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ESTUDOS TAXONÔMICOS, FILOGENÉTICOS E BIOGEOGRÁFICOS EM *AECHMEA* (BROMELIACEAE)

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Estudos taxonômicos, filogenéticos e biogeográficos em *Aechmea* (Bromeliaceae)

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal – PPGBV/UFPE como requisito necessário para a obtenção do título de Doutor em Biologia Vegetal.

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal, da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de Doutor em Biologia Vegetal.

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Dedico este trabalho à minha família

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RESUMO

Entender os processos e padrões evolutivos e ecológicos de grupos da Floresta Atlântica pode ajudar a caracterizar as forças responsávels pela biodiversidade da região. Exemplo disso são os processos responsáveis pelos padrões de distribuição disjuntas entre a Floresta Atlântica e Amazônica e a ocupação geográfica da Floresta Atlântica. Diante disto, o objetivo central dessa tese foi entender os processos que levaram aos padrões de distribuição em algumas espécies do gênero *Aechmea* e à diversificação de *Aechmea* subg. *Chevaliera*. Os resultados foram então sumarizados em oito artigos divididos em três partes da tese. Na primeira parte, uma abordagem taxonômica serviu para embasar os estudos subsequentes. Dessa forma ficou claro que o gênero *Aechmea* está representado na Floresta Atlântica ao Norte do Rio São Francisco por 27 espécies, três delas tendo distribuição disjunta entre a Floresta Atlântica e a Amazônica. Além disso, foi possível descrever mais uma nova espécie para o subgênero *Chevaliera*, que se junta às 29 formalmente já descritas. Na segunda parte, foi realizado um estudo sobre o grau de suficiência amostral, permitindo concluir que a representação do espaço ambiental das espécies da Floresta Atlântica ao Norte do Rio São Francisco não está relacionada ao número de ocorrências registradas e que a fragmentação florestal influencia a qualidade de informação dos seus habitats. Em consequência foram selecionadas duas espécies com suficiência amostral e distribuição disjunta para o estudo efeito de mudanças climáticas no estabelecimento de corredores de dispersão. Nos cenários climáticos pretéritos, a principal ligação entre a Floresta Atlântica Nordestina e a Amazônica se deu pelo litoral. Este resultado ressalta a importância do litoral como possível corredor enre as duas florestas em mudanças climáticas que aumentaram a pluviosidade e umidade na região ao invés da conexão pela caatinga como proposto na literatura. Por fim, na terceira parte foi estudada a evolução do subg. *Chevaliera*. Uma filogenia molecular datada (ETS, matK e phyC) e estudos de evolução morfológica e do nicho revelaram que o subgênero é polifilético. As espécies amazônicas previamente classificadas no subg. *Chevaliera* emergiram em distintos momentos da história evolutiva de Bromelioideae. A maioria das espécies atlânticas do subgênero emergiu formando dois grupos distintos. O primeiro grupo reuniu sete espécies previamente relacionadas ao complexo *Aechmea multiflora* e o segundo grupo possui onze espécies que formam o conceito restrito do subg. *Chevaliera*, chamado aqui de grupo *A. sphaerocephala*. Foi proposto transferir as espécies relacionadas ao complexo *A. multiflora* para um novo gênero, chamado *Gravatarum*. As análises morfológicas revelaram que os dois grupos convergem quanto ao grande volume corporal, forma de crescimento e nos aspectos da inflorescência, mas se diferenciam pela margem da bráctea floral e cor das pétalas. O estudo da dinâmica evolutiva dos dois grupos mostra que compartilham o mesmo espaço morfológico e geográfico, mas com dinâmicas distintas de ocupação da Floresta Atlântica, de dispersão nos habitats disponíveis e de evolução do espaço ambiental nos últimos três milhões de anos.

Palavras-chave: Bromelioideae. *Chevaliera*. Taxonomia. Biogeografia. Especiação. Floresta Atlântica. Pleistoceno.

