Paratype ♀: Body length 41.60 ; pronotum length 13.20 × 20.15 maximum width ; tegmen length 16.05 × 14.50 width; interocular width 2.9; interantennal width between sockets 6.0.

Coloration. Holotype ♂: General coloration sienna brown (Fig. 10A). Pronotum sienna brown with a brown anterior margin; central disk seal brown with scattered dark marks (Fig. 10B). Head reddish brown; clypeus and labrum amber. Antennae with basal segments dark brown pigmented and apical segments brown. Ocelli pale brown (Fig. 10C). Legs and spines dark brown; tarsal claws, pulvilli and arolia whitish brown. Tegmina sienna brown with marginal and scapular field with a buff brown part (Fig. 10A). Abdomen following general coloration of body.

Etymology. A term from the Tupi meaning taken out of the forest. Here it refers to the habitat and the color patterns of this species.

Distribution. Brazil (Sergipe). See Fig. 17 for details.

***Monastria itubera* Tarli, Grandcolas & Pellens sp. n.**

Male – Figure 11.

Female – Figure 12A–D.

Type material. Holotype ♂. Brazil, Bahia, Itubera, “Reserva ecologica Michelin”, 92-383m, 13°48'4.62''S, 39°10'23.2''W. 100km N Itabuna, Forêt semi-décidue, 28 VIII 2007, R. Pellens & P. Grandcolas rec. (MZUSP). Paratype: 1 ♂, 2 ♀, same data as holotype (MNHN)

Diagnosis. This species is characterized by having triangular head. L1 sclerite lateral branch slightly curved with some spines turned downwards and a slightly concave region with irregular distal margins with grooves ending in a long projection toward the front; L2d sclerite hook with subconical slightly narrow anterior region, short apical region, and a large space connecting them. Apex internal cavity concave with small lateral external margin and narrow subapical notch with pointy margin; R2 sclerite cleft curved inward with a conic opening at its base and with a sclerotized apex directed upwards. Sclerite N wider and near of R2 on the dorsal region, narrow and small in ventral surface. R3d narrow in the proximity of R2 and wider and rectangular in the distal region when in ventral view. R3v sclerite small, subtriangular, with rounded latero-distal end.

Description. Male. Head triangular, with narrow interocular space measuring approximately 1/6 of the distance between the antennal sockets. Ocelli developed and slightly deflected; frontal suture with a strong cuticular invagination (Fig. 11C). Pronotum transverse, pentagonal, dorsal surface rough with deep striae; anterior margin rounded; lateral margins with sharp angles, round ends and a conspicuous small protuberance; hind margin nearly straight (Fig. 11B). Legs short and robust. Fore-femora ventro-anterior margins with 20 or 18 spines of the same size; ventro-posterior margins with 4 small spines. Middle-legs ventro-anterior margins with 5 or 4 large spines. Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed with a slight invagination in the median portion. Subgenital plate asymmetrical with long styli, left funneled in the apical region, right with same caliper all long. L1 sclerite apical region with two distinct parts, a lateral branch slightly curved with some spines turned downwards and a slightly concave region with irregular distal margins with grooves ending in a long projection toward the front. Crown with a smaller number of robust spines in the posterior region (Fig. 11H, I). L2d sclerite, hook with subconical slightly narrow anterior region and short apical region, with a

large space connecting them. Apex internal cavity concave with small lateral external margin and narrow subapical notch with pointy margin (Fig. 11F, G). R2 sclerite cleft curved inward with a conic opening at its base and with a sclerotized apex directed upwards (Fig. 11D). Sclerite N wider and near of R2 on the dorsal region, and a narrow and small ventral surface. R3d narrow in the proximity of R2, and wider and rectangular in the distal region when in ventral view. R3v sclerite small, subtriangular, with rounded latero-distal end (Fig. 11D, E).

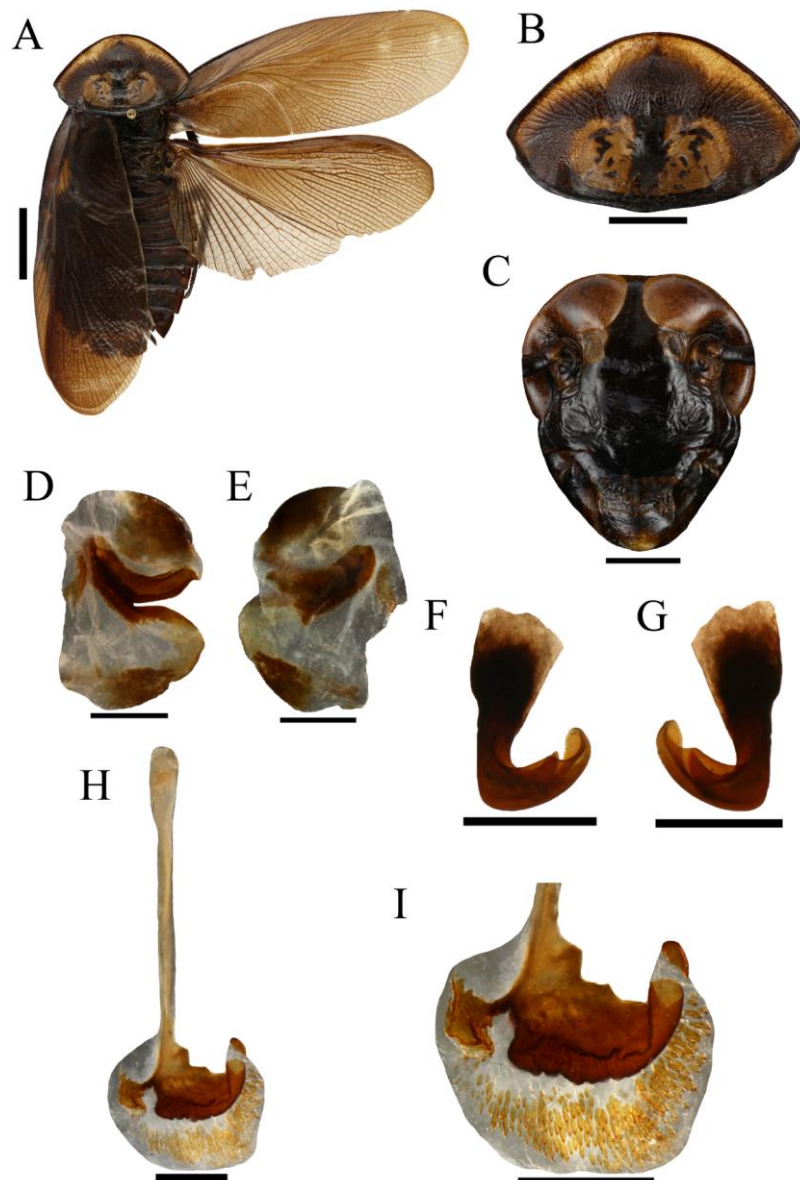


Figure 11. *Monastria itubera* sp. n., Holotype ♂: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Head, ventral view; **D)** Right phallomere, dorsal view; **E)** Right phallomere, ventral view; **F)** Left phallomere (L2d), ventral view; **G)** Left phallomere (L2d), dorsal view; **H)** Median sclerite (L1), dorsal view; **I)** Median sclerite (L1), detail (see Fig. 5 for abbreviations). Scales: Habitus=1cm, Pronotum=5mm, Head=2 mm, all other figures=1 mm.

Female (Paratype). Head rounded, with interocular space measuring approximately 1/3 of the distance between the antennal sockets. Eyes reniform with rounded interocular margin. Ocelli developed and deflected. Concavity between eyes and ocelli reaching the frontal suture. Frons with a prominence (Fig. 12D). Pronotum subtriangular, anterior region rounded with a depression near the margins; dorsal surface rough with deep striae, presence of small spine at the end of lateral region, hind margin nearly straight (Fig. 12B). Tegmina with rounded lateral anterior angle, hind margin truncated with a slight curvature in the region of radial vein and merging to the CuP vein at the end, not extending further than the second abdominal tergite (Fig. 12A). Legs short and robust. Fore-femora ventro-anterior margins with 21 or 20 spines of the same size, ventro-posterior margins with 4 spines. Middle-legs ventro-anterior margin with 8 spines, plus one near the apex. Supra-anal plate bilobed with a median incision and each lobe slightly rounded (Fig. 12C).

Measurements (mm). Holotype ♂: Body length 40.98; pronotum length 15.41×9.49 maximum width; tegmen length 31.22×11.23 width; interocular width 0.8; interantennal width between sockets 5.1.

Paratype ♀: Body length 35.79; pronotum length 9.70 × 17.05 maximum width; tegmen length 8.90 × 11.15 width; interocular width 1.5; interantennal width between sockets 4.5.

Coloration. Holotype ♂: General coloration brown (Fig. 11A). Pronotum brown with the anterior margin pale brown; central disk pale brown with scattered black marks (Fig. 11 B). Head dark brown/black; clypeus and labrum brown. Antennae with basal segments dark pigmented and apical segments whitish yellow. Ocelli light brown (Fig. 11C). Legs dark brown. Spines and tarsal claws brown, pulvilli and arolia pale brown. Tegmina and abdomen following general coloration of body but with tergites and sternites dark hind margins (Fig. 11A).

Etymology. The specific name refers to the type locality Itubera, state of Bahia, northeast Brazil

Distribution. Brazil (Bahia). See Fig. 17 for details.

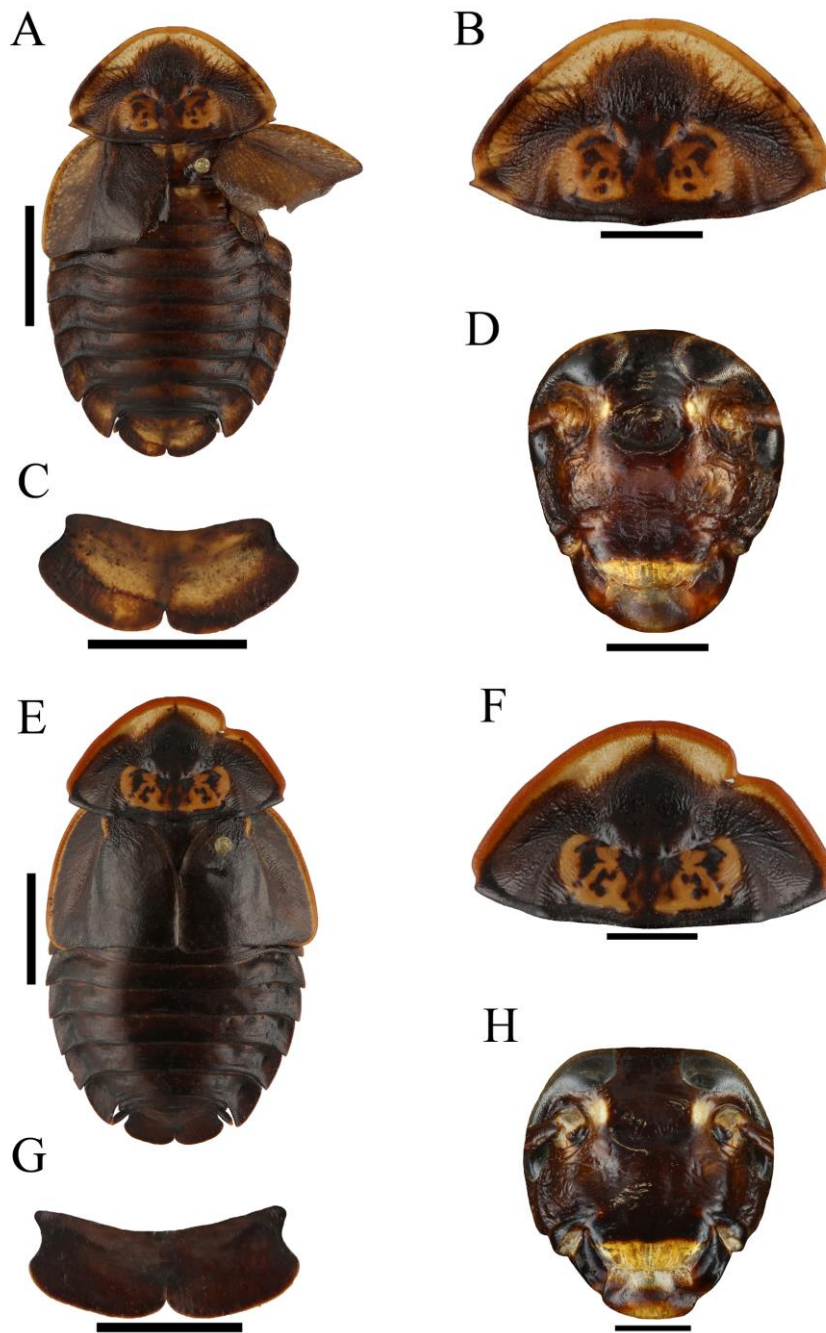


Figure 12. Figs. **A-D**, *Monastria itubera* sp. n., Paratype ♀: **A**) Habitus, dorsal view; **B**) Pronotum, dorsal view; **C**) Supra-anal plate, dorsal view; **D**) Head, ventral view. Figs. **E-H**, *Monastria itabuna* sp. n., Paratype ♀: **E**) Habitus, dorsal view; **F**) Pronotum, dorsal view; **G**) Supra-anal plate, dorsal view; **H**) Head, ventral view. Scales: Habitus=1cm, Pronotum=5mm, Supra-anal plate=5mm, Head=2 mm.

***Monastria itabuna* Tarli, Grandcolas & Pellens sp. n.**

Male – Figure 13.

Female – Figure 12E–H.

Type material. Holotype ♂, Brazil, Bahia, Itabuna. CEPLAC, Matinha. 14°46'20''S, 39°13'18''W. Elevation 46m, 11 V 2007, J. A. Rafael & F. F. Xavier F°, manual tronco (INPA). Paratype: 1 ♂, 1 ♀, same data as holotype. (INPA)

Diagnosis. This species is characterized by having L1 sclerite with apical region having a lateral branch slightly curved with some spines continuing until the crown in the posterior region. L2d sclerite, hook with short apical region, internal margin concave, lateral external margin strongly curved, with large sub-apical notch. R2 sclerite cleft curved inward with the apex directed forward. Sclerite N smaller in the dorsal region and with a large rough ventral surface. R3d narrow near R2 in dorsal view and wider, rectangular in the distal region when in ventral view. R3v sclerite large, subtriangular, with quadrangular and truncated latero-distal end. Caudal branch long, wide in the center and narrow in the apex very near R3d.

Description. Male. Head subtriangular, with narrow interocular space measuring approximately 1/6 of the distance between the antennal sockets. Ocelli developed and slightly deflected; frontal suture with a strong cuticular invagination. Clypeus distal half narrower transversally and orange brown (Fig. 13C). Pronotum transverse, pentagonal, dorsal surface rough with striae; anterior margin rounded; lateral margins slightly wider with sharp angles, round ends and a conspicuous small protuberance; hind margin nearly straight (Fig. 13B). Legs short and robust. Fore-femora ventro-anterior margins with 20 or 18 spines of the same size; ventro-posterior margins with 4 small spines. Middle-legs ventro-anterior margins with 5 or 4 large spines. Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed with a slight invagination in the median portion. Subgenital plate asymmetrical with long styles, left funneled in the apical region, right with same caliper all long. L1 sclerite with apical region with two distinct parts, a lateral branch slightly curved with some spines continuing until the crown of spines in the posterior region (Fig. 13G, H). L2d sclerite, hook with short apical region, internal margin concave, lateral external margin strongly curved, with large sub-apical notch (Fig. 13F, I). R2 sclerite cleft curved inward with the apex directed forward (Fig. 13D). Sclerite N smaller in the dorsal region and with a large rough ventral surface. R3d narrow near R2 in dorsal view and wider,

rectangular in the distal region when in ventral view (Fig. 13D, E). R3v sclerite large, subtriangular, with quadrangular and truncated latero-distal end. Caudal branch long, wide in the center and narrow in the apex very near R3d (Fig. 13E).

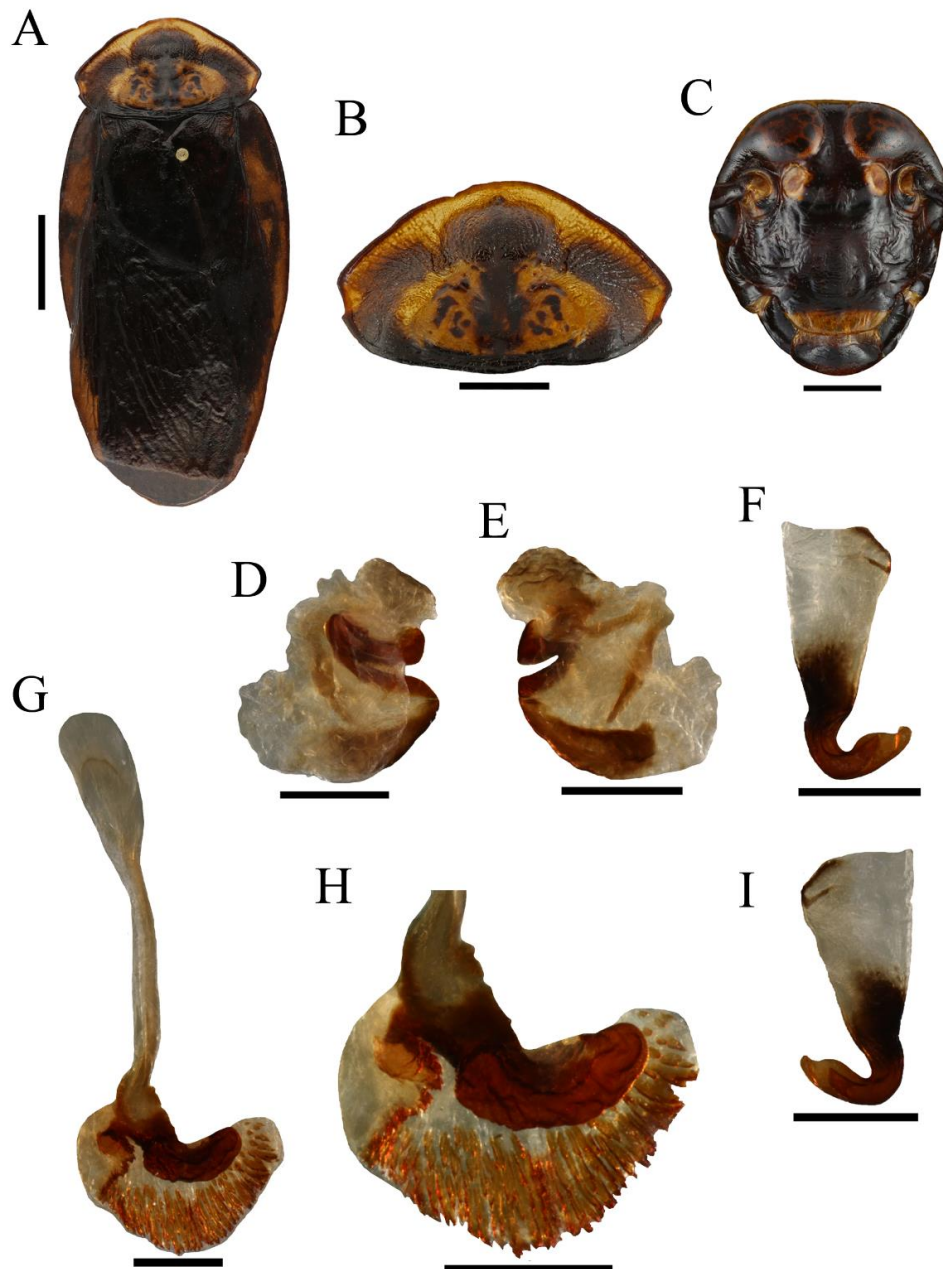


Figure 13. *Monastria itabuna* sp. n., Holotype ♂: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Head, ventral view; **D)** Right phallomere, dorsal view; **E)** Right phallomere, ventral view; **F)** Left phallomere (L2d), ventral view; **G)** Median sclerite (L1), dorsal view; **H)** Median sclerite (L1), detail; **I)** Left phallomere (L2d), dorsal view (see Fig. 5 for abbreviations). Scales: Habitus=1cm, Pronotum=5mm, Head=2 mm, all other figures=1 mm.

Female (Paratype). Head rounded, with wide interocular space measuring 1/2 the distance between the antennal sockets. Eyes with straight interocular margin. Ocelli developed and deflected. Frons broad, frontal suture with a cuticular invagination (Fig. 12H). Pronotum subtriangular, fore region rounded and slightly concave near the margins, dorsal region rough with deep striae, lateral margins rounded ending in a small corner, hind margin slightly curved in the median region (Fig. 12F). Tegmina with straight lateral anterior angle, hind margin truncated with a slight curvature in the region of radial vein; not extending further than the second abdominal tergite and lateral margin orange all along its extension (Fig. 12E). Legs short and robust. Fore-femora ventro-anterior margins with 19 small spines of the same size; ventro-posterior margins with 4 spines. Middle-legs ventro-anterior margins with 9 spines. Supra-anal plate bilobed with a median incision and each lobe slightly rounded (Fig. 12G). Tergite with slightly rounded lateral angles (Fig. 12E).

Measurements (mm). Holotype ♂: Body length 53.05; pronotum length 12.70 × 19.37 maximum width; tegmen length 40.40 x 15.55 width ; interocular width 0.9; interantennal width between sockets 5.4 .

Paratype ♀: Body length 40.70; pronotum length 11.25 × 19.80 maximum width ; tegmen length 12.30 x 13.00 width; interocular width - 3.0; interantennal width between sockets 5.7.

Coloration. Holotype ♂: General coloration dark brown (Fig. 13A). Pronotum dark brown with the anterior margin yellowish brown; central disk yellowish brown with scattered black marks (Fig. 13B). Head dark brown; clypeus and labrum yellowish brown. Antennae with basal segments dark pigmented and apical segments whitish yellow. Ocelli yellowish/pale brown (Fig. 13C). Legs and spines brown; tarsal claws, pulvilli and arolia yellowish brown. Tegmina and abdomen following general coloration of body but with tergites and sternites with brown posterior margin (Fig. 13A).

Etymology. The specific name refers to the type locality Itabuna, state of Bahia, northeast Brazil.

Distribution. Brazil (Bahia). See Fig. 17 for details.

***Monastria kaingangue* Tarli, Grandcolas & Pellens sp. n.**

Male – Figure 14.

Female – Figure 15.