ABSTRACT

Understanding evolutionary and ecological processes and patterns of Atlantic Forest species could help us to characterize the forces responsibles by biodiversity in the region. As example are the processes responsible by disjunct distribution patterns between Atlantic and Amazon forests. Therefore, the main aim of this work was understand process which allows disjunct distribution patterns in some species of *Aechmea* and diversification of *Aechmea* subg. *Chevaliera*. The results were summarized in eight papers organized in three parts on this thesis. In the first one, a taxonomical approach gave support to subsequents studies. Thus, the genus *Aechmea* is represented in Atlantic Forest at North of Sao Francisco River by 27 species and three of them are disjunct between Atlantic and Amazon Forest. Moreover, it was possible describing one new taxon to the subgenus *Chevaliera*. In the second part, a study about the sampling sufficiency of species was made, which allow conclude that good representation of environmental spaces of some species are not related to number of samples and forest lodge influences the quality of information about habitat of species. As consequence two species with sampling sufficiency and disjunct distribution were selected to analyse the effect of climatic changes in creating dispersion corridors. In past climatic scenarios the main connection between Northeastern Atlantic Forest and Amazon Forest was by coastal region of Brazilian Northeast. This results hightlight the importance of east coast as possible corridor between the two forest in climatic changes that increased pluviosity and humidity in South America instead the connection throughout caatinga, which is proposed in literature. In the last part, the evolution of subgenus *Chevaliera* was studied. A dated molecular phylogeny (ETS, matK e phyC) and studies of morphological and niche evolution revealed that the subgenus is polyphyletic. The Amazonian species previously classified as subg. *Chevaliera* emerges in distinct moments of evolutionary history of Bromelioideae. Two groups emerged gathering the majority of atlantic species. The first one included seven species related to *Aechmea multilora* complex. The second one gathered eleven species that form the restrict concept of subg. *Chevaliera*, named here as *A. sphaerocephala* group. We proposed tranfer to a new genus called *Gravatarum* all species related to *A. multiflora* complex. Morphological analyses show that *Gravatarum* and *A. sphaerocephala* group converg in body volume and growth form and in inflorescence aspect. However, they differentiate each other by floral bracts margins and petal color. The study of evolutionary dinamics of both groups shows that they share the same morphological and geographical spaces, but they had differents dynamics of occupation of Atlantic Forest, dispersion in available habitats and evolution in environmental spaces in the last three millions of years.

Keywords: Bromelioideae. *Chevaliera*. Taxonomy. Biogeography. Speciation. Atlantic Forest. Pleistocene.

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Sumário

1 Introdução

Ao longo dos últimos quatro anos elaboramos uma tese com objetivos que contemplassem um aprendizado amplo de ferramentas diversas que possam ser aplicadas em outros grupos biológicos. Dessa forma essa tese vai desde abordagens de taxonomia descritiva até a aplicação de ferramentas de macroevolução para entender os processos de diversificação na Floresta Atlântica.

Os três primeiros artigos tratam de estudos taxonômicos apresentando resultados da fase de coleta de dados de distribuição e de delimitação das espécies. O primeiro descreve uma nova espécie de *Aechmea* subg. *Chevaliera* para a ciência. O segundo artigo faz uma divulgação científica do esforço de coleta e sua importância para melhor conhecer as espécies de *A.* subg. *Chevaliera* e seus habitats. E por fim, o terceiro artigo apresenta pela primeira vez uma chave taxonômica para as espécies de *Aechmea* da Floresta Atlântica ao norte do Rio São Francisco. Todos os artigos dessa parte da tese estão publicados.

Os dois artigos seguintes usam a modelagem de nicho ecológico para aprofundar o conhecimento sobre o nicho das espécies analisadas nos estudos anteriores. O quarto capítulo reúne dados comparativos de espaços ambientais de distribuição potencial e observada das espécies da Floresta Atlântica ao Norte do Rio São Francisco. O quinto capítulo reúne os dados de paleomodelagem mostrando uma conexão entre as florestas Atlântica e Amazônica através de um corredor pelo litoral do Nordeste. Esse está aceito para publicação

Finalmente, os últimos três artigos abordam a evolução de *A.* sub. *Chevaliera*. O sexto capítulo faz uma abordagem da filogenia do subgênero *Chevaliera* com considerações sobre a evolução de alguns caracteres morfológicos e o impacto dos resultados para a biogeografia do grupo. Como consequência dos resultados da filogenia do subgênero *Chevaliera*, no sétimo capítulo é descrito um novo gênero. Por fim, um estudo de dinâmica evolutiva comparando o subgênero *Chevaliera* com o novo gênero, morfologicamente convergentes, esclarece a evolução do nicho e os impactos das mudanças climáticas nos grupos estudados.