Type material. Holotype ♂ . Brazil, São Paulo, Campinas. “Pico das Cabras”. 22°54'23.9"S 46°49'34.4"W. 14 october 2014, coll. V. M. Ghirotto (MZUSP). Paratype: 1♀ , same data as holotype (MZUSP).

Examined material. Brazil – Santa Catarina: 1♂, Urubici, “Parque Nacional de São Joaquim, Vacas Gordas”, 977m, 28°08'44.4"S, 49°37'09.3"W, 22 X 2015, coll. R. Pellens (MNHN). 2♂, 1♀, São Bonifacio, Santo Amaro da Imperatriz, -27.830854 -48.964832, 09 X 2014, P. Grandcolas & Vitor D. Tarli rec. (MNHN). São Paulo: 1♂ Bocaina, IV 1924, Luderm? “27” (MZUSP). 1♂ Bocaina, IV 1924, “29” (MZUSP). Rio Grande do Sul: 1♂, 2♀, Derrubadas, Parque Estadual do Turvo, 391m, -27.236413 -53.979640, 05 X 2014, R. Pellens & Vitor D. Tarli rec. (MNHN).

Diagnosis. This species is characterized by having two intercalated rows of spines in the ventro-anterior margins of fore-femora; one row with 5 or 6 spines, and another with 32 or 33 spines of the same size. L1 sclerite with lateral branch curved, rounded and smooth with some small spines, and a curved region with grooves in its interior and a projection with a rounded end directed upwards at its left side. L2d sclerite hook with long apical region, and rounded curvature of the margin near the notch. R2 sclerite cleft curved inward with a wide and sclerotized apex directed forward. R3d with a clear prominence like a tooth in ventral view. R3v sclerite with quadrangular and truncated latero-distal region, and caudal branch near the tooth from R3d sclerite.

Description. Male. Head subtriangular, interocular space approximately 1/3 distance between antennae. Frons slightly elevated. Ocelli developed and deflected. Frontal suture with a cuticular invagination (Fig. 14C). Pronotum pentagonal, fore margin rounded, with rounded lateral angles, hind margin slightly curved in the medial portion (Fig. 14B). Legs short and robust. Fore-femora ventro-anterior margins with two intercalated rows of spines, one with 6 or 5, and another with 33 or 32 spines of the same size; ventro-posterior margins with one large and a thin spine out of the row, 6 small spines. Middle legs ventro-anterior margins with 11 or 10 spines. Tegmina with orange lateral margins in the first half of its length (Fig. 14A).

Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed with a slight invagination in the median portion. Subgenital plate asymmetrical with long styles, left funneled in the apical region, right with same caliper all long. L1 sclerite with apical region with two distinct parts: a lateral branch curved, rounded and smooth with some small spines, and a curved region with grooves in its interior and a projection with a rounded end directed upwards at its left side (Fig. 14G, H). L2d sclerite hook with long apical region and rounded curvature of the margin near the notch (Fig. 14F, I). R2 sclerite cleft curved inward with a wide and very sclerotized apex directed forward (Fig. 14D). Sclerite N tiny in dorsal and large and wide in ventral view. R3d with a clear prominence like a tooth in ventral view (Fig. 14D, E). R3v sclerite with quadrangular and truncated latero-distal region, and caudal branch near the tooth from R3d sclerite (Fig. 14E).

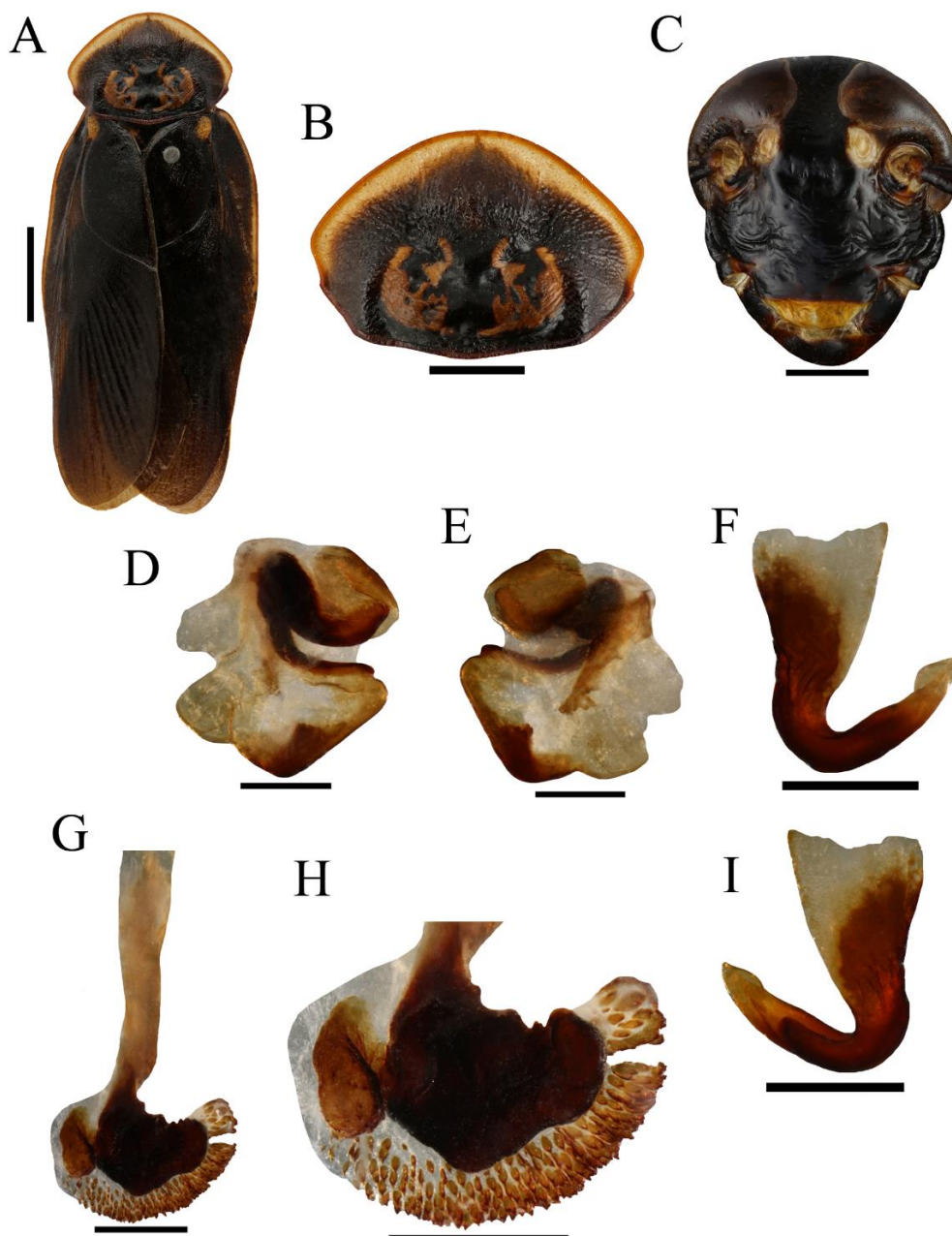


Figure 14. *Monastria kaingangue* sp. n., Holotype ♂: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Head, ventral view; **D)** Right phallomere, dorsal view; **E)** Right phallomere, ventral view; **F)** Left phallomere (L2d), ventral view; **G)** Median sclerite (L1), dorsal view; **H)** Median sclerite (L1), detail; **I)** Left phallomere (L2d), dorsal view (see Fig. 5 for abbreviations). Scales: Habitus=1cm, Pronotum=5mm, Head=2 mm, all other figures=1 mm.

Female (Paratype). Head rounded, with wide interocular space measuring approximately 1/2 the distance between the antennal sockets. Eyes with straight interocular margin. Ocelli developed and slightly deflected. Frontal suture with a cuticular invagination. Clypeus distal

half transparent yellow and larger (Fig. 15D). Pronotum subtriangular with anterior region rounded and slightly concave near the margins; dorsal region rough with deep striae, lateral angles rounded ending in a corner and hind margin slightly curved in the median region (Fig. 15B). Tegmina with little rounded lateral anterior angles, orange lateral margins, and rounded and curved hind margins. Long, reaching the fifth abdominal tergite (Fig. 15A). Legs short and robust. Fore-femora ventro-anterior margins with 31 or 32 spines of the same size; ventro-posterior margins with 3 spines. Middle legs ventro-anterior margins with 5 spines. Supra-anal plate bilobed with a very small median incision. Lobe lateral margins slightly rounded and posterior margin straight (Fig. 15C). Tergite with rounded lateral angles (Fig. 15A).

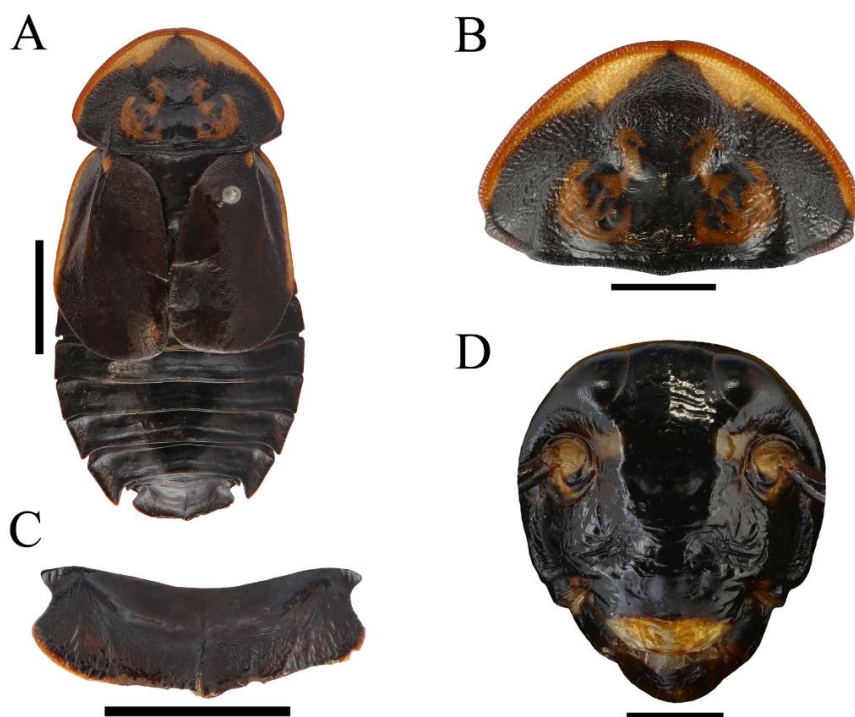


Figure 15. *Monastria kaingangue* sp. n., Paratype ♀: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Supra-anal plate, dorsal view; **D)** Head, ventral view. Scales: Habitus=1cm, Pronotum=5mm, Supra-anal plate=5mm, Head=2 mm.

Measurements (mm). Holotype ♂: Body length 52.80; pronotum length 12.05 x 17.35 maximum width; tegmen length 40.75 x 14.70 width; interocular width 1.7; interantennal width between sockets 5.5.

Paratype ♀: Body length 42.52; pronotum length 11.03 x 17.86 maximum width; tegmen length 17.05 x 12.55 width; interocular width 3.1; interantennal width between sockets 5.6.

Coloration. Holotype ♂: General coloration dark brown (Fig. 14A). Pronotum dark brown with the anterior margin yellowish brown; central disk orange brown with scattered dark brown marks (Fig. 14 B). Head dark brown; clypeus and labrum yellowish brown. Antennae with basal segments dark pigmented and apical segments whitish yellow. Ocelli pale brown (Fig. 14C). Legs dark brown and spines brown; pulvilli white, tarsal claws and arolia light brown. Tegmina with orange lateral margins and abdomen following general coloration of body (Fig. 14A).

Etymology. The word kaingang derives from the Tupi-Guarani. It is the name of an Indian group originally distributed from Sao Paulo to Rio Grande do Sul. The name is an allusion to the similarity of their distribution ranges and a tribute to this people that were certainly aware of the existence of this cockroach.

Distribution. Brazil (São Paulo, Santa Catarina, Rio Grande do Sul). See Fig. 17 for details.

***Monastria sagittata* Tarli, Grandcolas & Pellens sp. n.**

Figure 16.

Type material. Holotype ♂. Brazil, Minas Gerais, Serra do Cipó. March 1967, coll. D. Vital (MZUSP).

Diagnosis. This species is characterized by having pronotum with shallow, smooth and slightly striated dorsal surface; wide lateral margins with sharp angles. Tegmina anal field wide with the CuP vein perpendicular to the lateral. Subgenital plate asymmetrical with one small style. L1 sclerite with a distinct spear shaped apical region, hind margin with a large non-sclerotized projection, and fore region with a small projection directed upwards. Lateral branch small with strong teeth and spines. L2d sclerite, hook with subconical and narrow anterior region, very short and curved and internal ventral margin strongly convex.

Description. Male. Head subtriangular, with interocular space measuring approximately 1/3 of the distance between the antennal sockets. Ocelli developed and slightly deflected; frontal suture with a cuticular invagination (Fig. 16C). Pronotum broad, transverse and pentagonal; dorsal surface shallow, smooth and slightly striated; anterior margin rounded; lateral margins

wider with sharp angles; hind margin nearly straight (Fig. 16B). Tegmina characterized by a wide anal field with the CuP vein perpendicular to the lateral (Fig. 16A). Legs short and robust. Fore-femora ventro-anterior margins with 21 or 20 spines of the same size; ventro-posterior margins with 4 spines. Middle-legs ventro-anterior margins with 5 or 4 large spines. Supra-anal plate quadrangular with setae on the surface, hind margin straight and slightly rounded laterally, bilobed with narrower lobes and strong invagination in the median portion. Subgenital plate asymmetrical with one small style. L1 sclerite with a roughly triangular spear-shaped apical region, hind margin with a large non-sclerotized projection, fore region with a small projection pointing upwards, and lateral branch small with strong teeth and spines (Fig. 16G, H). L2d sclerite hook with subconical and narrow anterior region, very short, curved and internal ventral margin strongly convex (Fig. 16F, I). R2 sclerite cleft slightly curved inwards with the apex slightly sclerotized (Fig. 16D, E).

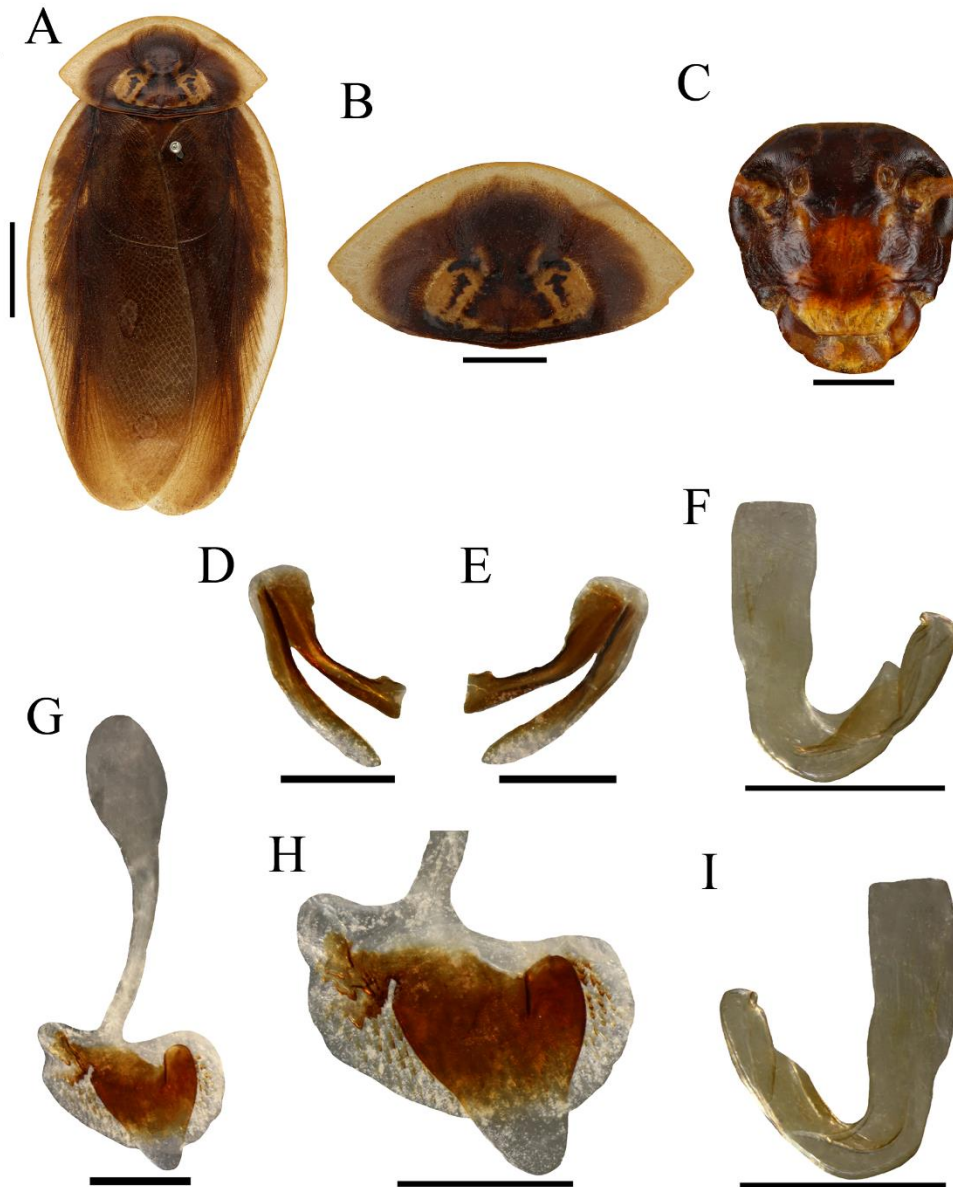


Figure 16. *Monastria sagittata* sp. n., Holotype ♂: **A)** Habitus, dorsal view; **B)** Pronotum, dorsal view; **C)** Head, ventral view; **D)** Right phallomere, dorsal view; **E)** Right phallomere, ventral view; **F)** Left phallomere (L2d), ventral view; **G)** Median sclerite (L1), dorsal view; **H)** Median sclerite (L1), detail; **I)** Left phallomere (L2d), dorsal view (see Fig. 5 for abbreviations). Scales: Habitus=1cm, Pronotum=5mm, Head=2 mm, all other figures=1 mm.

Female. Unknown

Measurements (mm). Holotype ♂: Body length 51.28; pronotum length 11.94 × 21.54 maximum width; tegmen length 41.97 × 17.00 width; interocular width 1.8; interantennal width between sockets 5.4.

Coloration. Holotype ♂: General coloration pale brown (Fig. 16A). Pronotum pale brown with a buff anterior margin; central disk brown ochre with scattered dark brown marks (Fig. 16B). Head with dark brown interocular space, orange frons and amber clypeus and labrum. Antennae with segments yellowish brown. Ocelli brown (Fig. 16C). Legs and spines yellowish brown; pulvilli yellow whitish, tarsal claws and arolia yellowish brown. Tegmina and abdomen following general coloration of body (Fig. 16A).

Etymology. The name “sagittata” derives from the Latin sagitta, meaning arrow, referring to arrow-shaped apex of the L1 sclerite.

Distribution. Brazil (Minas Gerais). See Fig. 17 for details.

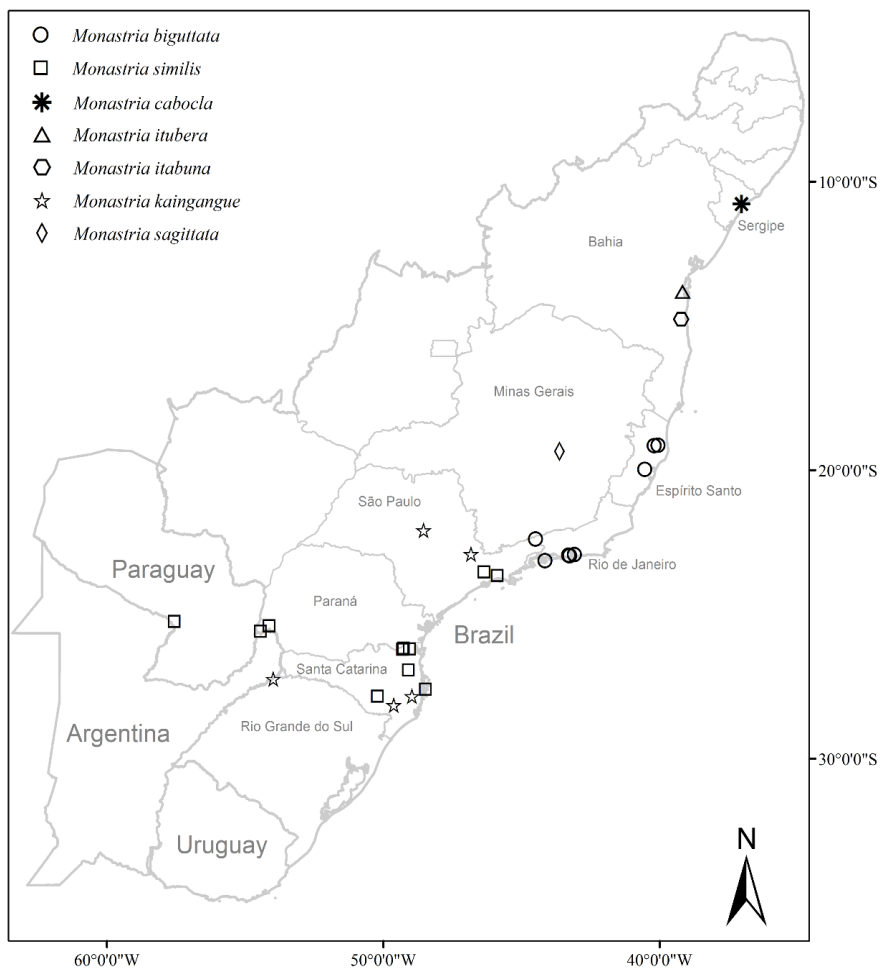


Figure 17. Geographic location of sites where the different species of *Monastria* were collected. *Monastria angulata* is not included in the map for it is only known from a specimen from Bahia, without any mention of locality.