Os artigos da tese não estão formatados conforme as normas das revistas para as quais serão ou foram submetidos ou publicados. Essa foi uma escolha meramente estética e não refletirá nenhuma dificuldade posteriormente.

2 Fundamentação teórica

2.1 Introdução

Pennington *et al.* (2004) defende que as filogenias tem um grande poder para explicar a origem de biomas e da biodiversidade. Isso nos leva a crer que um projeto apresentando padrões e processos que forjaram distribuições de espécies e suas dinâmicas de especiação pode ajudar a esclarecer como a biodiversidade de uma região se formou. Em especial a da Floresta Atlântica.

Esse debate vem se aprofundando desde meados do século XX quando começou a se notar uma grande incidência de espécies com padrões de disjunção entre as Florestas Atlântica Nordestina e Amazônica (Andrade-Lima 1953, 1966, 1982, Batalha-Filho *et al.* 2012, Bigarella *et al.* 1975, Cavalcanti & Tabarelli 2004, Ducke & Black 1954, Oliveira-Filho & Ratter 1995, Rizzini 1963, Santos *et al.* 2007, Siqueira-Filho & Leme 2006). Essas disjunções serviram como exemplos e foram explicadas pela Teoria dos Refúgios, que era hegemônica até então como o modelo de diversificação neotropical (Andrade-Lima 1982, Bigarella *et al.* 1975). Logo se notou como as mudanças climáticas poderiam ser a força geradora de biodiversidade na Floresta Atlântica.

Um avanço significativo no estudo da biodiversidade neotropical está acumulando informações mais detalhadas sobre processos de diversificação e de estabelecimento de distribuições. Porém, ainda relativamente pouco tem se avançado com grupos de plantas típicos da Floresta Atlântica. *Aechmea* Ruiz ex Pávon (Bromeliaceae-Bromelioideae) é um gênero candidato a ser modelo para entender as forças evolutivas e ecológicas por trás desses padrões devido a sua alta representatividade e diversidade nos ecossistemas neotropicais e especialmente na Floresta Atlântica. No entanto, sua sistemática confusa e com diversos aspectos a serem esclarecidos ainda limitam seu uso para inferências biogeográficas, ecológicas e evolutivas.

Mesmo assim, utilizamos *Aechmea* como um modelo para entender processos de especiação na Floresta Atlântica, aspectos ecológicos da distribuição de espécies do gênero e como as mudanças climáticas influenciaram a distribuição e especiação. Em particular, foi dado um foco para espécies da Floresta Atlântica ao Norte do Rio São Francisco e do subgênero *Chevaliera*, pois apresentam características morfológicas e ecológicas muito peculiares.

2.2 Contextualização taxonômica

A subfamília Bromelioideae é uma das oito reconhecidas para Bromeliaceae, possui 936 espécies e 33 gêneros (Butcher & Gouda cont. updated; ver figura 1). O monofiletismo de Bromelioideae é sustentado por sinapomorfias morfológicas, como o fruto baga e sementes sem apêndices (Barfuss *et al.* 2005, Crayn *et al.* 2004, Givnish *et al.* 2004, 2007, 2011, 2014, Horres *et al.* 2000, 2007, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008, Silvestro *et al.* 2014, Terry *et al.* 1997). Datações baseadas em dados nucleares e plastidiais propõem que Bromelioideae evoluiu nos últimos 10Ma, com uma possível origem ancestral andina e um evento de colonização e irradiação no leste do Brasil, sendo a subfamília monogenérica Puyioideae seu grupo irmão (Givnish *et al.* 2004, 2007, 2011, 2014, Silvestro *et al.* 2014).