Acknowledgements

Many people facilitated our work along the several sessions in the field. We thank ICMBio for authorizing the fieldwork (License No. 44118-1), and the people directly working on the conservation units we visited; Jose Wellington de Moraes (Instituto Nacional de Pesquisas da Amazônia) for support with fieldwork license; the people working for the environment and agricultural secretaries from Joinville, Campo Alegre and Florianópolis, for assuring our access to reserves from these municipalities; and people that gave us access to private reserves under their responsibilities: the owner of Hotel Dona Francisca in Joinville (SC), Sr. Gilson and Sr. Egon in Campo Alegre (SC), Kevin Flesher from the reserve of Society Michelin at Ituberá (BA), and John Keller and Igu in Foz de Iguaçu (PR). We are also very grateful to Luciana Ribeiro, from Instituto Latino-Americano de Economia, Sociedade e Política, Patricia Garcia Carvalho, Joaquim Buchaim from Faculdades Anglo, for facilitating our study in Foz do Iguaçu, Aurora do Iguaçu, and at Estação Ecológica Ari Cavalca. Finally, we thank the curators of several collections who loaned the material to this study: Eliana Marques Canello (Museu de Zoologia – University of São Paulo), José Albertino Rafael (Instituto Nacional de Pesquisas da Amazônia), Sônia Maria Lopes Fraga (Museu Nacional do Rio de Janeiro), George Beccaloni (Natural History Museum of London), Peter J. Schwendinger (Muséum d'histoire naturelle de la Ville de Genève). We would also like to thank Hans Mejlou (Uppsala University) for the pictures of the type *Monastria biguttata*. We thank Simon Poulain (MNHN) for the support with the digital images. VDT also thanks CAPES Foundation – Ministry of Education, Brazil for the scholarship (Grant Number – 6062/13-0). We thank the ATM “Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme : le message systématique” and ATM “Savoirs Naturalistes, expertise et politiques de la biodiversité” (MNHNP) for financial support for field work.

**C) Chapitre III –
Diversification and distribution of the genus
Monastria Saussure, 1864 in the Brazilian Atlantic
Forest**

Diversification and distribution of the genus *Monastria* Saussure, 1864 in the Brazilian Atlantic Forest

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Abstract

The Atlantic forest biome is characterized by extremely high species richness and threat. Stretching over more than 27 degrees of latitude (3300 km) along the Atlantic Coast, and more than 800 km from the coast to the continent, it comprises a rich diversity of landscapes, ecosystems, and multiple histories of diversification. Here we aim to contribute to a better understanding of these histories by focusing on the diversification of an endemic genus of cockroach, *Monastria* Saussure 1864, limited to forest ecosystems and with limited dispersal ability. The phylogenetic analysis retrieved only 3 monophyletic species (in 8 or 9), indicating that the diversification of the genus was more intense in the Northeast (NE), and suggesting the existence of molecular polymorphism or introgression in the most widespread species. In the NE range size is smaller and richness is higher, contrarily to Southeast(SE)-South(S). An analysis of the distribution of 111 variables indicates the temperature in the Last Glacial Maximum (LGM) and the difference of temperatures between present and LGM are the most important in terms of information gain and interaction. It puts in evidence a greater climatic stability along the coast and a contrasting pattern between the NE, where climate was more stable and temperatures was higher, and

SE-S, where the area was much larger but much more impacted by fluctuations in aridity and temperatures. Based on it, we suggest that the lower number of species with wider distribution range in the S, associated to the presence of species in islands isolated during the Holocene, is due to a presence before the LGM in scattered forests followed by a recent dispersion. In contrast, the higher richness and narrow range in NE is likely to be the result of long term climatic stability and continuity of forest, followed by the present fragmentation of forests in this range.

Introduction

The Atlantic forest is the forest biome stretching along the coast of Brazil, and extending to the West as far as in Assumption in Paraguay and Misiones in Argentina. It comprises a large diversity of ecosystems, from Araucaria forests in the South, to perennial forests in Southeast, and semi-deciduous forests in Espírito Santo and Northeast. This is widely known as one biodiversity hotspots due to numerous threats faced by its rich biodiversity (Myers et al. 2000; 2003). For many decades, this forest has remained infinitely less studied than the Amazon, except through the numerous inventories made concerning fauna and flora. The last twenty years have, however, seen a great deal of in-depth work on the history of this forest (eg Costa et al., 2000, Cardoso da Silva, 2004, Cabanne et al., 2008, Carnaval & Moritz, 2008, Mello Martins, 2011).

Cockroaches of the genus *Monastria* Saussure, 1864 belong to the Neotropical subfamily Blaberinae (Grandcolas, 1993, 1996; Legendre et al. 2015). The genus includes described species, and probably one more, that needs the observation of male specimens to be confirmed. Species of this genus are historically known from the Brazilian Atlantic Forest (Princis 1963), occurring from the State of Ceará to the Rio Grande do Sul in the South of

Brazil (03° to 30°S), and from the Atlantic coast to the furthest inland forests of this biogeographical domain, in Misiones (Argentina) and in Assumption (Paraguay). Individuals of *Monastria* live on the underside of dead trunks lying on the forest ground, have a generation time of about 2 years, are very sedentary, gregarious, and females care the brood during about 20 days. In addition to that, females are short winged, so unable to fly. This makes that species of *Monastria* have very limited ability to disperse and found new populations (Pellens and Grandcolas 2003, 2007; Pellens et al. 2010). This limited ability to disperse, and the need of forest to live, makes that the diversification of this genus may have followed the distribution of forests, and we wonder what factors associated have been involved.

In this study, we aim to understand the diversification of this genus and their present distribution in the Atlantic forest. Are the species clearly separated? Are there groups of species clearly separated in the geographical space? Where did it originate? What factors could explain the present diversity and distribution? For doing this, we studied the phylogenetic relationship of specimens collected in the whole range of distribution of the genus. Due to the lack of fossil records, we were unable to date the tree. In order to overcome this difficulty, and try to have an estimate of the time of diversification, we sampled some specimens in two islands assumed to be isolated during the LGM, namely Ilha Grande (RJ), and Florianopolis (SC). In addition to the phylogeny, we also studied the distribution of the genus with Ecological Niche Models (ENM), and then assessed the variables [altitude, velocity of climate change, and climate (present and three times in the past)] that contribute more to explain this pattern.

Material and Methods

Taxonomic and character sampling

We sampled 31 specimens belonging to 6 (or 7) species of *Monastria* (out of 8 (or 9) known species (75%) and three outgroup species, namely *Blaberus discoidalis*, *Byrsotria fumigata* and *Petasodes* sp. The two-remaining species *M. cabocla* and *M. angulata* were not sequenced because the material available is only from old specimens. We used four molecular markers to reconstruct *Monastria* phylogenetic relationships: 12S rRNA (~355 bp), 16S rRNA (~500 bp), 28S rRNA (~495 bp) and cytochrome oxidase subunit I (COI, 658 bp). Primers and molecular techniques were described in Legendre *et al.* (2008). We provided 111 sequences and complemented them with 10 sequences from Legendre *et al.* (2015; KP986272, KP986317, KP986385, KP986429), Legendre *et al.* (2014; KF372445, KF372514), Pellens *et al.* (2007; EF363290, EF363262), Inward *et al.* (2007; DQ874032) and Kambhampati (1995; U17769). We sampled 82.4% of the taxa for 12S, 94.1% for the 16S, 91.2% for the 28S and 88.2% for the COI.

Alignment and phylogenetic analyses

All sequences were blasted before any analysis. Then, we used MUSCLE (Edgar, 2004) as implemented in Seaview v.4 (Gouy *et al.* 2010) to align molecular sequences and refined the alignment manually. We also checked that the alignment for COI was congruent with codon reading frame. We used the software SequenceMatrix 1.7.8 (Vaidya *et al.* 2011) to concatenate the markers. It resulted in a final alignment of 2038 nucleotides.

We used PartitionFinder v.1.1.1 (Lanfear *et al.* 2012) to select the best partitioning strategy, which involved five partitions: 12S-16S, 28S, COI-1, COI-2 and COI-3. The selected

models were either a General Time Reversible model with a gamma distributed rate variation among sites (GTR+G) or a GTR+G with a proportion of invariant sites (GTR+G+I). However, because G and I are strongly correlated (Sullivan et al. 1999) and using models mixing these parameters could bias their estimation, we used a GTR+G model for each partition.

Maximum Likelihood analyses were conducted using RAxML 7.4.2 (Stamatakis 2006). We first performed 500 ML replicates using the rapid hill-climbing algorithm on the combined dataset and the optimal solution was selected. We then estimated bootstrap support values from 1000 replicates using the rapid bootstrap algorithm (Stamatakis *et al.* 2008).

Records of occurrence, climate variables, and niche model

We modeled the niche of the genus *Monastria* using 61 records of presence coming from our sampling plus data issuing from Natural History Collections. This included 31 records of species from the phylogeny and 30 additional records (Fig. 1b). As recommended by Tarli et al. (in preparation- chapter 4 of this thesis), we tested for biases and then rarefied the data by excluding 21 records in the most biased environmental space. The methods used are strictly the same used in this work. This strategy enhances model's sensitivity so allowing to detect more possible suitable areas. In other words, this allows for avoiding that some suitable areas are excluded by overrepresentation of samples in one climate class (see Tarli et al. for details). Climate data were obtained from WorldClim version 4. From the 19 Bioclim we eliminated correlating variables where Pearson's $r > 0.80$. The variables retained were those with the most correlations with others, and those without significant correlation. The niche was modeled with MaxEnt 3.3.3 (Phillips et al. 2004). The same variables were

used to model the niche of the species with sufficient number of records (*M. similis*, *M. biguttata*, and *M. kaingangue*). For the other species, the records of occurrence were too few or too near each other to use the data model their niche. So, we used hydrosheds as units of delimitation, assuming that the range of each species were limited to the geographical sub-basin of Level 4 (IBGE 2011). Sub-basins are often used as planning units in Brazil, due to their natural and biogeographically meaningful boundaries.

Variables and assessment of variable importance for the distribution of the genus *Monastria*

We used 111 variables to assess the factors that could explain the present pattern of distribution of *Monastria*. Seventy-two of them correspond to the values of climate variables in four different periods: Present, MidHolocene (MiH) (6 ky¹), Last Glacial Maximum (LGM) (22ky²) and Last inter-glacial (LIG) (120ky³). For MiH and LGM these variables were used in three different scenarios of green-house gas emission. Thirty-six other variables come from layers produced with the function Minus in ArcGis 10.3, used to calculate the difference between present and past values for each climate variables (LGM and LIG). The remaining 3 variables were altitude, velocity of climate change and probability of suitability of each area calculated from the niche model of *Monastria*. The variables, data used, models, and their respective sources are presented in Table 1.

These values of each variable were extracted to points from layers at 2.5-minute of a latitude/longitude degree spatial resolution (i.e., 4.5 km at the equator). The points of extraction were obtained through the transformation of one Bioclim layer to grids of the same size and placement of the raster cells followed by the transformation of grids to points.

The resultant map had 198,210 points regularly distributed in the spatial surface of the Atlantic forest *lato sensu* in Brazil, Paraguay and Argentina.

Table 1 – Variables used and data source. Bioclim data were used for the Present, Mid-Holocene (MiH) (6 ky), Last Glacial Maximum (LGM) (22ky), Last inter-glacial (LIG) (120ky). Data from LGM and LIG were based on three different Atmospheric-Oceanic Global Circulation Models, CCSM4 (CC), MIROC-ESM (MR), MPI-ESM-P (ME).

Abbreviation	Variable	Source*
Bio01	Annual Mean Temperature	WorldClim 1.4
Bio02	Mean Diurnal Range	WorldClim 1.4
Bio03	Isothermality	WorldClim 1.4
Bio06	Min Temperature of Coldest Month	WorldClim 1.4
Bio12	Annual Precipitation	WorldClim 1.4
Bio15	Precipitation Seasonality	WorldClim 1.4
Bio16	Precipitation of Wettest Quarter	WorldClim 1.4
Bio18	Precipitation of Warmest Quarter	WorldClim 1.4
Bio19	Precipitation of Coldest Quarter	WorldClim 1.4
Alt	Altitude	WorldClim 1.4
Vel	Velocity of climate change	Sandel et al. 2011
Niche	Probability of suitability	Maxent 3.3.3

* data from LIG comes from Otto-Bliesner et al. (2006).

We used Random Uniform Forest (RUF) in R (<http://CRAN.R-project.org/package=randomUniformForest>) to characterize variable importance in predicting the distribution *Monastria*. This is a machine learning algorithm designed for classification, regression and unsupervised learning. It works by building many unpruned and randomized binary decision trees, using random cut-points to grow the tree, and bootstrap and subsampling (Ciss, 2015). RUF is non-parametric and thus can be used on data with a large number of variables of various types, and do not depend on the assumptions of normality and heteroscedasticity. Its application in ecology (e.g. Cutler et al. 2007) and forest management (e.g. Oliveira et al. 2012) suggests that it can be very powerful particularly when non-linear trends exist. We used the classification function in RUF for assessing global

variable importance and variable importance based on interactions, using 111 variables in 198,210 lines, each corresponding to point a point of data extraction as explained above.

Results

Phylogenetic relationship of Monastria

In the best tree (ln L=-8873.208050), *Monastria* is monophyletic with a high bootstrap support value (BS=94). *M. itubera* is the first species diverging from the remainder within *Monastria*, a result also well supported (BS=91). Then, two clades are distinguished (BS=91), one comprising the monophyletic *M. kaingangue* and *M. itabuna*, then *M. sagittata*, one specimen of *M. similis*, one of *M. biguttata* and a last one of a not confirmed specimen of *M. biguttata* (BS=58). The other main clade comprises only specimens of *M. biguttata* and *M. similis* (BS=55).

For the four markers considered, species from the second clade are less divergent than species belonging to the first. The first clade includes species occurring in the whole range of the genus, with *M. kaingangue* in the southern part of the range and the others found in isolated localities from Minas Gerais (*M. sagittata*) to the Northeast. Three of these species are only known from single localities. The species of the second clade have large distribution range: *M. biguttata*, from Bahia to the south of Rio de Janeiro; and *M. similis*, from Minas Gerais to the extreme southern and western distribution of the genus (Fig. 1B; Table 2).

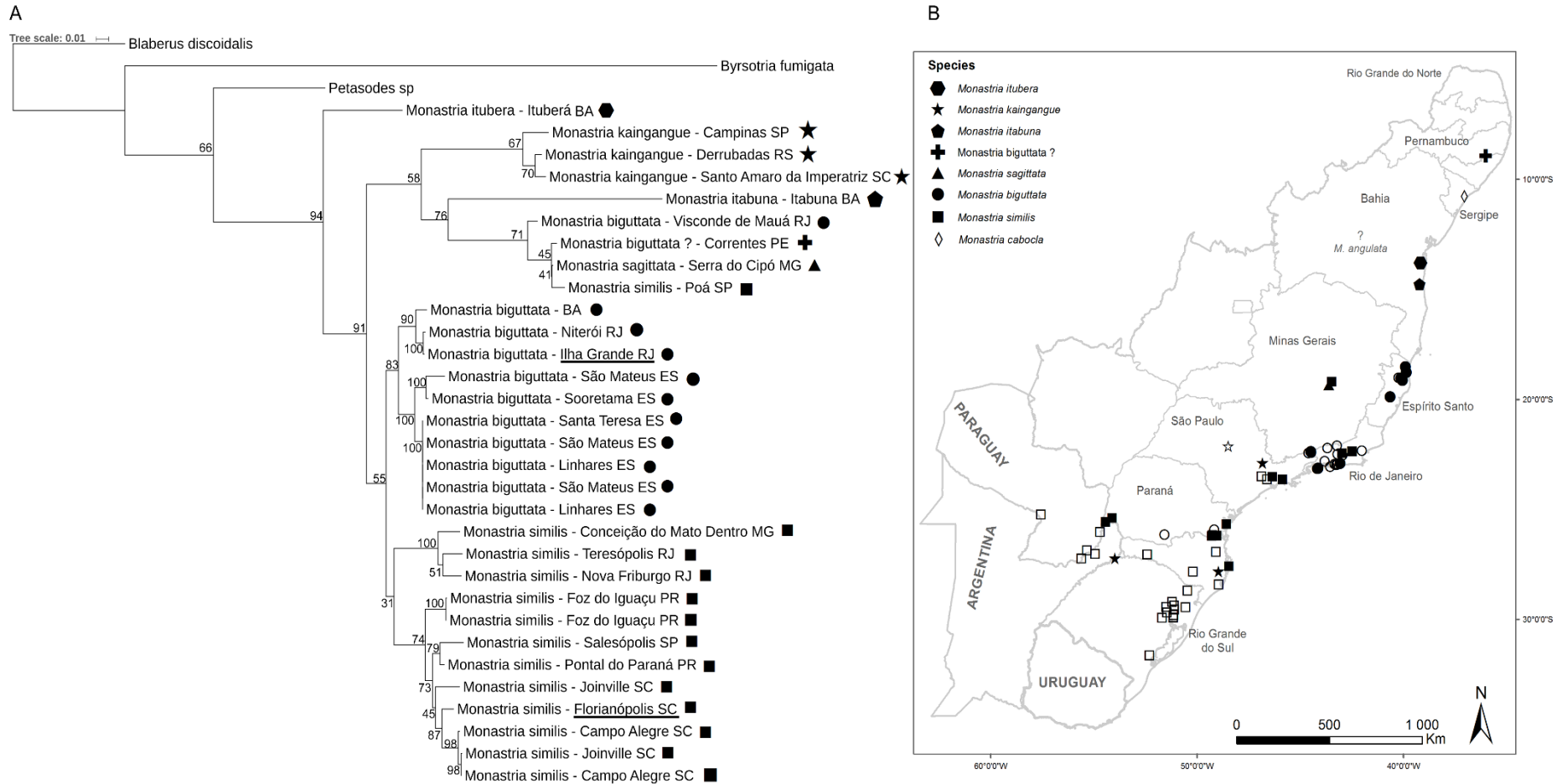


Figure 1. A) Maximum likelihood-based tree inferred from the four molecular markers. Bootstrap values are shown at each node. The characters next to the localities correspond to the species of *Monastria* shown in figure B. B) Geographic location of sites where the different species of *Monastria* were collected. Full characters: 31 records of species from the phylogeny. Empty characters: 30 additional records.

Note that although *M. biguttata* and *M. similis* are not monophyletic due to two specimens identified in other clades, this main trend of distribution is maintained, except for the specimen *M. biguttata?* in Correntes, PE. (The only specimen of this locality is a female that strongly resembles *M. biguttata*. But, the lack of male genitalia precludes the Fig. 1B confirmation of this species). But, contrarily to what could be expected by the distance of this point in Correntes to the nearest point in Bahia, the addition of this record in the niche model did not increase markedly the area suitable for *M. biguttata* (Table 2). This indicates that their distribution must be very scattered in this region.

Table 2. Area of distribution of the species of *Monastria* inferred with Ecological Niche Model (area with probability of suitability ≥ 0.68), or from the area of the Hydrographic basin level 4 of the occurrence record.

Species	Niche area (PoS) (Km ²)	Hydrographic basin area (Km ²)
<i>Monastria itubera</i>		2,730
<i>Monastria itabuna</i>		4,648
<i>Monastria sagitatta</i>		27,630
<i>Monastria cabocla</i>		3,255
<i>Monastria similis</i>	71,780	
<i>Monastria biguttata</i> *	28,160	
<i>Monastria biguttata</i> **	32,220	
<i>Monastria kaingangue</i>	77,950	
<i>Monastria angulata</i>	NA	NA

* without the record from Correntes, PE; ** including the record of Correntes, PE

This makes that two main patterns of distribution are observed in the main clades of the genus, one concerns the species from the Northeast, that have more restricted range. Note that *M. cabocla* and *M. angulata* (not sequenced in this study) are also known from single localities at the Northeast. This pattern from the northeast is contraposed by that of the species occurring in the southern part of the range, *M. kaingangue*, *M. biguttata* and *M. similis*, with much larger distribution ranges. Another point indicated by this topology is that

specimens from the islands are not particularly separated in the tree. Both (*M. biguttata* in Ilha Grande, and *M. similis* in Florianopolis) are found within the clade with the specimens from the nearest localities.

The distribution of the genus *Monastria*

The high training AUC (0.9429) indicates a good performance of MaxEnt in the ENM. The niche model indicates that one area of 107,400 km² has high probability of suitability for *Monastria*. This corresponds to 28.1% of total area used in this study. The analysis of contribution of the different variables indicated that Bio02 was the one with highest regularized trained gain, with 38.1%, followed by Bio03 (22.2%) and Bio12 (15.1%) (Table 3).

Table 3. Relative contributions and permutation importance of the nine variables used for modeling the niche of *Monastria*.

Variable	Percent contribution	Permutation importance
Bio02	38.1	38.3
Bio03	22.2	26.2
Bio12	15.1	13.5
Bio18	12.7	0.1
Bio16	7.1	3
Bio06	2	1.1
Bio19	1.6	8.5
Bio01	0.7	5.8
Bio15	0.2	0.2

The niche model indicates a distribution strongly matching the distribution of main forests along the coast, and spreading to west until Argentina and Paraguay in moist regions around Iguaçu and Turvo River. In general, suitable areas are much wider and more continuous in the Southeast and South than in the Northeast (Fig. 3A)

The results of RUF indicate a high contribution of the temperature of the LGM in the patterns observed. This is shown by the high importance of the variable Bio01 in the LGM, and by the difference between present and LGM of Annual Mean Temperature (Bio 01) in

the two Atmospheric-Oceanic Global Circulation Models, Minimum Temperature of Coldest Month (Bio 06) and Mean Diurnal Range (Mean of monthly (max temp - min temp) (Bio 02) (Fig. 2).

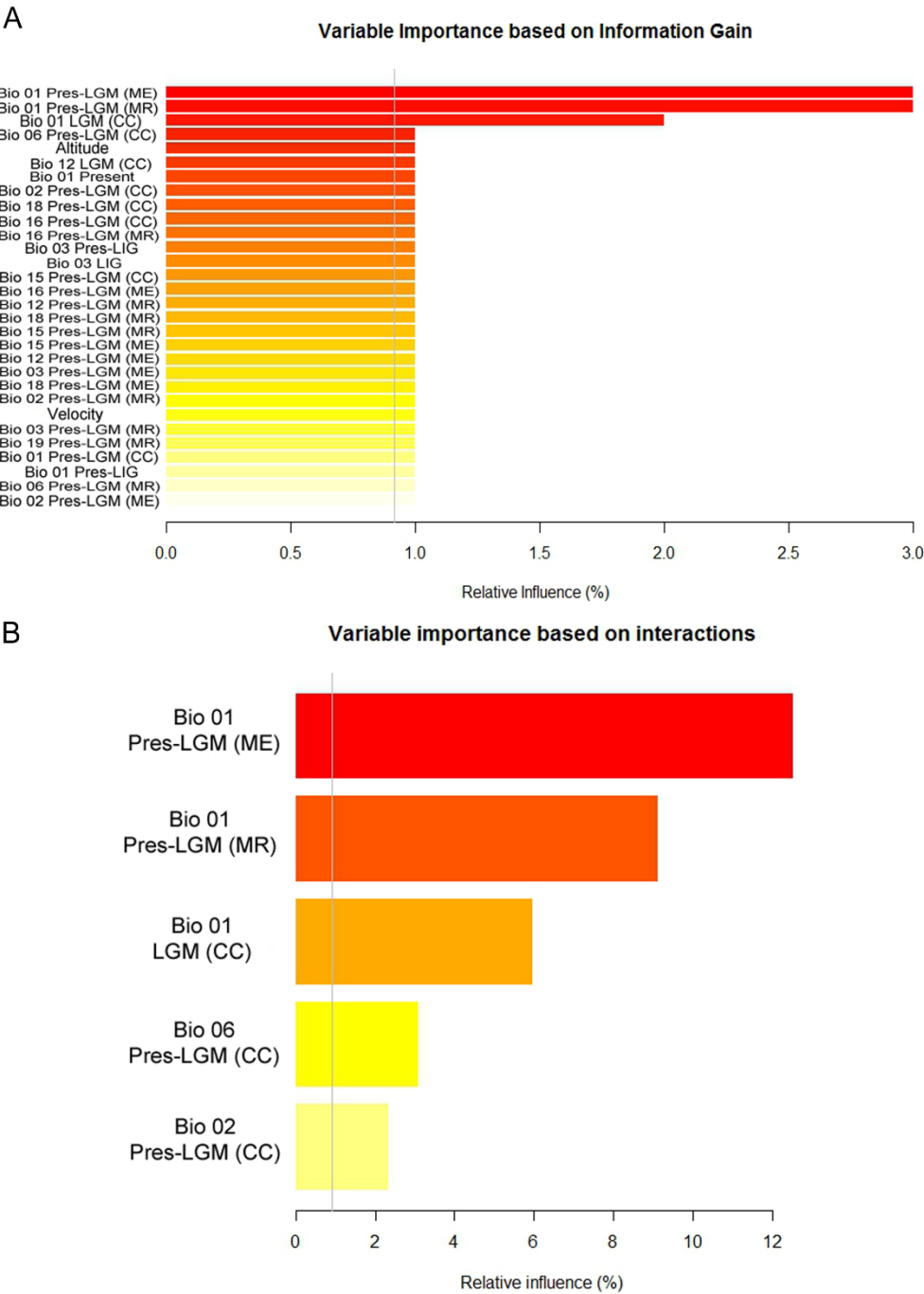


Figure 2. Classification of 30 variables with Random Uniform Forest. A) Variable importance based on information gain; B) Variable importance based on interactions

The correlation between the probability of suitability of areas for *Monastria* and the values of Bio01 in LGM or the difference between present and past climate are negative for all variables, except for the difference of Bio06 (Table 4). This means that suitable areas for *Monastria* are where Bio01 and Bio02 changed less from the LGM to the present, and where the minimum temperature of the coldest month increased more (Fig. 3B-F). A close look at Fig. 3 shows that it was above all along the coast that the lower differences of temperature was observed in this time frame, so indicating the importance of this variable to the general distribution of the genus.

Table 4. Values of Pearson correlation between the probability of suitability of the niche model and the variables with highest importance in terms of interaction in Fig. 2. For abbreviations see table 01.

Variables	r	p-value
Bio01 LGM (CC)	-0.3716326	< 2.2e-16
Bio01 Pres-LGM (ME)	-0.4471289	< 2.2e-16
Bio01 Pres-LGM (MR)	-0.06781511	< 2.2e-16
Bio06 Pres-LGM (CC)	0.4064031	< 2.2e-16
Bio02 Pres-LGM (CC)	-0.4157254	< 2.2e-16

The Bio01 in the LGM (Fig. 3B) and the difference of Bio06 between present and LGM (Fig. 3C) show that, in addition to this trend separating the coast from the inland, there were also important differences between the North and the South. In the LGM, the South was much colder, and the increase in the temperature of the coldest month was much higher in the South than in the Northeast (Fig. 3B; Supplementary Material). In addition to that, the present distribution *Monastria* in the northeast finely matches the distribution of the highest differences of Bio06 between present and LGM in this region (Fig. 3 A, C).

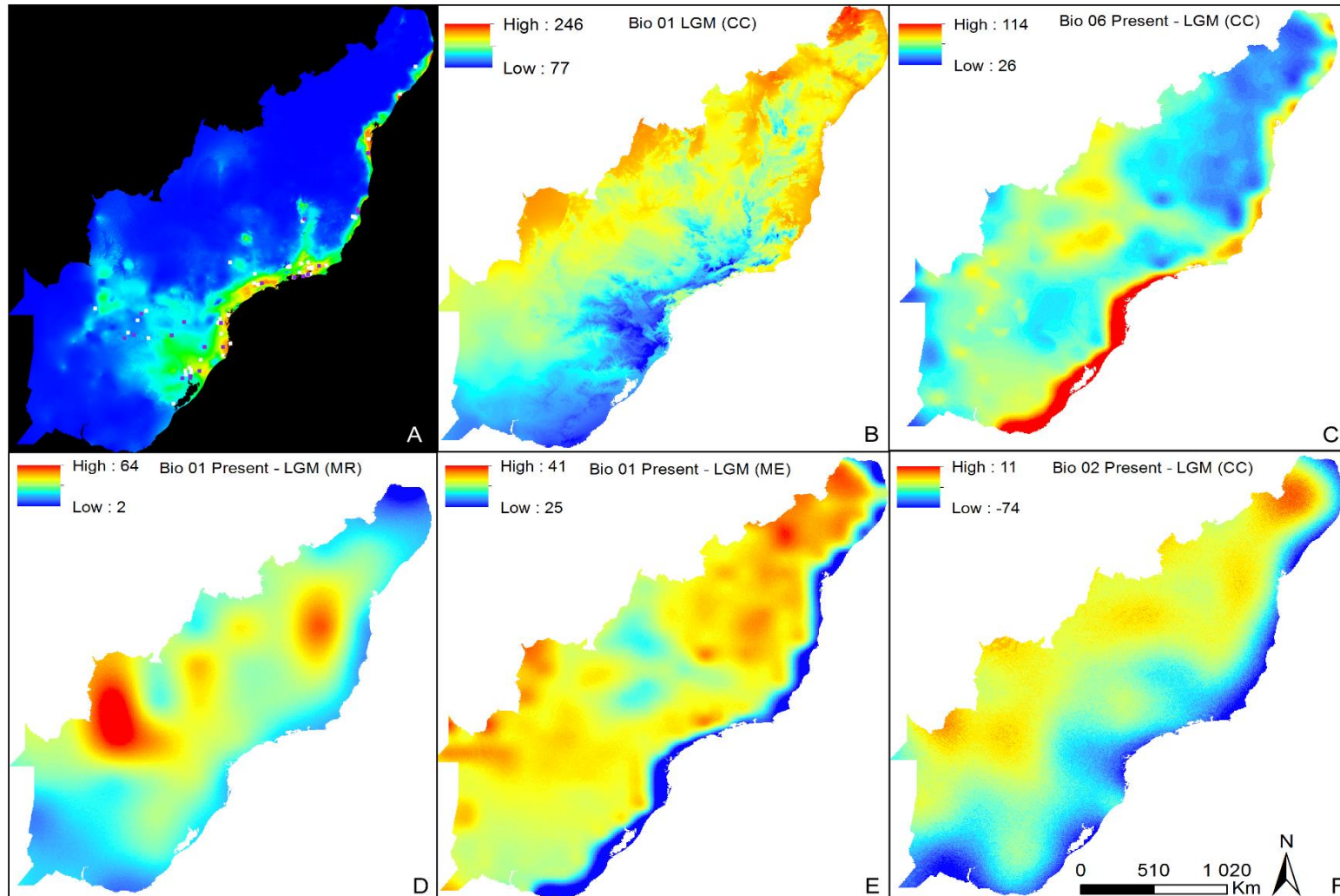


Figure 3. Niche of the genus *Monastria* and Bioclim layers from different variables resulting from the RUF analyses. A) Niche of the genus *Monastria* using 61 records of presence. B) Bioclim layer of Bio 01 in the LGM (Model CC). C) Bioclim layer of Bio 06 with difference between present and LGM (Model CC). D) Bioclim layer of Bio 01 with difference between present and LGM (Model MR). E) Bioclim layer of Bio 01 with difference between present and LGM (Model ME). F) Bioclim layer of Bio 02 with difference between present and LGM (Model CC)

Discussion and Conclusion

Phylogenetic and systematics of the genus Monastria

This study confirms the monophyly of only three out of six species studied here (out of eight already described based on the morphology), *M. itubera*, *M. itabuna*, *M. kaingangue* (Tarli et al. *submitted*). For the remaining species, this question is opened, and certainly more specimens could help to solve some of them. For example, from the morphological point of view *M. sagittata* is markedly different of *M. biguttata* and *M. similis* concerning several characters (the shape of the pronotum, the distribution of the veins in the tegmina, and male genitalia) (Tarli et al. *submitted*). So, why this molecular similarity? Another point is that *M. similis* is found in very near localities where we collected *M. sagittata* (Serra do Cipó and Conceição Mato Dentro - about 60km). But it is not the specimen from this place that is in the clade with *M. sagittata* (it is the specimen from Poá, about 800km far away, in São Paulo). Is this phylogenetic similarity indicating genetic exchange, or hybridization between the two species in the past? Or is it indicating that natural selection is acting on interspecific differences in cases on sympatry, and relaxing in populations that are far away? From the present results both possibilities could be true. Curiously, the specimens of *M. biguttata* in this clade come from the two limits of distribution of this species. The specimen from Correntes, PE at the extreme North, and the one from Visconde de Mauá (at the limit of Rio de Janeiro and São Paulo). All this suggests the existence of ancestral polymorphism or hybridization.

Despite the fact that *M. biguttata* and *M. similis* are not monophyletic, their distribution range is quite coherent, making with *M. kaingangue* three groups with distributed mostly at the south of Espírito Santo. *M. biguttata* is mainly distributed along the coast from Rio de Janeiro to the Northeast, whereas *M. similis* is found in areas much farther

in the continent (as far as in Misiones, Argentina and Assumption, Paraguay) from Minas Gerais to Rio Grande do Sul. The only exception concerns *M. biguttata?* from Correntes, PE, one of the most extreme localities from where *Monastria* is known in the Northeast, which is likely to belong to an isolated population.

The origin of the genus Monastria

The phylogeny indicates that the first divergent lineage of *Monastria* is now found in a very small forest remnant in the State of Bahia in the Northeast, *M. itubera*. Based on it, the most parsimonious hypothesis of diversification is that the genus originated in the Northeast, from where it dispersed and reached the entire domain of the Atlantic forest. The fact that species from the southern region are also found far away in the Northeast (even if by ancestral polymorphism or introgression as hypothesized above) also corroborates this hypothesis. This suggests that the NorthEastern route may have been the most important for the origin of the genus in the Atlantic Forest (Por, 1992; Ledo & Colli, 2017), which means an arrival in the Atlantic forest from the Amazonia through the Northeast (see also Costa 2003). This hypothesis can be tested in a near future with a phylogenetic study of Blaberinae in the different biomes in South-America, or with a study specifically designed to assess the routes of diversification of Blaberinae between the Atlantic forest and the Amazon.

Dating

One major problem concerning the phylogenetic study of recent groups of Blattaria is the scarcity of fossils records that could be used to date the inner group (Legendre et al. 2015). This is not an exception for *Monastria*, for which no fossil records are available. This makes that the only calibration points would be from external groups (those used in

Legendre et al. 2015 for Dictyoptera), making *Monastria* a very old clade (about 56My), and with extremely large confidence intervals.

Unfortunately, contrarily to what we expected, the use of specimens from islands that were connected to the continent during the LGM and are isolated during the last 14 000 years did not add any contribution to date the tree, letting this point opened to further studies. Nevertheless, as the females of *Monastria* are wingless and unable to fly (Pellens and Grandcolas, 2003) the main way of spread of their populations is by walking or by drift grasped on dead trunks where they live. So, from it we can assume that it is very likely that the presence of species of *Monastria* in islands strongly precedes their isolation from the continent during the Holocene. In the next section we discuss the contribution of this information to understand the distribution of these two species.

Patterns of distribution

The main pattern of distribution of *Monastria* is the contraposition between the large ranges of species occurring from Espírito Santo to the South, and narrow distribution range of species occurring in the Northeast. In addition to that, there are more species in the Northeast than from Espírito Santo to the South [5 (or 6) vs 3], despite the fact that the total area of forest is much smaller.

The analysis using climate variables from present and three past periods puts in evidence the important role of the temperature in the LGM, in particular the minimum temperature of the coldest month, in marking the differences between northern and southern region of the Atlantic forest. In addition, studies based on palynological records suggest that climatic fluctuations and the impact of Pleistocene arid phases were also more important in this Southern region (Por, 1992). Nevertheless, we must recall that, in the

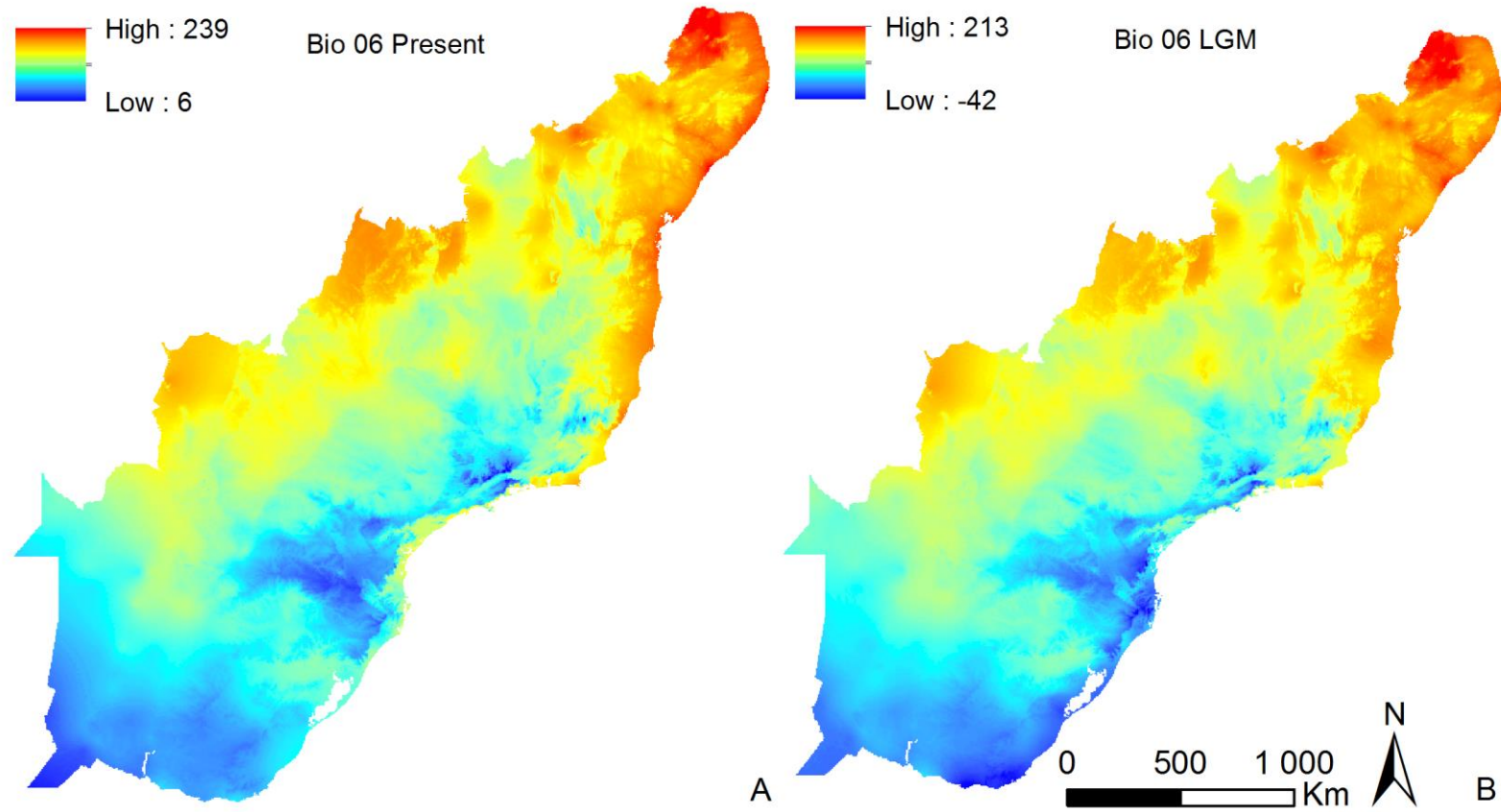
South, terrestrial surface of the Atlantic coast was much larger during the LGM because the continental platform goes much farther away than in Northeast (Leite et al. 2016). These areas were retracted with the sea level rise in the Holocene.

Based on it and on the fact that populations on islands are not particularly recent when compared to those from the continents we hypothesize that the colonization of the South precedes the LGM. Nevertheless, due to the lower temperatures and higher aridity in the South during this period (Por, 1992), it is very likely that populations were scattered, limited to some regions nearby the coast, or towards the West in the South. In fact, the historical suitability of this area in the LGM explains better the present distribution of *Monastria* to this region than present climate (see Fig. 3, A, B).

Contrarily to the South, several scenarios suggest that the climate in the Northeast remained more stable and that forests were more continuous, particularly in the Last Interglacial (about 120my) (Leite et al. 2016). In addition, the region of Bahia where two species, *M. itubera* and *M. itabuna*, were recorded is hypothesized as one of the major climatic refuges within the Atlantic forest during LGM (Carnaval & Moritz 2008; Carnaval et al. 2009; Mello Martins 2001). So, historical climatic stability is quite likely to be the most important reason for the higher species richness in the Northeast. Nevertheless, the niche of the genus, as well as the distribution of different species in the Northeast, strongly matches the distribution of the Atlantic forest (forests existing before deforestation by modern civilization) (SOS *Mata Atlântica* & Instituto Nacional de Pesquisas Espaciais 1993, 2014). This leads to the hypothesis of wider distribution range in the past, followed by the extinction of multiple populations, and isolation of each of them in one of the isolated forests.

To conclude, much remains to be discovered about the factors that lead to the present distribution of biological diversity in the Atlantic forest. The study of the genus *Monastria*, a group of cockroach totally dependent on forest for its survival and with very restricted possibility of dispersion brings significant insights to understand the distribution of biodiversity in this hotspot. It shows that even if the genus is likely to be old, the climate change in recent past periods (22 and 120 ky) were strongly important to shape its distribution.

Supplementary Material



Bioclim layers from Min Temperature of Coldest Month (Bio06). A) Bioclim layer of Bio 06 in the Present. B) Bioclim layer of Bio 06 in the LGM (Model CC)

**D) Chapitre IV –
The informative value of Museum collections for
ecology and conservation: a comparison with target
sampling in the Brazilian Atlantic forest**

The informative value of Museum collections for ecology and conservation: a comparison with target sampling in the Brazilian Atlantic forest

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Abstract

Since two decades the richness and potential of natural history collections (NHC) were rediscovered and emphasized, promoting a revolution in terms of access on data of species occurrence, and fostering the development of several disciplines. Nevertheless, due to their inherent erratic nature, NHC data embody several biases. Understanding these biases is a major issue, particularly because ecological niche models (ENMs) are based on the assumption that data is not biased. Based on it, a recent body of research have focused on searching adequate methods of dealing with biased data and proposed the use of filters in geographical and environmental space. Although the strength of filtering in environmental space has been shown with virtual species, nothing has yet been tested with a real dataset including field validation. In order to contribute to this task, we explore this issue by comparing a dataset from NHC to a recent targeted sampling of the cockroach genus *Monastria* in the Brazilian Atlantic forest. We showed that, despite strong similarities, the area modeled with NHC data was much smaller. These differences were due to strong climate biases, which increased model's specificity and reduced sensitivity. By applying two forms of rarefaction in the environmental space, we showed that deleting points at random in the most biased climate class is a powerful way for increasing model's sensitivity, so increase the possibility to predict more suitable areas of occurrence than those more sampled.

Keywords: natural history collections, species distribution models, target sampling, biases, MaxEnt, field validation, rarefaction, filtering, environmental space, climatic bias, overrepresentation

Introduction

NHCs were designed to keep vouchers of the living world several centuries ago. More than a simple repository for taxonomic studies, these collections are memories of the past and present life on earth, and represent important references of biodiversity in time and space. In the last two decades, the richness and the huge potential of these collections have been rediscovered and emphasized (Graham et al. 2004; Suarez and Tsutui 2004; Lavoie 2013). Many possible uses have been listed for specimens housed in collections (Funk 2003; McLean et al. 2016), as for example, tracking invasions (Muller 2015), defining trends in populations of pathogens and parasites (Pinto et al. 2010), revealing the history of diseases (Persing et al. 1990; Marshall et al. 1994), analyzing responses to environmental changes (Robbirt et al. 2011; Lister et al. 2011), building seed banks (Muller 2015), following phenotypic and genotypic changes in populations and documenting many aspects of the evolutionary process (Holmes et al. 2016).

This recent emphasis on NHC data however brings more benefit for studies of macroecology. The international enterprise of rendering available data from specimen's labels (and associated information from field notes and expedition logs), and more recently, traits and pictures of the specimens, is powering this research field, which is becoming central in ecology and biodiversity conservation. The massive amount of data available in national databases and some data federators like GBIF www.gbif.org along with environmental data interpolated at high spatial resolution (e.g. Hijmans et al. 2005; Fick and Hijmans 2017) and powerful methods of analysis is not only allowing for unraveling main patterns of biodiversity distribution, but also for understanding the processes leading to them (see Beck et al. 2012 for a review).

However, specimens found today in collections were not necessarily collected based on protocols and standardized samplings. Most of them come from the accumulation of erratic and irregular field works over more than two centuries. So, assembling them to answer a specific question requires considering the biases that they may span, as, for example, the well-known biases towards places of easy access [as along main rivers (e.g. ter Steege et al. 2016), near roads (e.g. Kadmon et al. 2004)], with high population density (e.g. Araujo 2003 for Europe, but see Yang et al. 2016 for China), with better academic (Mooerman and Eastbrook

2006; Pautasso and McKinney 2007), or socio-economic structure (Golding et al. 2010)]; and biases away from remote regions (e.g. Schulman et al. 2007).