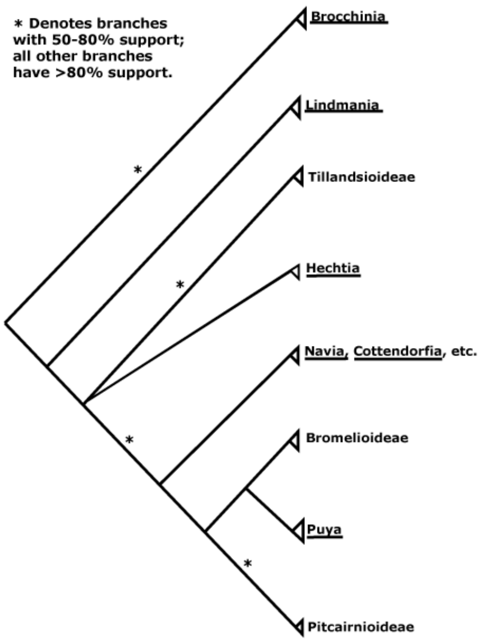

Figura 2.1. Filogenia de Bromeliaceae. Nessa figura é possível reconhecer as oito linhagens que representam as oito subfamílias atualmente estabelecidas: Brochhinioideae, Lindmanioideae, Tillandsioideae, Hechtioideae, Navioideae, Bromelioideae, Puyioideae e Pitcairnioideae. (Reproduzido de http://www.mobot.org/MOBOT/research/APweb/)

É possível distinguir duas linhagens em Bromelioideae (Schulte *et al.* 2009, Silvestro *et al.* 2014; figura 2). A primeira reúne quase todas as espécies com rosetas que não acumulam água. A segunda linhagem (Sass & Specht 2010) reúne essencialmente gêneros e espécies com roseta formando o tanque típico da família Bromeliaceae.

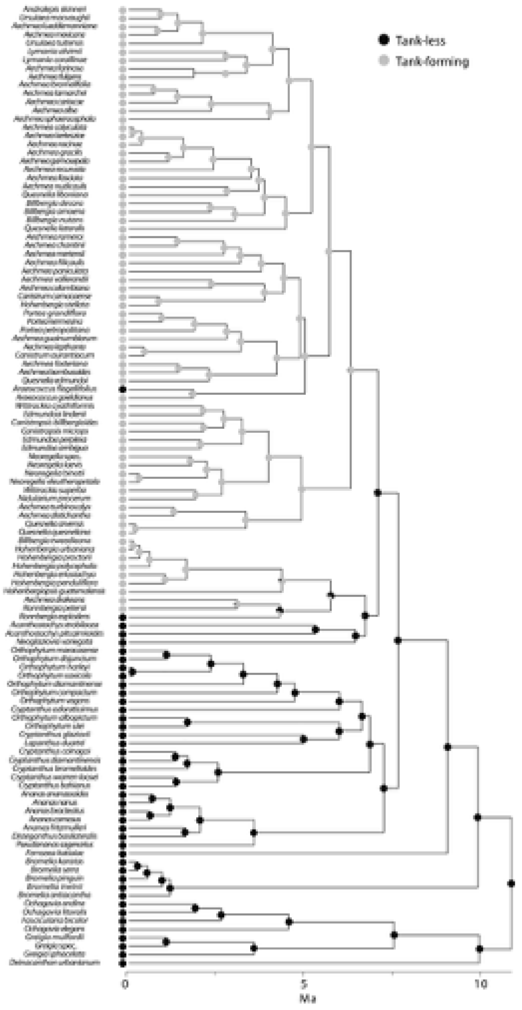

Figura 2.2. Filogenia de Bromelioideae. Aqui é possível ver as duas principais linhagens da subfamília. A linhagen não tanque tem os gêneros *Cryptanthus, Ananas, Bromelia* e *Ortophytum*, como os mais representativos. A linhagem tanque é que agrupa o maior número de espécies e onde se encontra o conceito não monofilético de *Aechmea*. A maior parte das espécies de Bromelioideae-Core (destacado na figura) pertence ao gênero *Aechmea*. (Adaptado de Silvestro *et al.* 2014).

Diversos autores relatam as dificuldades de esclarecer relações filogenéticas em Bromelioideae (Aguirre-Santoro *et al.* 2015, 2016, Evans *et al.* 2015, Faria *et al.* 2004, Heller *et al.* 2015, Horres *et al.* 2000, 2007, Louzada *et al.* 2014, Sass & Specht 2010, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008). Essa dificuldade se dá principalmente por que em Bromelioideae-core se inserem diversos gêneros parafiléticos (Sass & Specht 2010, Smith & Downs 1979). Parte desses padrões morfológicos é resultado de convergências ou paralelismos com nítida conservação geográfica nos agrupamentos (Sass & Specht 2010).