Depending on the constraints of access, and on the regional environmental variability, these biases have important implications on the environmental range sampled (Kadmon et al. 2004; Loiselle et al. 2008), and on the inferences of species distribution range (e.g. Schulman et al. 2007; Feeley and Silman 2011). This makes the use of NHC data is very challenging, particularly because ENMs as estimated in MaxEnt (the most powerful method modeling species distribution) are based on the assumption that distribution records are not biased. Due to this, a whole body of research has been devoted to the characterization of biases in collection databases and to the search of solutions in order to minimize errors on estimates based on ENMs (Kramer-Schadt et al. 2013, Boria et al. 2014). However, the lack of field validation still represents a major constraint for evaluating and understanding models' outcomes (Anderson et al. 2016; Robbirt et al. 2011).

During a biogeographic study in the Brazilian Atlantic forest, we took advantage of a long-term survey of the insect genus *Monastria* Saussure, 1864 (Dictyoptera, Blaberidae) to mobilize data for this kind of study. We referred to all Museum collections in the world that harbored specimens of *Monastria* and we conducted a field sampling designed to characterize their distribution in the biome and to define the limits of their distribution range. The main interest of focusing on species of this genus is that they are not specialized, so they are not constrained by specific resources like a host plant, and not well-known like many vertebrates, even if first records date back to the beginning of the 18th century (Pellens and Grandcolas 2003, 2007).

Here we used all distribution records available to the species of this genus aiming to explore whether data issuing from NHC dataset would be enough to predict the entire distribution range of the genus, as validate by the recent sampling dataset. Based on it, we explored how sampling biases could be responsible for the result. Then, we developed and compared two strategies of rarefaction and the way the influence the outcomes of ENMs.

Material and Methods

Monastria

Cockroaches of the genus *Monastria* belong to the Neotropical subfamily Blaberinae (Grandcolas, 1993, 1996; Legendre et al. 2015). The genus includes nine species. Three of them with large and partially overlapping distribution range, and six other known from single

localities (Tarli *et al.* in press). Species of this genus are historically known from the Brazilian Atlantic Forest (Princis 1963), occurring from the State of Ceará to the Rio Grande do Sul in the South of Brazil (03° to 30°S), and from the Atlantic coast to the furthest inland forests of this biogeographical domain, in Misiones (Argentina) and in Assumption (Paraguay). They were observed in a large array of forest ecosystems composing this biome, ranging from semi-deciduous forests in the Northeast to the humid montane forests in the central region and the *Araucaria* forests in the South. Individuals of *Monastria* live on the underside of dead trunks lying on the forest ground, live about 2 years, are very sedentary and gregarious, and adults reach the size of small mammals (about 3cm in length x 1.5cm in width). They are collected by direct search on their specific habitats, or, indirectly, by collectors searching for other xylophagous insects. Adult males can be captured with light traps, although it rarely occurs (Pellens and Grandcolas 2003, 2007; Pellens et al. 2010).

Collection data

We searched for *Monastria* in the literature and in collections of Natural History Museums. This led to a dataset issuing from 23 references (S1 Appendix) and 11 collections (S1 Table). We assigned geographical coordinates to every specimen with enough information at the level of a locality or with more details. Specimens with information of occurrence at very coarse resolution (level of the continent, a country, a state, or a big city) were discarded.

Target sampling

We designed a sampling protocol aimed at checking the occurrence in different forest physiognomy within the Atlantic Forest and at characterizing longitudinal, latitudinal and altitudinal limits of distribution. Since the Atlantic forest is now reduced to less than 5% of its original surface and distributed in a multitude of scattered fragments (SOS Mata Atlantica and Instituto Nacional de Pesquisas Espaciais 2014), we focused mainly on officially protected areas. But some forests in private properties in regions where reserves do not exist were also sampled. In a first study, we verified that individuals of *Monastria* were not present in tree plantations, or secondary regrowth forests, even when they were very near forests where they were abundant (i.e. less than 1km) (Pellens and Grandcolas, 2007). So, we limited our fieldwork to forests with at least three strata, and with areas where dead trunks and branches were observed in the understory. Every forest physiognomy of the biome and all forests

located at the extreme of distribution of the Atlantic forest were sampled. This made a total of 26 sites with presence and 21 with absences.

Sampling was made through walks perpendicular to main trails looking for their microhabitat, i.e., dead trunks lying in the forest ground. Each trunk observed was turned in order to search for individuals. This procedure was repeated until finding the first individual for declaring presence. Nevertheless, we often collected some more individuals in order to have exemplars for taxonomic and molecular studies. Absences were assumed after 8 hours of field search, period in which at least 20 clumps of dead trunks were prospected. The great majority of the absences recorded here are related to the present quality of site. I.e. in some regions the only forest remaining are either very disturbed native forests or secondary old regrowth. This environment markedly reduces the chances of finding *Monastrinia*.

Climate Data

We used Bioclim variables obtained in WORLDCLIM Version 1.4 database (<http://www.worldclim.org>; Hijmans et al. 2005), in 30-arc second resolution. In order to reduce collinearity (e.g. Kramer-Schadt et al. 2013), we eliminated variables where Pearson's $r > 0,80$ and retained the variables correlated with more variables. So, the analysis was limited to only eight of them (Table 1).

Analysis

ENMs were modeled with MaxEnt 3.3.3 (Phillips et al. 2004). We chose to use this method due to its excellent predictive performance when compared to several other ENM methods, independently if they are based on presence only or if they characterize background with a sample (Elith et al. 2006; 2011; Hernandez et al. 2006). In all analyses performed in this study, 70% of the data was used in training and 30% was retained as test points. We employed the subsample parameter for the replicates and set “maximum training sensitivity plus specificity” as the threshold, which means that habitats are labeled as suitable when probability \geq threshold.

The parameters for the maximum number of interactions and replicates were set as 5000 and 20, respectively, and all analyses were based on the mean of the 20 replicates. The similarity between the two ENM's was quantified with the I-statistics using the program ENMTools (Warren et al. 2008). This statistic compares the overlap of full grid-cells in a given area, producing results varying from 0 (no overlap) to 1 (identical models).

MaxEnt predictions are presented in a continuous cumulative probability field. We transformed this probability field into binary maps of “suitable” (upper class) versus “unsuitable” for calculating and comparing the distribution area. These maps were transformed into polygons used to calculate the final area with ArcGis 10.4.

Assessing biases and analyzing its effect in the dataset

Biases in the dataset were assessed in two ways. The first was the estimation of the aggregation of points in the geographic space. It was tested with Averaged Nearest Neighbor calculated in ArcGis 10.4. The second was the evaluation of sample biases in climate space. This was done through the assessment of differences in probability of occurrence between observed and expected number of points (Kadmon et al. 2004; Loiselle et al. 2008). Following the basic MaxEnt output, the climate space was divided into 9 equal-interval bins based on the range observed within the Atlantic Forest. Then we calculated the number of sampling points and the proportion of points expected based on the area covered by each bin. For each climate variable, bias was calculated as

$$Bias_d = \frac{n_d - p_d N}{\sqrt{p_d(1 - p_d)N}}$$

where n_d is the number of localities collected within climate bin_d, p_d is the probability that a collecting locality falls within climate bin d given the area covered by that bin, and N is the total number of collecting localities.

In order to check the implications of climate biases on the ENMs of collection data we designed a rarefaction strategy to delete points in order to make subsets of the dataset, which was used to model the niche and then to compare the area estimated and AUC training and test. We limited this analysis to Annual Precipitation based on the fact that this variable is the one with greatest difference in range covered between the niches with the two datasets. Two forms of rarefaction were employed. In the first we eliminated 30%, 40%, 45% and 55% of the points from the most skewed climate class (11, 15, 17 and 21 points, respectively) chosen at random. In the second, we deleted the same number of points at random from the entire dataset. Comparisons were made with results of twenty replicates for each situation.

Results

Characterization of the Datasets

Our dataset was composed of 82 occurrence data: 56 from Museum collections and literature (hereafter NHC) resulting from 23 independent samples (S1 Appendix), and 26 from the called target sampling (TS). Twenty additional locations were studied with the target sampling without finding *Monastria* (Fig 1).

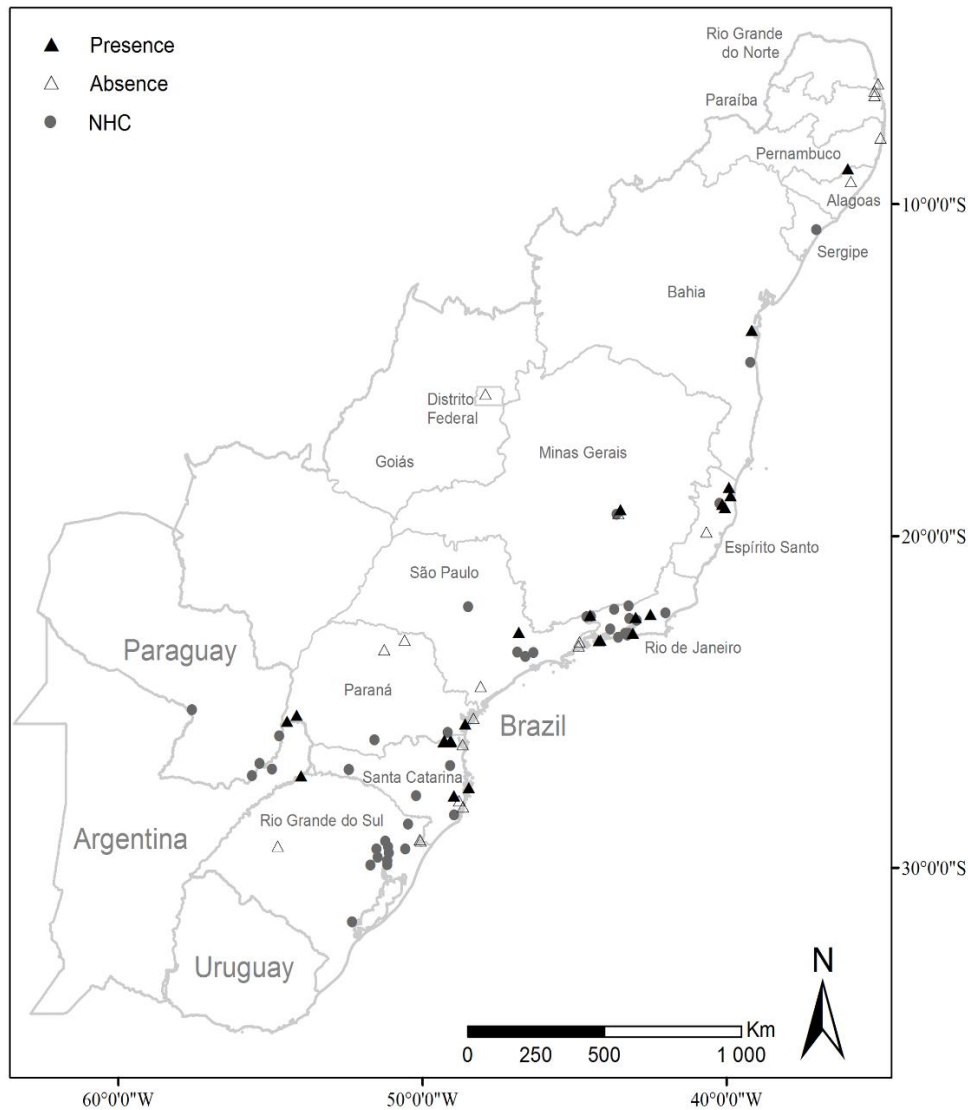


Fig 1. Distribution of the sampling records of *Monastria* in the Brazilian Atlantic forest. Full circle: Data from NHC; fTriangles: Data of presence (full triangle) and absence (empty triangle) obtained with target sampling.

As most of these absences looked associated to the present degradation of forests, they were not used as pseudo-absences. Both occurrence records cover about the entire range of

the Atlantic forest. But NHC dataset includes records much further in the south and west whereas the TS dataset includes presences in the extreme northeast. Despite these differences in the geographical space, the range of the occurrence in environmental space is quite similar (Table 1).

Table 1. The eight Bioclim variables used in this study. Abbreviation, full name, and minimum and maximum values (and respective difference) of the occurrence records with a target sampling (TS), and a dataset from natural history collections and literature (NHC).

Abbreviation	Variable	TS		NHC		TS - NHC		SD
		Min	Max	Min	Max	Min	Max	
bio01	Annual Mean Temperature	154	242	152	255	2	-13	-11
bio02	Mean Diurnal Range	63	130	64	140	-1	-10	-11
bio03	Isothermality	46	69	47	67	-1	2	1
	Max Temperature of Warmest							
bio05	Month	233	321	248	338	-15	-17	-32
bio12	Annual Precipitation	1197	2102	1177	2171	20	-69	-49
bio13	Precipitation of Wettest Month	173	313	132	338	41	-25	16
bio14	Precipitation of Driest Month	11	124	8	156	3	-32	-29
bio15	Precipitation Seasonality	10	81	9	86	1	-5	-4

SD - Sum of the difference

Assessing distribution with the two different datasets

MaxEnt performed well in both analyses. The training AUC (area under the receiver operating characteristic curve) was slightly higher for the ENM with collection data (0.9429), than in the ENM with data from our samples (0.9381). In both cases it strongly rejected the hypothesis that test points were predicted no better than by a random prediction. No locality point fell outside the total distribution area predicted by the model, although some of them were found in areas with low predicted suitability (Fig. 2). The I-statistics indicates that the entire area of ENMs estimated with the two datasets strongly overlap ($I=0.92$).

The analysis of contribution of the different variables indicated that Bio02 was the one with highest regularized trained gain, with 31.1% and 29.2%, followed by Bio03 and Bio14 for collection and target sampling, respectively. It shows that the most suitable areas for *Monastria* were those with low mean diurnal range in temperature (Bio02 and Bio03), which, in this region, was mainly determined by variations in precipitation during the driest month (Bio 14) (Table 2).

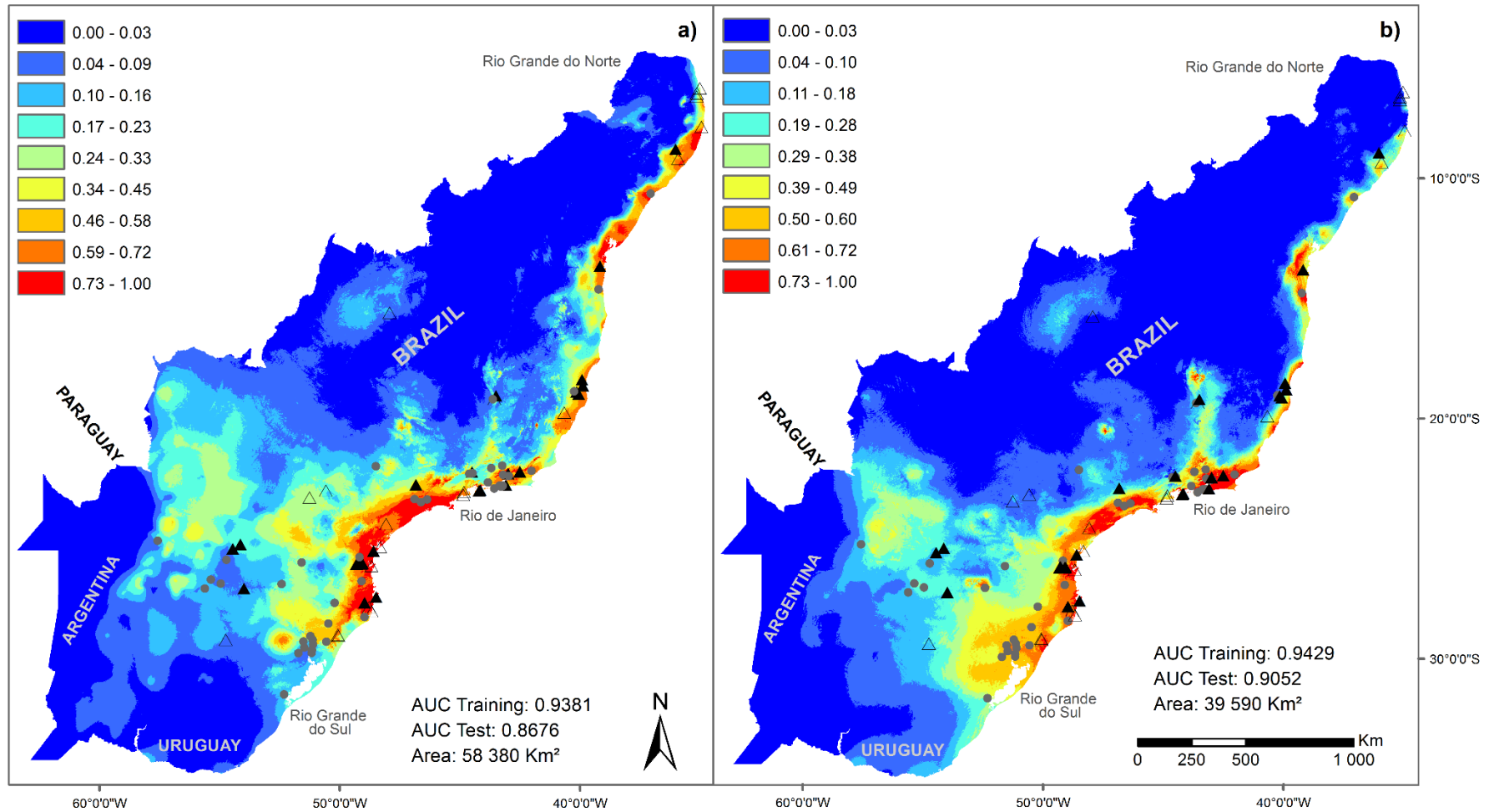


Fig 2. Ecological niche models of the cockroach *Monastria* in the Neotropical Atlantic Forest made with two different datasets. A) Data from a target sampling aimed at detecting the occurrence in different phyto-physiognomies of the biome and the altitudinal, latitudinal and longitudinal extreme limits of distribution. B) Data from Natural History Collections and literature. Values of AUC training, test and area are the mean of 20 replicates.

Table 2. Relative contributions and permutation importance of the variables used for modeling the niche of *Monastria* with data issuing from two different datasets.

Variable	TS		NHC	
	Percent contribution	Permutation importance	Percent contribution	Permutation importance
bio01	0.2	0.2	0.7	1.2
bio02	29.2	20.4	31.1	25.2
bio03	1.4	7.6	24.5	48.2
bio05	16.7	6.5	8.6	2.1
bio12	0.5	0.1	12.9	16
bio13	20.1	33.8	2.7	0.8
bio14	27	27.9	18.8	1.9
bio15	4.9	3.6	0.7	4.6

In spite of this, the ENMs differed markedly in extent of suitable area. The range estimated with NHC data corresponded to only 67% of that with our recent sampling, indicating suitable areas much concentrated in the humid forests at the central region of the biome, particularly in the region of Rio de Janeiro. The model produced with the TS dataset showed additional suitable areas in the Northeast, where *Monastria* was not known before. Another important difference was detected in the extreme south at the interior of Rio Grande do Sul, both with several records in the NHC dataset, but not identified as suitable with the model produced with it (Fig. 2). As a result of this failure to detect suitable areas at the extreme northeast, the range of two out of nine species of this genus were not or very poorly detected with the dataset from NHC (Fig. 3). The response curves show that annual precipitation (Bio12) was the environmental variable with highest difference between the two models, with a range about 1/3 wider in the models with data from the target sampling (Fig. 4).

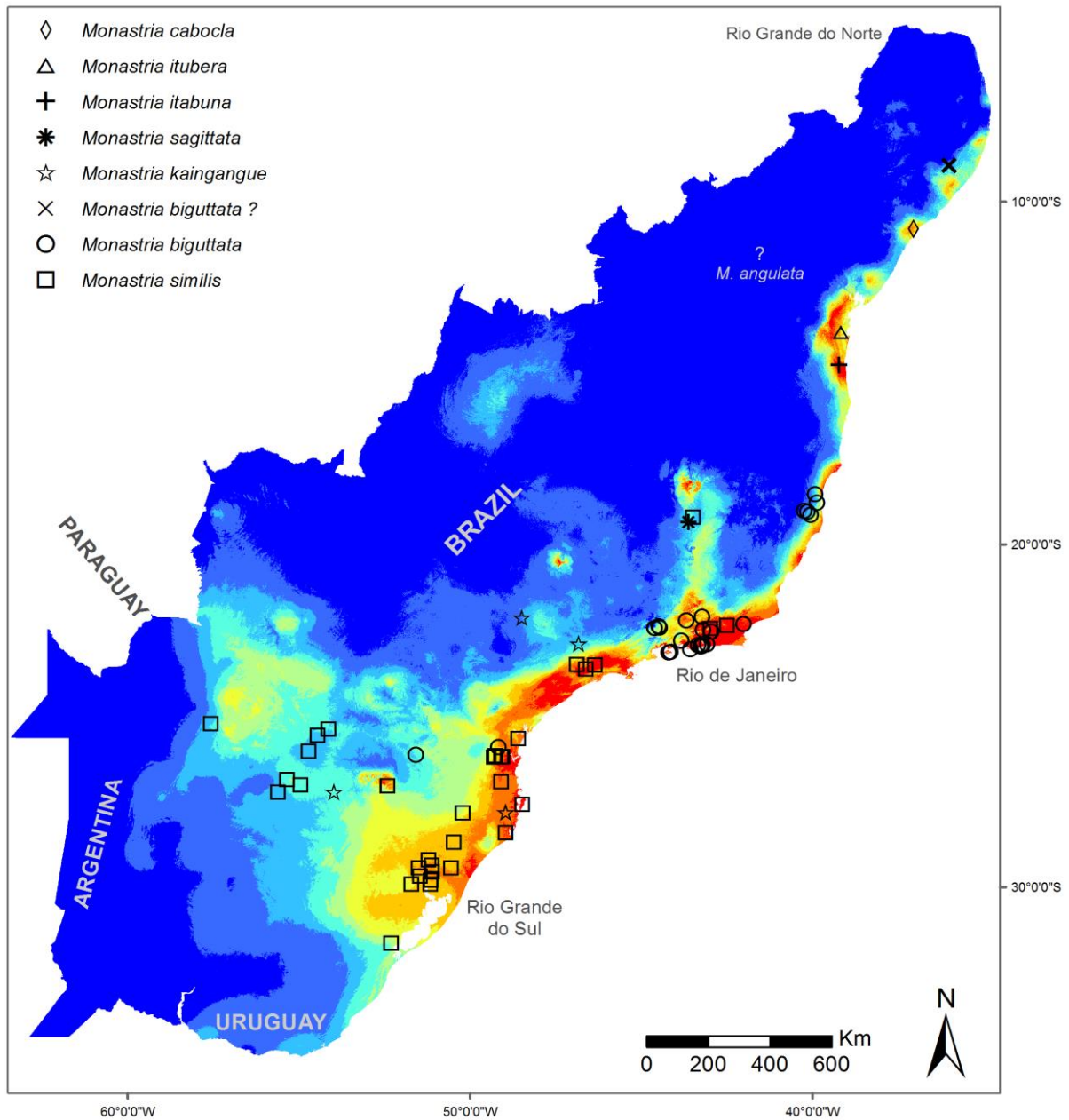


Fig 3. Distribution of the nine species of *Monastria* in the ENM's dataset from Natural History Collections and literature.