Um dos principais gêneros parafiléticos é *Aechmea*, com 288 espécies classificadas em oito subgêneros (Butcher & Gouda cont. updated, Smith & Downs 1979). A maioria das espécies de *Aechmea* ocorre na Floresta Atlântica, onde são encontradas 140 espécies, sendo 88% delas endêmicas dessa região (BFG 2015, Martinelli *et al.* 2008). As espécies de *Aechmea* apresentam em geral independência ao substrato como tantas outras da família Bromeliaceae (Benzing 2000). Isso faz com que seus padrões de distribuição sejam limitados principalmente por aspectos climáticos, o que torna o grupo um bom modelo para estudos de modelagen de nicho ecológico. Além disso, as espécies de *Aechmea* possuem frutos carnosos que são dispersos por animais como aves e morcegos ou até mesmo formigas que desempenham papel fundamental na dispersão secundária (Benzing 2000, Carrias *et al.* 2012, Céreghino *et al.* 2011).

Em 1794, Hipólito Ruiz & José Pavón estabeleceram *Aechmea* pela primeira vez na *Flora Peruvianae et Chilensis*, mas sem atribuir nem descrever nenhuma espécie para o gênero. Só em 1802, os autores descreveram uma única espécie, *Aechmea paniculata*, tornando obrigatório o uso dela como typus do gênero. Porém, Michel Adanson havia proposto *Hoiriri* em 1763, tendo como typus *Bromelia nudicaulis* (=*Aechmea nudicaulis* (L.) Griseb), que passou a ter então prioridade sobre a publicação de Ruiz & Pavón. Mas o nome *Aechmea* se manteve como *nomen conservandum* e atualmente *Hoiriri* é um nome rejeitado (Grant & Zijlstra 1998).

O nome *Aechmea* deriva do grego 'aichmea' que significa lança, por conta da sépala com ápice caudado e espinescente de *Aechmea paniculata* (Figura 3). Nas descrições de Ruiz & Pavón em 1794 e 1802, *Aechmea* se caracterizaria pelas inflorescências paniculadas e flores com dois apêndices petalíneos. Essa delimitação inicial foi muito ampliada posteriormente, quando Baker (1879, 1889) e Smith & Downs (1979) sinonimizaram diversos gêneros sob *Aechmea*.

Figura 2.3. Flor e botão floral de *Aechmea paniculata* apresentada na prancha VIII por Ruiz & Pávon em 1794. Observar o detalhe do ápice da sépala que levou os autores a aplicar o nome *Aechmea* para o novo gênero que descreviam então. *Aechmea paniculata* é a espécie typus do gênero está classificada atualmente no subgênero *Aechmea*. Aparentemente ocorre como epífita nas matas úmidas premontanas de Pasco, no distrito Huánuco no Peru. No entanto a espécie não foi mais coletada desde o séc. XIX. León et al. (2006) classificou a espécie como criticamente ameaçada de extinção.

Dessa forma, a definição de *Aechmea* apresentada por Smith & Downs (1979) circunscreve uma ampla variação morfológica, onde são encontradas espécies com inflorescências simples e compostas, flores sésseis ou estipitadas, sépalas livres ou conadas usualmente assimétricas, pétalas livres com dois apêndices basais que podem estar ausentes ou reduzidos em algumas espécies, estames inclusos e livres ou em séries adnatos às petalas, pólen bi a multiporados e óvulos caudados. Tais características são compartilhadas com diversos outros gêneros da subfamília Bromelioideae.

Figura 2.4. Representantes de subgêneros de *Aechmea.* Numa interpretação livre da classificação subgenêrica mais aceita de *Aechmea* é possível observar uma tendência em agrupar as espécies pelo nível de ramificação das inflorescências. Nessas fotos podemos ver essa tendência e a diversidade de formas de inflorescência nos sete primeiros subgêneros de *Aechmea*, seguindo a mesma sequência da classificação de Smith & Downs (1979): a-b. *