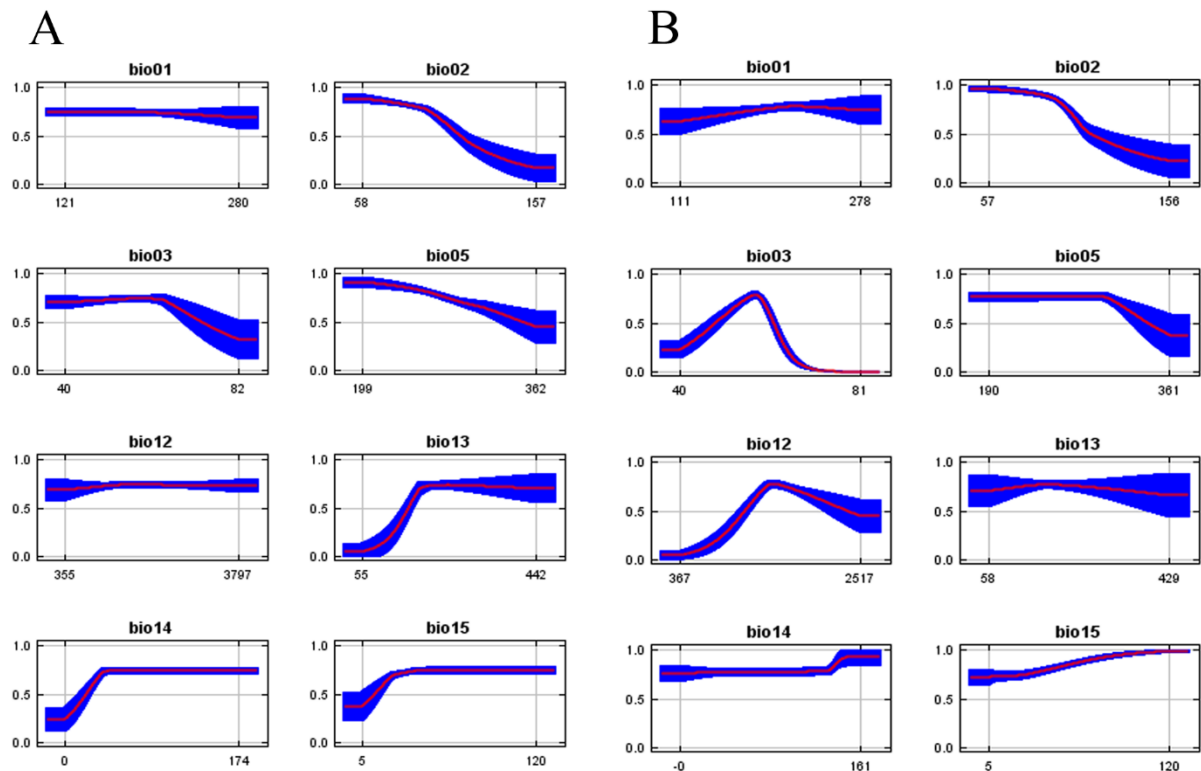


Fig 4. The response curves of the eight bioclim variables used in this study. The curves show the mean response of the 20 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

Testing for possible biases in the datasets

The test of spatial aggregation showed that, although values were significant for both datasets, they were much higher in the data from NHC (Z -score= -5,892; $p < 0,0001$) than that in the target sampling (Z -score= -2,2901; $p = 0,022$). It means that the observed average distance between points was much lower than expected at random, especially in the NHC dataset.

The analysis of climatic biases shows that points of occurrence from the two datasets were recorded in the same climate classes, and that the intermediate climate class 4 was the most biased one. Nevertheless, biases were much higher (more than twofold) in NHC than in TS dataset, particularly for Bio2, Bio5 and Bio12 (Table 3).

Table 3. Values of Bias_d calculated with data from a target sampling (TS) and data from natural history collections and literature (NHC) for eight climatic variables used to estimate ENMs of *Monastria* in the Brazilian Atlantic forest.

Climate classes	Bio01		Bio02		Bio03		Bio05		Bio12		Bio13		Bio14		Bio15	
	TS	NHC	TS	NHC	TS	NHC	TS	NHC	TS	NHC	TS	NHC	TS	NHC	TS	NHC
1	-2.17	-2.08	-0.61	0.00	0.00	3.56	2.46	-1.62	-1.02	-2.34	-1.02	-1.44	-1.63	-0.94	-1.02	4.04
2	-3.40	-2.67	0.00	-0.52	2.04	2.88	1.47	2.37	-1.84	-2.59	-2.17	0.40	0.74	0.36	-1.23	0.43
3	1.00	0.00	1.84	1.30	1.47	0.00	-0.61	0.00	1.47	0.00	0.00	0.00	2.46	0.38	-1.63	-1.82
4	-2.42	0.70	5.15	9.34	1.47	1.82	0.00	6.09	4.35	9.77	0.00	0.00	-1.09	-0.40	5.44	-2.18
5	-1.40	1.73	-1.09	-2.18	1.02	1.91	-1.23	-0.93	3.07	0.86	-0.74	-0.34	3.68	-0.40	3.68	1.78
6	-0.93	1.73	-1.00	0.34	-0.54	-2.29	-1.47	1.19	-1.49	0.52	2.17	-0.43	1.47	2.02	-1.63	1.30
7	-1.40	0.86	-1.40	-1.73	0.47	0.52	1.63	-1.82	-1.84	-3.06	-0.74	1.19	-0.61	0.52	-1.02	-1.62
8	-0.47	0.43	-1.02	-3.14	-2.79	-3.91	-1.23	-2.42	-2.17	-2.34	0.74	1.73	-2.49	-2.42	-1.09	1.78
9	-2.49	-0.94	-1.02	-1.44	-0.74	-1.78	-1.47	-0.52	-1.02	-2.83	1.23	-1.15	-1.02	1.44	-1.84	-2.16

The larger Bias_d values are given in bold

Effect of rarefaction on the collection dataset

Since Bio12 was the environmental variable with highest difference in range between the two models (Fig. 4) we chose to use it to test the effect of rarefaction on the environmental space.

As expected, AUC values were significantly reduced with rarefied data, especially AUC training (One-way ANOVA $F= 4.4185$ $p<0.0001$ $DF=8$; and $F= 2.9906$; $p=0.004$; $DF=8$ for AUC training and test, respectively). But, the estimated suitable areas were significantly higher (One-way ANOVA $F= 11.72348$ $p<0.0001$ $DF=8$).

The comparison of two ways of rarefaction showed important differences concerning AUC training and area. AUC training varied markedly and not linearly when the dataset was rarefied by deleting points in the most biased climate class. But, when 21 points was deleted, the values from the two modes of rarefaction were very similar and also similar to the that estimated with all the NHC dataset. The values of AUC test were very variable among the 20 models produced for each situation (see standard deviation bars in Fig. 5), so showing no significant differences between ways of rarefaction, except for the interaction (Table 4). Concerning suitable area, the differences between the two ways of rarefying increased with the number of points deleted. In the class with 21 points (55%) deleted, the area estimated with data rarefied in the most biased climate class was even broader than that obtained with target sampling (Table 4; Fig. 5).

Table 4. Results of two-ways ANOVA comparing the effect of rarefaction on the collection data (See Fig. 2 for more information)

	Mean Square	d.f.	F-value	Significance
AUC Training				
Entire dataset X Most Biased dataset	0.002	1	18.0288	< 0.0001
Number of Points Deleted	0.0003	3	2.7477	0.0449
Interaction	0.0002	3	2.1301	0.0987
AUC Test				
Entire dataset X Most Biased dataset	0.003	1	2.9773	0.0864
Number of Points Deleted	0.0021	3	2.0755	0.1058
Interaction	0.0046	3	4.5134	0.0046
Area				
Entire dataset X Most Biased dataset	500478428	1	3.1422	0.0782
Number of Points Deleted	1700097789	3	10.674	< 0.0001
Interaction	593681737	3	3.7274	0.0127

Bold numbers correspond to a statistical significance ($p < 0.05$)

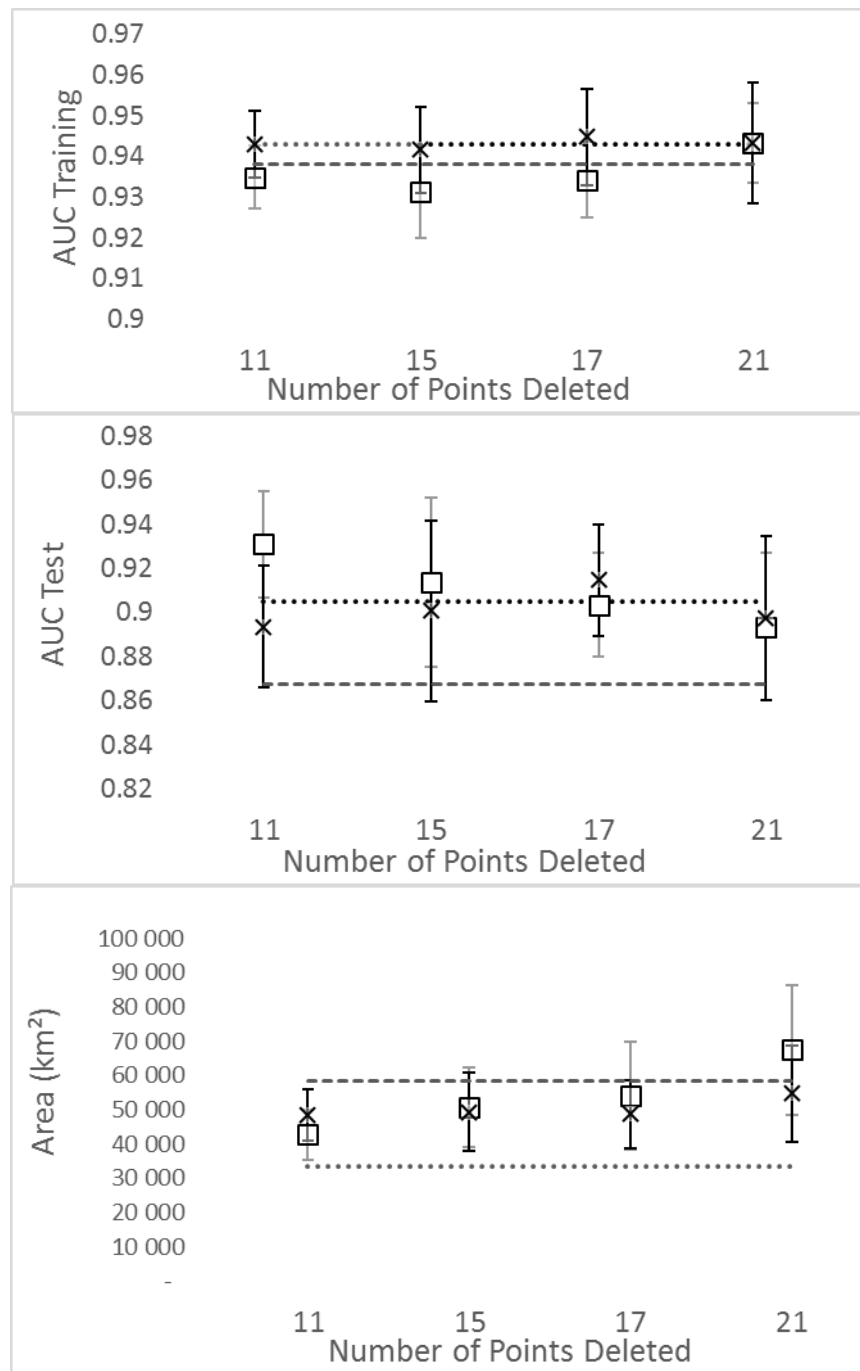


Fig 5. AUC training, AUC test and area estimated with NHC and literature data rarefied in two different ways. □ Mean and SD (gray line) using a dataset in which points were deleted at random only from the most biased climate class of Annual Precipitation (class 4 in Table 2); × Mean and SD (black line) using a dataset in which points were deleted at random in the entire dataset. In both cases the same number of points was deleted. They represented 30, 40, 45 and 55% of the points in the most biased climate class. Dotted line: Mean values estimated with NHC and literature data. Dashed Line: Mean values estimated with data from the target sampling.

Discussion

In both cases, the model performance was particularly high, especially because of the important breadth of the distribution range (Fig. 4) (Barbet-Massin et al. 2012). Nonetheless, the TS dataset allowed for better prediction of suitable areas for *Monastria* than the NHC dataset. Had we used the model with the NHC dataset to predict where to find new species of *Monastria*, we had excluded two out of nine species of this study. The differences between the two datasets were not only in regions under-sampled by the NHC collection dataset, as in the northeast, but also in regions well sampled in the south and southwest. This suggested that the problem was not in the geographic, but in the environmental space.

This hypothesis was confirmed by the analysis of climate biases, which showed significant differences in representation in different climate bins between the two datasets. Biases in sampling arise by (1) overrepresentation of samples in some climate classes (positive values), (2) absence or low representation in others (negative), or (3) a combination of both. Here we identified that collection data of *Monastria* is strongly overrepresented in moderate climate ranges.

The results of the rarefaction confirmed the conclusions on the importance of sampling biases for explaining the differences in area in ENMs estimated with the two datasets. The increase in estimated suitable area with rarefaction independently of the way data were deleted brings one more argument to the importance of filtering. Some studies have shown that suitable areas also increase when filtered in geographical space (Kramer-Schadt et al., 2013; Boria et al. 2014), i.e., by deleting redundant points occurring at an arbitrary distance from each other. However, a recent study comparing the effects of filtering in geographical and environmental space for virtual species shows that the utility of geographic filters is quite unlikely generalized to several places. In fact, it can increase climate biases in areas with heterogeneous and repeated environments across different geographic scales (Varela et al., 2014).

The second point contributing to this conclusion was that rarefaction did not necessarily imply in a decrease in model performance, as shown by variations in AUC. This is contrary to that observed by Kramer-Schadt et al. (2013) and Varela et al. (2014) when using spatial filters, and in accordance with the observation of Varela et al. (2014) when using environmental filter. It indicates that, when environmental bias is reduced, other combination of variables become evident, so leading to robust models with much less data (Fig. 5).

Excluding data is a crucial choice when dealing with NHC datasets, particularly because very often the number of data available is not enough to make good inferences on the species distribution range (Feeley and Silman 2011). Nevertheless, as shown by the present results, and also by Kramer-

Schadt et al. (2013), Boria et al. (2014), and Varela et al. (2014) if biases are detected it is necessary to find a way to reduce it.

Our results show that testing for climate biases (Kadmon et al. 2004; Loiselle et al. 2008) is a very important step in this evaluation. It shows that, overrepresentation of samples in a climate class favors the maximization of model's specificity. This means that the suitable areas are predicted in climate spaces with higher number of records. In other words, the model outcomes are very good at finding true positives, but it fails in predicting some false negatives, i.e. it does not predict the presence in some places where the species really occurs.

The second outcome of this study is how to filter in order to enhance model's sensitivity. By comparing two strategies of deleting points at random in the environmental space, we showed that acting on the most biased climate class is more effective so allowing detecting other suitable areas.

This calls the attention to the importance of clearly defining the aim of the study when using SDMs in order to decide the best way to use the data available (Guillera-Arroita et al. 2015). For example, if we are looking for the best site to place a reserve, it is desirable to maximize specificity (i.e. the chances that the species occur in the site). So, considering all points may be the good choice, as it reduces the chances of commission errors, i.e., the probability of inferring the presence when a species is not there. Nonetheless, if the aim is to screen all possible habitats in order to find new species of the same genus as was in the case in this study, or to make inferences about future availability of suitable habitats, sensitivity is highly important. In this case, detecting environmental biases and rarefying by reducing the number of occurrences on the most biased class can be a straightforward strategy, as it leads to robust models enlarging the possibility of places to be screened.

To conclude, NHC is a goldmine of data available to biodiversity prospection. But, these data embody several biases, and there is an urgent need to find ways to deal with them in order to make better prediction. In this respect, field validation is crucial, as it is the only way to test the predictions (Robbirt et al. 2011, Anderson et al. 2016). The study of genus *Monastria* in the Brazilian Atlantic forest showed the need to look for climate biases in models with MaxEnt, and the solution proposed here is likely to be useful in any situation where this kind of bias is detected.

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Supporting information

S1 Appendix. Twenty three references with location records used in NHC dataset.

1. Becker CJ (1984) Preliminary survey of the Blattaria of the state of Rio Grande do Sul, Brazil. *Revista Brasileira de Entomologia* 28: 87-98.
2. Brunner von Wattenwyl C (1865) *Nouveau Système des Blattaires*.
3. Couri M, Nessimian, J., Mejdalani, G., Monne, M.L., Fraga, S.M.L., Mendonca, M.C., Monteiro, R.F., Buys, S.C. & Carvalho, R. A. (2009) Levantamento dos insetos da Mata Atlântica do Estado do Rio de Janeiro. *Arquivos do Museu Nacional do Rio de Janeiro* 67: 151-154.
4. F. W (1868) *Catalogue of the specimens of Blattarie in the collection of the British Muse: British Museum*. 239 p.
5. M. H (1921) South American Blattidae from the Museum National d'Histoire Naturellen Paris, France. *Proceedings of the Academy of Natural Sciences of Philadelphia* 73: 193-304.
6. Pellens R, Grandcolas P (2003) Living in Atlantic forest fragments: life habits, behaviour, and colony structure of the cockroach *Monastria biguttata* (Dictyoptera, Blaberidae, Blaberinae) in Espírito Santo, Brazil. *Canadian Journal of Zoology* 81: 1929-1937.

7. Pellens R, Grandcolas P (2007) The conservation-refugium value of small and disturbed Brazilian Atlantic forest fragments for the endemic ovoviviparous cockroach *Monastria biguttata* (Insecta : Dictyoptera, Blaberidae, Blaberinae). *Zoological Science* 24: 11-19.
8. Pellens R, Grandcolas (2008) Catalogue of blattaria (insecta) from Brazil. *Zootaxa*: 1-109.
9. Princis K (1946) Colombianische Blattodeen, gesammelt von Herrn G. Dahl und Frau M. Althin-Dahl in den Jahren 1936–1939. *Kungl Fysiografiska Sällskapet i Lund Förhandlingar* 16: 172 pp.
10. Princis K (1963) Blattariae: Suborde Polyphagoidea: Fam.: Homoeogamiidae, Euthyrrhaphidae, Latindiidae, Anacompsidae, Atticolidae, Attaphilidae; Subordo Blaberoidea: Fam. Blaberidae. In: Beier M (Ed.) *Orthopterorum Catalogus, Pars 4*. Uitgeverij Dr. W. Junk's - Gravenhage. pp. pp. 77–172.
11. Rehn JAG (1913) A contribution to the knowledge of the orthoptera of argentina. *Proceedings of the Academy of Natural Sciences of Philadelphia* 65: 273-379.
12. Rehn JAG (1920) Records and descriptions of Brazilian Orthoptera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 72: 214-293.
13. Rocha e Silva Albuquerque I (1964) Checklist dos Blattaria brasileiros. *Boletim do Museu Paraense Emilio Goeldi (Nova Serie) Zoologia* 41: 1-37.
14. Rocha e Silva Albuquerque I (1971) Sobre alguns Blattaria de Santa Catarina, Brasil (Dictyoptera). *Revista Brasileira de Biologia* 31: 329-335.
15. Rocha e Silva Albuquerque I (1972) Inventario dos Blattaria da Amazonia, com descricao de tres especies novas. *Boletim do Museu Paraense Emilio Goeldi (ns) Zoologia* 76.
16. Rocha e Silva Albuquerque I (1982) Lista dos Blattodea do Municipio do Rio de Janeiro, RJ, Brasil – (Dictyoptera). *Boletim do Museu Nacional, Nova Serie, Zoologi* 304: 1-20.
17. Rocha e Silva Albuquerque I (1987) Nova contribuição ao conhecimento da fauna de Blattaria (Dictyoptera) do Alto da Mosela, Petrópolis, RJ, Brasil, com descrição de três espécies novas. *Boletim museu nacional do Rio de Janeiro, Nova Série, Zool, Rio de Janeiro*, 312: 1-19.
18. Roth LM (1970) Evolution and Taxonomic Significance of Reproduction in Blattaria. *Annual Review of Entomology* 15: 75-&.
19. Saussure H (1864) Orthopteres de L' Amerique Moyenne. *Mémoires pour servir à l'histoire naturelle du Mexique*, . 255 p.
20. Saussure H (1864) Blattarum novarum species aliquot. *Revue et Magasin Zoologie* 2: 341-349.
21. Stål C (1855) Entomologiska Notiser. *Ofversigt af Kongliga Vetenskaps-Academien förhandlingar* 12: 342-355.

22. Thunberg CP (1826) *Blattarum novae species descriptae*. 276 p.
23. Vanschuytbroeck P (1969) *Catalogue des Blattariae conservés dans les collections entomologiques de l'Institut royal des Sciences naturelles de Belgique. Polyphagoidea et Blaberoidea*. *Bulletin of the Royal Belgian Institute of Natural Sciences* 45: 1-21.

S1 Table. Eleven collections used in NHC dataset.

Abbreviation	Institution	Locality
MZUSP	Museu de Zoologia da Universidade de São Paulo	Sao Paulo, Brazil
MNRJ	Museu Nacional do Rio de Janeiro	Rio de Janeiro, Brazil
INPA	Instituto Nacional de Pesquisas da Amazônia	Manaus, Brazil
MNHN	Muséum National d'Histoire Naturelle	Paris, France
MHNG	Muséum de Histoire Naturelle de la Ville de Genève	Geneva, Switzerland
NRM	Swedish Museum of Natural History	Stockholm, Sweden
MZLU	Lund Museum of Zoology	Lund, Sweden
ME	Museum of Evolution	Uppsala, Sweden
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig	Bonn, Germany
NHM	Natural History Museum	London, United Kingdom
IRSNB	Institut royal des Sciences naturelles de Belgique	Brussels, Belgium

**E) Chapitre V –
Discussion, Conclusion et Perspectives de la Thèse**

Discussion, Conclusion et Perspectives de la Thèse

La taxonomie des Blaberinae et *Monastria*

L'étude de Blattaria du nouveau monde, notamment du Brésil a été marqué par des vagues de descriptions d'espèces et révisions de quelques genres. Tout cela dans un cadre de taxonomie classique portant sur des échantillonnages soit focalisés sur un endroit - comme par exemple Alto da Mosela (Rocha e Silva Albuquerque & Lopes, 1977; Rocha e Silva & Vasconcelos, 1987), les collectes réalisés en Nova Teutônia, SC (Rocha e Silva Albuquerque, 1971), Caruaru, PE (Rocha e Silva Albuquerque, 1974), et Sinop, MT (Rocha e Silva & Aguiar, 1977), soit utilisant des données accumulées dans les collections pendant de longues périodes. Ce cadre erratique fait qu'il n'y a pas de connaissances taxonomique et spatiale homogène pour les Blattaria en général, ce qui rend difficile de répondre aux questions concernant la complétude des connaissances taxonomiques, la distribution, l'origine, et la diversification de Blattaria. C'est d'autant plus dommageable que les données disponibles sur la biodiversité ne constituent pas seulement un grand répertoire taxonomique mais aussi un fond de connaissances qui devraient pouvoir être utilisées à tous égards. Cette thèse a contribué principalement à mieux comprendre ce problème et à proposer des solutions statistiques pour les utilisations futures.

La sous-famille des Blaberinae est un groupe néotropical particulier, avec des adultes de grande taille, souvent très visibles et donc en général pas complètement méconnus. Mais les genres endémiques de la forêt atlantique, dont *Monastria* Saussure, 1864 fait partie, comprennent des Blattes très spécialisées et inféodées à des habitats particuliers (Grandcolas, 1993; 1998;

Pellens et al., 2007). Les individus réfugiés dans leurs habitats sont donc rarement récoltés par des pièges lumineux ou des pièges de Malaise. Par conséquent, bien que les premières espèces de ces genres soient décrites depuis le début du XVIIIème siècle (Thunberg, 1826; Princis, 1963; Pellens & Grandcolas, 2008), les Blaberinae de la forêt atlantique restent passablement méconnues et ne sont pas les plus communes dans des collections d'histoire naturelle. La capture des individus reste en effet très dépendante d'une recherche dirigée vers leurs habitats (Shao & Bell 1986; Grandcolas 1994; Pellens 2002).

Même dans le cas de ce groupe de taille moyenne présent dans les collections naturalistes, l'étude taxonomique réalisée dans cette thèse a montré que moins de la moitié des espèces était connue et que trois de ces espèces ont été découvertes grâce à des échantillonnages très récents: *M. kaingangue*, *M. itubera* et *M. itabuna*. Ce travail a aussi mis en évidence les problèmes liés à des travaux indépendants menés par plusieurs taxonomistes anciens sur les mêmes spécimens, qui ont amené à une nomenclature chargée et complexe, avec une multiplication des noms pour les mêmes espèces. Le présent travail de taxonomie a permis la résolution de ces problèmes nomenclaturaux.

Un autre aspect de la taxonomie de ce groupe concerne l'ancienneté des descriptions, souvent basées sur un seul spécimen ou sur des caractères très généraux (couleur, forme du pronotum, forme de l'aile). La recherche des caractères morphologiques et les échantillonnages récents ont été ainsi très importants pour la re-définition des espèces en se basant sur des individus des deux sexes. Dans cette étude, on a exploré et inclus par la première fois plusieurs autres caractères morphologiques ainsi que la description des genitalia, mâles et femelles. Ceux-ci étaient totalement inconnus pour ce genre et même pour les autres genres de Blaberinae endémiques de la région.

L'élaboration d'une clé de détermination pour les jeunes des Blaberinae endémiques de la forêt atlantique a été un autre point important de cette étude. Les larves sont trouvées beaucoup plus souvent que les adultes et des élevages sont très fréquemment nécessaires pour l'obtention des adultes nécessaires à la réalisation de diverses études, même taxonomiques (Pellens & Grandcolas, 2003). En outre, les individus des différents genres sont facilement confondus et peuvent cohabiter. Par exemple, un tronc d'arbre en décomposition sur le sol peut abriter larves de *Petasodes* sous l'écorce, de *Monastria* sur l'écorce sous le tronc, et de *Minablatta* dans la poussière, le sable ou la sciure en décomposition en dessous du tronc (Grandcolas, 1991; 1994; Pellens, 2002). Pouvoir caractériser les genres avec des larves se révèle donc indispensable pour tous ceux qui souhaitent travailler sur cette faune. Enfin, ce travail nous a permis de vérifier une fois de plus que les concepts d'espèces ne devaient pas être idéalisés et gagnaient à la confrontation d'analyses morphologiques, moléculaires, phylogénétiques et populationnelles (Sites & Marshall, 2004). Dans le cas présent, il sera intéressant dans le futur que des études supplémentaires puissent renseigner sur les raisons des non-monophylies constatées chez au moins deux espèces du genre *Monastria*.

La diversification de *Monastria* et des Blaberinae

L'étude de la diversification du genre dans la forêt atlantique a aussi apportée des résultats nouveaux et intéressants, mettant en évidence le rôle du climat passé assez ancien dans la distribution actuelle des espèces. Ces résultats sont en accord avec des études récentes qui montrent toute la grande importance de la stabilité climatique en particulier au NE de la forêt atlantique pour la diversification et la survie de cette diversité à travers des périodes de temps longues (Carnaval et al., 2009; de Mello Martins, 2011). Dans le cas de notre étude, il est

intéressant de montrer que l'épisode maximum glaciaire le plus ancien (22000 ans) est celui qui semble être lié le plus significativement à la répartition et à la diversification de *Monastria*.

L'étude d'autres groupes endémiques de la forêt atlantique pourra contribuer à éclairer la mesure dont ces facteurs ont impacté différents organismes dépendant des écosystèmes forestiers (de Mello Martins, 2011). Parmi eux, une étude sur le genre *Petasodes* est faisable dans le court terme. *Petasodes* a été le groupe le plus récolté pendant les recherches de terrain destinées à étudier *Monastria*. Les individus de *Petasodes* ont plus d'aptitude à se disperser, car mâles et femelles ont de longues ailes et peuvent voler; ils ont été trouvés dans des forêts avec de degrés de perturbations très divers (Pellens and Grandcolas, unpublished). Donc, le fait d'être des espèces plus mobiles et moins dépendantes des forêts très préservées comme *Monastria*, pourra renseigner sur d'autres facteurs qui ont amené à la diversification dans cette région. Cependant, comme pour *Monastria*, il serait nécessaire de commencer par une révision taxonomique et par la description des nouvelles espèces, car la taxonomie de *Petasodes* est aussi en grand besoin de révision (Pellens & Grandcolas, 2008).

Parmi les grands biomes du Brésil, la faune de Blattaria est sans doute plus riche dans les biomes forestiers avec 227 espèces connues de l'Amazonie et 519 répertoriées dans la forêt atlantique (environ 26% et 65%, respectivement, des occurrences dans différents états du pays) (Pellens & Grandcolas, 2008). Quand on observe les différences de surface entre ces deux biomes, on s'aperçoit que d'autres facteurs que l'état réel de la diversité biologique sont responsables pour les différences observées. En effet, les biais d'échantillonnage sont en faveur des régions les plus peuplées et les plus actives au plan économique, ce qui augmente l'accès à plus de sites par plus de collecteurs et donc augmente au final la diversité capturée (e.g. Araujo, 2003; Golding et al. 2010). Dans la région de la forêt atlantique, les universités et les centres de recherche sont ainsi

beaucoup plus nombreux qu'en Amazonie, ce qui amène bien plus d'opportunités de prospection de la biodiversité (Mooerman & Eastbrook, 2006; Pautasso & McKinney, 2007).

Si l'on se permet d'inférer la richesse d'un biome à partir de ce qui est connu dans un autre où l'échantillonnage est plus complet, on peut donc espérer qu'une grande richesse spécifique de Blattaria est encore à découvrir en Amazonie. Ceci met en évidence l'intérêt d'intensifier les échantillonnages dans cette région dans un futur proche. Pour l'instant, la faune de Blattes de l'Amazonie est bien connue dans la région de la Guyane Française (e.g. Grandcolas 1994), et autour de Manaus (e.g. Lopes et al., 2014). Des échantillonnages couvrant d'autres parties du territoire, ainsi qu'un échantillonnage dans la diagonale sèche (i.e. le Cerrado et la Caatinga), pourront contribuer à mieux comprendre la transition entre ces deux biomes forestier majeurs et des facteurs qui ont amené à l'endémisme dans ces régions (Costa, 2003; Ledo & Colli, 2017; Sobral-Souza et al., 2015).

Données, biais et aire de répartition actuelle et future

La troisième étude développée dans le cadre de cette thèse a mis en évidence le grand besoin de considérer les biais d'échantillonnage lors de l'utilisation des données des collections naturalistes pour inférer la distribution spatiale des organismes. C'est une problématique actuelle importante. Dans l'urgence scientifique ou de la gestion des territoires, il est important de pouvoir s'appuyer sur toutes les données disponibles, d'autant qu'elles peuvent en outre renseigner sur des tendances récentes d'évolution des faunes et des flores (Suarez & Tsutui, 2004). Les spécimens trouvés dans les collections résultent des échantillonnages erratiques qui portent des biais spatiaux et environnementaux. Malgré le fait que plusieurs études avaient déjà montré l'importance de ces biais avec des espèces virtuelles (Varela et al., 2014) ou en utilisant des filtres temporels (Feeley &

Silman, 2011) ou spatiaux (Kramer-Schadt et al., 2013; Boria et al., 2014), très peu d'études sur ces biais ont été faites en les contrôlant avec des validations par des échantillonnages sur le terrain (Anderson et al., 2016). Notre étude nous a permis de voir que les inférences faites à partir des données de collections n'informaient pas correctement sur l'aire d'occurrence de *Monastria* et que la cause était que la plupart des échantillons avaient été collectés dans des forêts humides, provoquant une sur-représentation des données dans une classe de climat bien particulière. Pour contrer ce biais, nous avons donc développé une stratégie de raréfaction se focalisant sur l'espace climatique qui permet d'arriver à des résultats plus en conformité avec la réalité.

Cette stratégie mise au point dans le cas particulier de l'étude de *Monastria* a potentiellement une utilité très générale dans le cadre des études de distribution basées sur des données de collection, études qui sont appelées à se développer fortement.

Cette stratégie est aussi très utile et nécessaire pour la modélisation des futures aires de répartitions dans le cadre des changements globaux et notamment climatiques. Dans ce contexte, une étude qui nous sommes en train de développer traite de la disponibilité de habitats adéquats pour *Monastria* dans des scénarios de changement climatique dans un futur très proche, soit 2050 ou 2070. Cette question est importante pour la forêt atlantique déjà très fragmentée, car plusieurs scénarios indiquent une intensification des conditions climatiques qui sont déjà extrêmes dans cet intervalle de temps très court, surtout au Nordeste où la richesse en espèces est plus importante mais les aires de répartition sont plus petites. Cette situation peut amener à des changements importants dans la distribution des forêts, qui sont déjà devenues rares et distribuées de manière très éparse pendant la fin du XXème siècle. En outre, les fragments de forêt sont séparés les uns des autres par des villes, des parcs industriels, ou des champs agricoles (SOS Mata Atlantica, Inpe 2017). Ceci réduit encore plus la probabilité déjà faible pour les Insectes de pouvoir suivre

l'évolution des surfaces forestières avec le changement climatique (« track the climate change ») et de s'installer aux endroits où les conditions environnementales seraient devenues adéquates.

L'étude de *Monastria* pourra être utile pour mieux comprendre l'effet de ces changements climatiques sur des organismes avec une faible capacité de dispersion dans un environnement morcelé et fragmenté. Ce trait de vie, associé aux rugosités du paysage mentionnées ci-dessus, font que l'avenir à long terme du genre *Monastria* est très dépendant de la continuité des forêts là où les populations de ces Insectes se trouvent maintenant.

En partant de cette hypothèse, on a réalisé un ensemble d'analyses en se basant sur deux différents scénarios d'émission de carbone et deux modèles de climat pour 2050 et 2070 couplées avec la distribution des forêts dans le temps présent. Les résultats montrent une situation très alarmante où dans le meilleur scénario seulement 4,38% de l'aire de répartition *Monastria* serait adéquate dans un futur proche (Figure 1). En regard de la structure extrêmement fragmentée des paysages dans la forêt atlantique, et des difficultés énormes de dispersion des organismes entre fragments, cette question se pose en outre pour une forte partie de la biodiversité de ce biome.

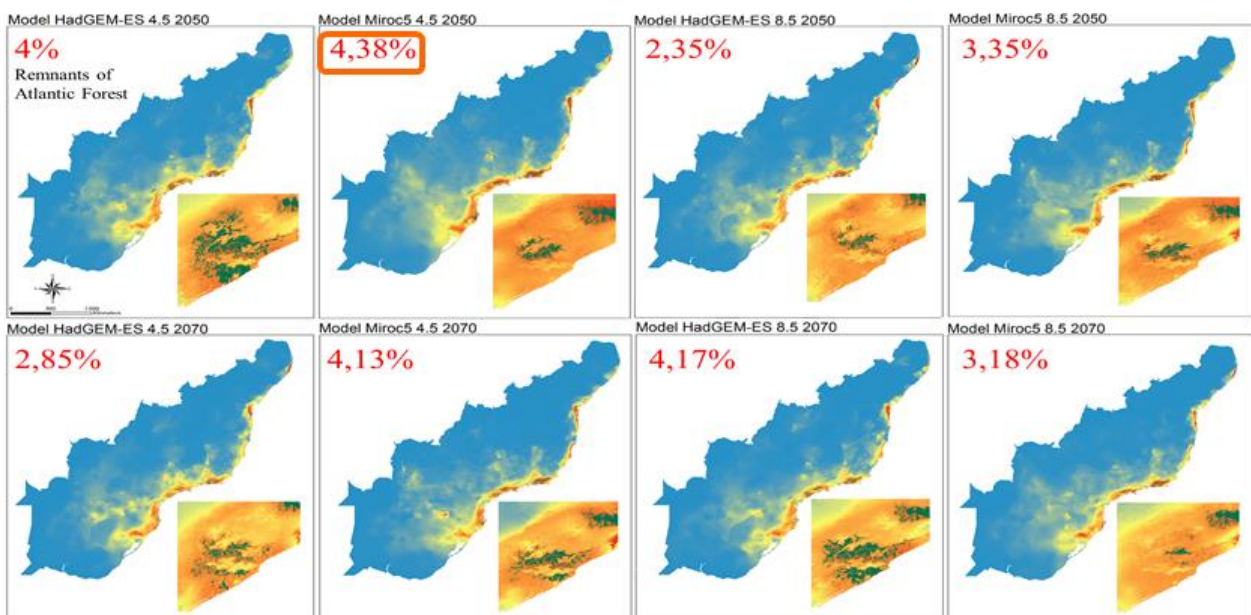


Figure 1. Fragments actuels de la forêt atlantique basé sur deux scénarios d'émission de carbone et deux modèles de climat pour les années 2050 et 2070

Il restera à étudier comment ces évènements impacteront la diversité phylogénétique du genre (Faith, 1992; Pellens & Grandcolas, 2015). Si les espèces qui sont au Nordeste (i.e. *M. itabuna*, *M. itubera*, *M. saqittata* et *M. sp 9*) ont des aires de répartition aussi petites qu'elles sont inférées à partir des modélisations sur les données existantes, il est fort possible que l'espèce sœur des autres *Monastria* soit très menacée, ce qui amènerait à une grande perte dans l'histoire évolutive de ce genre.

La thèse a donc révisé et augmenté un corpus de connaissances taxonomiques à la suite d'un indispensable échantillonnage de terrain. Du fait de la redéfinition des espèces, cette révision a permis de mobiliser toutes les données actuellement disponibles sur le genre étudié dans les collections, et de montrer quels sont à la fois les forces et les défauts de l'utilisation d'un tel lot de données. Le présent travail fait donc le lien entre les nécessités incontournables dans l'étude de la biodiversité, celles pratiquées depuis longtemps - études systématiques et échantillonnages ciblés - et celles à venir dans un monde numérique, - mobilisation des données disponibles. Il permet également de donner un aperçu de la diversité et de la complexité d'un point sensible de biodiversité - la forêt atlantique brésilienne - dont le futur apparaît malheureusement bien sombre dans le contexte des changements globaux.

Références bibliographiques

- Ab'Saber NA (1977) Os domínios morfoclimaticos da América do Sul. Primeira aproximação. *Geomorfologia* 53:1–23
- Alkimim FF (2015) Geological Background: A Tectonic Panorama of Brazil *In: Vieira BC, Salgado AAR, Santos LJC, Landscapes and Landforms of Brazil*. Springer, Dordrecht, 230 pp.
- Anderson OF, Guinotte JM, Rowden AA, Clark MR, Mormede S, Davies AJ, Bowden DA (2016) Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: implications for the use of broad scale models in fisheries management. *Ocean Coast Manage* 120: 110–126.
- Araújo MB (2003) The coincidence of people and biodiversity in Europe. *Glob Ecol Biogeogr.* 12: 5–12. doi:10.1046/j.1466-822X.2003.00314.x
- Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *J Biogeogr.* 33: 1677–1688. doi:10.1111/j.1365-2699.2006.01584.x
- Arruda DM, Schaefer CEGR, Fonseca RS, Solar RRC, Fernandes Filho EI (2018) Vegetation cover of Brazil in the last 21 ka: New insights into the Amazonian refugia and Pleistocenic arc hypotheses. *Global Ecology Biogeography*;27:47–56. <https://doi.org/10.1111/geb.12646>
- Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Meth Ecol Evol* 3: 327–338
- Beck J, Ballesteros-Mejia L, Buchmann CM, Dengler J, Fritz SA, Gruber B, Hof C, Jansen F, Knapp S, Kreft H, Schneider AK, Winter M, Dormann CF (2012) What's on the horizon for macroecology? *Ecography* 35: 673–683.
- Behling H (2002) South and southeast Brazilian grasslands during Late Quaternary times: A synthesis. *Palaeogeogr Palaeoclimatol Palaeoecol* 177:19–27.

- Behling, H, Pillar, VP, Orloci, L, & Bauermann, SG (2004) Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 203, 277–297.
- Behling H, Pillar VD (2007) Late quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and Grassland ecosystems. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 362: 243–251.
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* 275: 73–77.
- Brunner von Wattenwyl, C. (1865) *Nouveau Système des Blattaires*. Vienne : G. Braumüller, 426 pp.
- Burmeister, H (1838) *Blattina*. In: *Handbuch der Entomologie*, Berlin: I.C.F. Enslin, 2, 469– 517.
- Cabanne GS, d'Horta FM, Sari EHR, Santos FR, Miyaki CY (2008) Nuclear and mitochondrial phylogeography of the Atlantic forest endemic *Xiphorhynchus fuscus* (Aves: Dendrocolaptidae): Biogeography and systematics implications. *Molecular Phylogenetics and Evolution* 49, 760–773.
- Caesar, M, Grandcolas, P, Pellens, R (2017) Outstanding micro endemism in New Caledonia: More than one out of ten animal species have a very restricted distribution range. *Plos ONE* 12, e0181437.
- Cancello EM, Silva RR, Vasconcellos A, Reis YT, Oliveira LM (2014) Latitudinal Variation in Termite Species Richness and Abundance along the Brazilian Atlantic Forest Hotspot. *Biotropica*, 46: 441–450. doi:10.1111/btp.12120
- Cardoso da Silva JM, Cardoso de Sousa M, Castelletti CHM (2004) Areas of endemism for

- passerine birds in the Atlantic forest, South America. *Global Ecology and Biogeography* 13, 85–92.
- Carnaval AC, Moritz C (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography* 35, 1187–1201.
- Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science* 323: 785–789.
- Carnaval AC, Waltari E, Rodrigues MT *et al.* (2014) Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20141461.
- Caruso F, Suguio K, Nakamura T (2000) The quaternary geological history of the Santa Catarina southeastern region (Brazil). *Anais da Academia Brasileira de Ciências*, 72, 257–270.
- Colombo AF, Joly CA (2010) Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. *Brazilian Journal of Biology* 70: 697–708
- Costa LP, Leite YLR, da Fonseca GAB, da Fonseca MT (2000) Biogeography of South American Forest Mammals: Endemism and Diversity in the Atlantic Forest. *Biotropica* 32, 872–881.
- Costa LP. (2003) The historical bridge between the Amazon and the forest of Brazil: a study of molecular phylogeography with small mammals. *J Biogeogr.* 30: 71–86. doi:10.1046/j.1365-2699.2003.00792.x
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT (2007) Random forests for classification in ecology. *Ecology* 88: 2783–2792.
- Dalman JW (1823) *Analecta entomologica*. Typis Lindhianis, Holmiae, 104 pp.
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32:1792–1797.

- Elith J, Graham CH, Anderson RP et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129-151.
- Elith J, Phillips S, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *DiversDistrib* 17: 43-57.
- Eschscholtz JF (1822) *Entomographien*. Erste Lieferung. Berlin, G. Reimer, 128 + 3 pp, 2 col. pls.
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61: 1-10.
- Feeley KJ, Silman MR (2011) Keep collecting: accurate species distribution modelling requires more collections than previously thought. *Divers Distrib* 17: 1132-1140.
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *IntJ Climatol* 37: 4302-4315
- Finot, A (1897) Catalogue des Orthoptères de l'Amérique Méridionale décrits jusqu'a ce jour, 1896. *Actes de la Société Scientifique du Chili*, 7, 169-220.
- Funk VA (2003) 100 uses for an herbarium (well at least 72). *Am Soc Plant Taxon* 17: 17-19.
- Galindo-Leal C, Câmara IG (Eds.) (2003) *The Atlantic Forest of South America: Biodiversity Status, Threats and Outlook*. CABS and Island Press, Washington.
- Golding J, Güsewell S, Kreft H, Kuzevanov VY, Lehvavirta S, Parmentier I, Pautasso M (2010) Species-richness patterns of the living collections of the world's botanic gardens: a matter of socio-economics? *AnnBot* 105: 689-696.
- Gouy M, Guindon S, Gascuel O (2010) SeaView Version 4: A Multiplatform Graphical User Interface for Sequence Alignment and Phylogenetic Tree Building. *Mol. Biol. Evol.* 27:221-224.
- Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends Ecol Evol* 19: 497-503.
- Grandcolas P (1991) Descriptions de nouvelles Zetoborinae Guyanaises avec quelques remarques

- sur la sous-famille. *Bulletin de la Société Entomologique de France*, 95, 241–246.
- Grandcolas P (1993a) Monophylie et structure phylogénétique des [Blaberinae + Zetoborinae + Gyninae + Diplopterinae] (Dictyoptera : Blaberidae). *Annales de la Société entomologique de France (N.S.)*, 29, 195–222.
- Grandcolas P (1993b). The origin of biological diversity in a tropical cockroach lineage: a phylogenetic analysis of habitat choice and biome occupancy. *Acta Oecologica*, 14, 259–270.
- Grandcolas P (1996) The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Canadian Journal of Zoology*, 74, 508–527.
- Grandcolas P (1998) The evolutionary interplay of social behavior, resource use and anti-predator behavior in Zetoborinae + Blaberinae + Gyninae + Diplopterinae cockroaches: a phylogenetic analysis. *Cladistics*, 14, 117–127.
- Grandcolas P, Pellens R. (2012) Capitulo 27. Blattaria. In: Rafael, J.A., Rodrigues de Melo, G.A., Barros de Carvalho, C.J., Casari, S.A. & Constantino, C.J. (Eds.), *Insetos do Brasil. Diversidade e Taxonomia*. Ribeirao Preto, Holos Editora, pp. 333–346.
- Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, et al. Is my species distribution model fit for purpose? Matching data and models to applications. *Glob Ecol Biogeogr.* 2015;24: 276–292. doi:10.1111/geb.12268
- Hebard, M. (1921) South American Blattidae from the Museum National d'Histoire Naturelle, Paris, France. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 73, 193–304.
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29: 773-785.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated

- climate surfaces for global land areas. *Int J Climatol* 25: 1965-1978.
- Holmes MW, Hammond TT, Wogan GOU, Walsh RE, Labarbera K, Wommack EA, Martins FM, Crawford JC, Mack KL, Bloch LM, Nachman MW (2016) Natural history collections as windows on evolutionary processes. *Mol Ecol* 25: 864-881.
- IBGE (2011) Mapa de compartimentos do relevo. In. Instituto Brasileiro de Geografia e Estatística, Brasília, DF, Brasil.
- Inward D, Beccaloni GW, Eggleton P (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol. Lett.* 3: 331–5.
- Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytol*, 204: 459–473. doi:10.1111/nph.12989
- Kadmon R, Farber O, Danin A (2004) Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecol Appl* 14: 401-413.
- Kambhampati S (1995) A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. *Proc. Natl. Acad. Sci. USA.* 92: 2017– 2020.
- Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowickic C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the USA* 106, 9322 9327.
- Kirby WF (1904) *A sinonimic catalogue of Orthoptera. Euplexoptera, Cursoria et Goessinia (Forficulidae, Hemimeridae, Blattidae, Mantidae, Phasmidae)*. British Museum, London, 501 pp.
- Kirby WF (1910) *A Synonymic Catalogue of Orthoptera (Orthoptera Saltatoria, Locustidae vel Acridiidae)* British Museum, London, 562–567.
- Kramer Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, et al (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Divers*

Distrib. 19: 1366–1379. doi:10.1111/ddi.12096

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.* 29:1695–1701.

Lavoie C (2013) Biological collections in an ever-changing world: herbaria as tools for biogeographical and environmental studies. *Perspect Plant Ecol* 15: 68-76.

Ledo RMD, Colli GR (2017) The historical connections between the Amazon and the Atlantic Forest revisited. *J Biogeogr.* 44: 2551–2563. doi:10.1111/jbi.13049

Ledru MP, Salatino MLF, Ceccantini G, Salatino A, Pinheiro F, Pintaud JC (2007) Regional assessment of the impact of climatic change on the distribution of a tropical conifer in the lowlands of South America. *Diversity and Distributions* 13: 761–771.

Ledru MP, Mourguiart P, Riccomini C (2009) Related changes in biodiversity, insolation and climate in the Atlantic rainforest since the last interglacial. *Palaeogeography Palaeoclimatology Palaeoecology* 271:140–152.

Legendre F, Whiting MF, Bordereau C, Canello EM, Evans TA, Grandcolas P (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: Implications for the evolution of the worker and pseudergate castes, and foraging behaviors. *Mol. Phylogenet. Evol.* 48: 615–627.

Legendre F, D’Haese C, Deleporte P, Pellens R, Whiting MF, Schliep K, Grandcolas P (2014) The evolution of social behaviour in Blaberid cockroaches with diverse habitats and social systems: phylogenetic analysis of behavioural sequences. *Biol. J. Linn. Soc.* 111: 58–77.

Legendre F, Nel A, Svenson GJ, Robillard T, Pellens R, Grandcolas P (2015) Phylogeny of Dictyoptera: Dating the Origin of Cockroaches, Praying Mantises and Termites with Molecular Data and Controlled Fossil Evidence. *Plos ONE* 10, e0130127.

- Leite YLR, Costa LP, Loss AC, Rocha RG, Batalha Filho H et al. (2016) Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proceedings of the National Academy of Sciences*, Volume 113, Issue 4, 2016, pp.1008 1013
- Linnaeus C (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. [1–4], 1–824. Holmiæ.
- Lister AM, Grp CCR (2011) Natural history collections as sources of long-term datasets. *Trends Ecol Evol* 26: 153-154.
- Loiselle BA, Jorgensen PM, Consiglio T, Jimenez I, Blake JG, Lohmann LG, Montiel OM (2008) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *J Biogeogr* 35: 105-116.
- Lopes SM, Oliveira EH, Tarli V (2014) Five new species of *Ectobiidae* (*Blattodea*) collected in the Reserva Ducke, Amazonas, Brazil *Biota Neotropica*, 14, p. e20130079
- Marshall WF, Telford SR, Rys PN, Rutledge BJ, Mathiesen D, Malawista SE et al. (1994) Detection of *Borrelia burgdorferi* DNA in museum specimens of *Peromyscus leucopus*. *J Infect Dis* 170: 1027-1032.
- McKittrick FA (1964) Evolutionary studies of cockroaches. *Cornell University Agriculture Experimental Station*, 389, 1–197.
- McLean BS, Bell KC, Dunnum JL, Abrahamson B, Colella JP, Deardorff ER, Weber JA, Jones AK, Salazar-Miralles F, Cook JA (2016) Natural history collections-based research: progress, promise, and best practices. *J Mammal* 97: 287-297.
- Mello Martins F (2011) Historical Biogeography of the Brazilian Atlantic Forest and the Carnaval–Moritz Model of Pleistocene Refugia: What Do Phylogeographical Studies Tell Us? *Biol J Linn Soc* 104: 499 509.

- Mittermeier RA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB (2004) Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. *University of Chicago Press*, Chicago, IL
- Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Global biodiversity conservation: the critical role of hotspots. In: Zachos FE, Habel JC. (Eds.), *Biodiversity Hotspots: Distribution and Protection of Priority Conservation Areas*. Springer Verlag, Berlin, pp. 3–22
- Moerman DE, Estabrook GF (2006) The botanist effect: Counties with maximal species richness tend to be home to universities and botanists. *J Biogeogr.* 33: 1969–1974. doi:10.1111/j.1365 2699.2006.01549.x
- Muller S (2015) Intérêt des herbiers pour la connaissance des dynamiques spatio-temporelles des invasions biologiques *Rev Ecol* 70: 229-235.
- Myers N, Mittermeier RARA, Mittermeier CG, da Fonseca GAB, Kent J, Fonseca GAB, et al. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403: 853–8. doi:10.1038/35002501
- Myers N. (2003) Biodiversity Hotspots Revisited. *Bioscience*. 53: 916. doi:10.1641/0006 3568(2003)053[0916:BHR]2.0.CO;2
- Oliveira Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil, and the influence of climate. *Biotropica* 32: 793–810.
- Oliveira S, Oehler F, San Miguel Ayanz J, Camia A, Pereira JMC (2012) Modeling spatial patterns of fire occurrence in Mediterranean Europe using Multiple Regression and Random Forest. *Forest Ecology and Management* 275: 117 129.
- Otto Bliesner BL, Marshall SJ, Overpeck JT, Miller GH, Hu A, Members CLIP (2006) Simulating Arctic Climate Warmth and Ice Sheet Sensitivity for the Last Interglacial. *Science* 311 (24

March): 1751–1754.

Pautasso M, McKinney ML (2007) The botanist effect revisited: Plant species richness, county area, and human population size in the United States. *Conserv Biol* 21(5):1333-40. doi: 10.1111/j.1523-1739.2007.00760.x

Pellens R (2002) Fragmentação florestal em Mata Atlântica de Tabuleiros: os efeitos da heterogeneidade da paisagem sobre a diversidade de artrópodos edáficos. PhD thesis. Universidade Federal de Rio de Janeiro.

Pellens R, Grandcolas P, Silva Neto ID (2002) A new and independently evolved case of xylophagy and the presence of intestinal flagellates in cockroaches: *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of Brazilian Atlantic Forest. *Canadian Journal of Zoology* 80, 350-359.

Pellens R, Grandcolas P (2003) Living in Atlantic forest fragments: life habits, behaviour and colony structure of the cockroach *Monastria biguttata* (Dictyoptera, Blaberidae, Blaberinae) in Espírito Santo, Brazil. *Canadian Journal of Zoology* 82, 1929-1937.

Pellens R, Arhends A, Hollingsworth P, Grandcolas P (2016) Assessing Hotspots of Evolutionary History with Data from Multiple Phylogenies: An Analysis of Endemic Clades from New Caledonia. In: Pellens, R., Grandcolas, P. (Eds.), *Biodiversity Conservation and Phylogenetic Systematics: preserving our evolutionary heritage in an extinction crisis*. Springer Open, pp. 237-262.

Pellens R, D'Haese C, Bellés X, Piulachs MD, Legendre F, Wheeler W, Grandcolas P (2007a). The evolutionary transition from subsocial to eusocial behavior: phylogenetic and ecological evidence for modification of the "shift-in-dependent-care" hypothesis with a new prototermite model. *Molecular Phylogenetics and Evolution* 43, 616-626.

Pellens R, Legendre F, Grandcolas P (2007b) Phylogenetic analysis of social behavior evolution in

- [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] cockroaches: an update with the study of endemic radiations from the Atlantic forest. *Studies in Neotropical Fauna and Environment* 42, 25–31.
- Pellens R, Grandcolas P (2007) The conservation refugium value of small and disturbed Brazilian Atlantic forest fragments for the endemic ovoviviparous cockroach *Monastria biguttata* (Insecta: Dictyoptera, Blaberidae, Blaberinae). *Zoological Science* 24, 11–19.
- Pellens R, Garay I, Grandcolas P (2010) Biodiversity conservation and management in the Brazilian Atlantic forest: every fragment must be considered. In: Rescigno, V., Maletta, S. (Eds.), *Biodiversity Hotspots*. Nova Publishers, Hauppauge, NY pp. 1–37.
- Pellens R, Grandcolas P (2008) Catalogue of Blattaria (Insecta) from Brazil. *Zootaxa* 1709, 1–109.
- Pellens R, Grandcolas P, eds. (2016) *Biodiversity Conservation and Phylogenetic Systematics: Preserving Our Evolutionary Heritage in an Extinction Crisis*, Topics in Biodiversity and Conservation: Springer Open, 2016.
- Persing DH, Telford SR, Rys PN, Dodge DE, White TJ, Malawista SE, Spielman A (1990) Detection of *Borrelia burgdorferi* DNA in museum specimens of *Ixodes dammini* ticks. *Science* 249: 1420–1423.
- Pessenda LCR, De Oliveira PE, Mofatto M, Medeiros VB, Garcia RJF, Aravena R, et al. (2009) The evolution of a tropical rainforest/grassland mosaic in southeastern Brazil since 28,000 14C yr BP based on carbon isotopes and pollen records. *Quaternary Research*, 71, 437–452.
- Phillips JF, Dudik M, Schapire RE (2004) A Maximum Entropy approach to species distribution modeling. *Twenty-First International Conference on Machine Learning*. Banff, Canada, 655–662.
- Pinto CM, Baxter BD, Hanson JD, Mendez-Harclerode FM, Suchecki JR, Grijalva MJ, Fulhorst CF, Bradley RD (2010) Using museum collections to detect pathogens. *Emerg Infect Dis* 16: 356–

357.

Por FD (1992) Sooretama: The Atlantic Rain Forest of Brazil. The Hague: SPB Academic Publishing.

Princis K (1946) Colombianische Blattodeen, gesammelt von Herrn G. Dahl und Frau M. Althin-Dahl in den Jahren 1936–1939. *Kungliga Fysiografiska Sällskapet I Lund Förhandlingar*, 16, 162 pp.

Princis K (1949) The Blattaria described by Carl Peter Thunberg. *Opuscula Entomologica*, 14, 61–67.

Princis K (1951) Neue und wenig bekannte Blattarien aus dem Zoologischen Museum, Kopenhagen. *Spolia Zoologica Musei Hauniensis*, 12, 1–72

Princis K (1958) Revision der Walkerschen un Kirbyschen Blattarientypen im British Museum of Natural History, London. II. *Opuscula Entomologica*, 23, 59–75.

Princis K (1963) Pars 4: Blattariae: Subordo Polyphagoidea: Fam.: Homoeogamiidae, Euthyrrhaphidae, Latindiidae, Anacompsidae, Atticolidae, Attaphilidae. Subordo Blaberoidea: Fam. Blaberidae. In *Orthopterorum catalogus*. M. Beier. Uitgeverij Dr. W. Junk, 's-Gravenhage. pp. 75-172.

Proosdij ASJ, Sosef MSM, Wieringa JJ, Raes N (2015) Minimum required number of specimen records to develop accurate species distribution models. *Ecography* 38: 1-11.

Rabineau M, Berne S, Olivet JL, Aslanian D, Guillocheau F, Joseph P (2006) Paleo sea levels reconsidered from direct observation of paleoshoreline position during Glacial Maxima (for the last 500,000 yr). *Earth Planet Sci Lett* 252:119–137.

Rehn JAG (1911) Notes on Paraguayan Orthoptera, with descriptions of a new genus and four new species. *Entomological News*, 22, 247–258.

Rehn JAG (1913) A contribution to the knowledge of the Orthoptera of Argentina.

- Proceedings of the Academy of Natural Sciences of Philadelphia*, 65, 273–379.
- Rehn JAG (1915) A further contribution to the knowledge of the Orthoptera of Argentina. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 67, 270–292.
- Rehn JAG (1920) Records and descriptions of Brazilian Orthoptera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 72, 214–293.
- Rehn JAG (1937) New or little known Neotropical Blattidae (Orthoptera). Number four. *Transactions of the American Entomological Society*, 63, 207–258.
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FvJ, Hirota, MrM (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142, 1141–1153.
- Robbirt KM, Davy AJ, Hutchings MJ, Roberts DL (2011) Validation of biological collections as a source of phenological data for use in climate change studies: a case study with the orchid *Ophrys sphegodes*. *J Ecol* 99: 235–241.
- Rocha e Silva Albuquerque I (1971) Sobre alguns Blattaria de Santa Catarina, Brasil (Dictyoptera). *Revista Brasileira de Biologia*, 33, 329–335.
- Rocha e Silva Albuquerque I (1974) Blattaria de Caruaru, Pernambuco, Brazil. *Revista Brasileira de Biologia*, 34, 237–247.
- Rocha e Silva Albuquerque I, Aguiar GM (1977) Blattariae da Amazônia. Família Blaberidae da localidade Sinop, estado de Mato Grosso, Brasil (Dictyoptera). *Boletim do Museu Paraense Emílio Goeldi (Ser. Zoologia)*, 88, 1–30.
- Rocha e Silva Albuquerque I, Lopes SM (1977) Blattaria (Dictyoptera) do Alto da Mosela, Petrópolis, RJ. *Revta bras. Biol.*, Rio de J., 37(3):499–520.
- Rocha e Silva I, Vasconcelos S (1987) Nova contribuição ao conhecimento da fauna de Blattaria (Dictyoptera) do Alto da Mosela, Petrópolis, RJ, Brasil, com descrição de três espécies novas.

- Boletim Museu Nacional do Rio de Janeiro, Nova Série, Zoologia., Rio de Janeiro, 312:1 19.
- Roth LM (1970) Evolution and taxonomic significance of reproduction in Blattaria. *Annual Review of Entomology*, 15, 75–96
- Roth LM (2003) Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Oriental Insects*, 37, 1–186. <http://dx.doi.org/10.1080/00305316.2003.10417344>
- Saussure H (1864a) *Orthoptères de L'Amérique Moyenne*. Mémoires pour servir à l'histoire naturelle du Mexique, Genève, 255 pp.
- Saussure H (1864b) Blattarum novarum species aliquot. *Revue et Magasin de Zoologie*, 2, 341–349.
- Saussure H (1870) Famille des Blattides. In: *Recherches zoologique pour servir a l'histoire de la faune de l'Amérique Centrale et du Mexique*. Imprimerie Impériale, Paris. Vol. 4, pp. 120.
- Schal C, Bell WJ (1986) Vertical community structure and resource utilization in neotropical forest cockroaches. *Ecol Entomol.* 11: 411–423.
- Schulman L, Toivonen T, Roukolainen K (2007) Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *JBiogeogr* 34: 1388–1399.
- Scudder SH (1868) *Catalogue of the Orthoptera of North America described previous to 1867*. Smithsonian miscellaneous collections, 189, 13 pp.
- Scudeller VV, Martins FR, Shepherd GJ (2001) Distribution and abundance of arboreal species in the Atlantic Ombrophilous Dense Forest in southeastern Brazil. *Plant Ecology* 152: 185–199.
- Serville JGA (1831) Revue méthodique des insectes de l'Ordre des Orthoptères. *Annales des Sciences Naturelles*, 22, 262-292.
- Serville JGA (1839) *Histoire Naturelle des Insectes - Orthoptères*. Librairie encyclopédique de Roret, Paris, 776 pp.
- Shelford RMA (1908) Studies of the Blattidae. The Blattidae described by Linnaeus, De Geer and

- Thunberg. *Transactions of the Entomological Society of London*. 4, 455–470.
- Silva JMC, Casteleti CHM (2003) Status of the biodiversity of the Atlantic Forest of Brazil. In: Galindo Leal C, Câmara IG, eds. *The Atlantic Forest of South America: biodiversity status, trends, and outlook*. Washington, DC, USA: Center for Applied Biodiversity Science & Island, 43–59.
- Sites JW, Marshall JC (2004) Operational criteria for delimiting species. *Annual Review of Ecology, Evolution, and Systematics* 35: 199–227.
- Sobral Souza T, Lima Ribeiro MS, Solferini VN (2015) Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. *Evolutionary Ecology* 29, 643–655.
- SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais. (1993) *Evolução dos remanescentes florestais e ecossistemas associados do domínio da Mata Atlântica no período 1985–1990*. Fundação SOS Mata Atlântica, São Paulo.
- SOS Mata Atlantica, Instituto Nacional de Pesquisas Espaciais (2017) *Atlas dos remanescentes florestais da Mata Atlântica: período 2015–2016*. São Paulo.
- Stål C (1855) Entomologiska Notiser. *Öfversigt af Kongliga Vetenskaps-Academien Förhandlingar*, 12, 342–355.
- Stamatakis A (2006) RAxML VI HPC: maximum likelihood based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*. 22:2688–90.
- Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML Web servers. *Syst. Biol.* 57:758–71.
- Suarez AV, Tsutsui ND (2004) The Value of Museum collections for research and society. *Bioscience* 54: 66–74.
- Sullivan J, Swofford DL, Naylor GJP (1999) The effect of taxon sampling on estimating rate

- heterogeneity parameters of maximum likelihood models. *Mol. Biol. Evol.* 16:1347– 1356
- Tarli VD, Grandcolas P, Pellens R (2018) The informative value of Museum collections for ecology and conservation: a comparison with target sampling in the Brazilian Atlantic forest. *PLoS One* (submitted).
- Tarli VD, Grandcolas P, Pellens R 2018. Taxonomic revision of the genus *Monastria* Saussure, 1864 (Blattodea: Blaberidae, Blaberinae). *Zootaxa* (submitted).
- Ter Steege H, Vaessen RW, Cárdenas-López D, Sabatier D, Antonelli A, De Oliveira SM, et al. (2016) The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. *Sci Rep.* 6: 1–15. doi:10.1038/srep29549
- Thunberg CP (1826) *Blattarum novae species descriptae*. Mémoires de l'Académie impériale des sciences de St. Pétersbourg, 10, 276 pp.
- Vaidya G., Lohman D.J., Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi gene datasets with character set and codon information. *Cladistics.* 27:171–180.
- Varela S, Anderson RP, García-Valdés R, Fernández-González F. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. *Ecography (Cop).* 2014;37: 1084–1091. doi:10.1111/j.1600-0587.2013.00441.x
- Vieira BC, Gramani MF (2015) Serra do Mar: The Most “Tormented” Relief in Brazil *In: Vieira BC, Salgado AAR, Santos LJC, Landscapes and Landforms of Brazil.* Springer, Dordrecht, 230 pp. doi: 10.1007/978 94 017 8023 0
- Walker F (1868) *Catalogue of the specimens of Blattariae in the collection of the British Museum.* British Museum, London, 239 pp
- Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62: 2868-2883.

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: Pattern, process, scale and synthesis. *Annual Review of Ecology, Evolution, and Systematics*. 34: 273–309.

Wilson, EO (1988) *Biodiversity*. National Academies Press Washington.

Yang WJ, Ma KP, Kreft H (2014) Environmental and socio-economic factors shaping the geography of floristic collections in China. *G Ecol Biogeogr* 23: 1284-1292.

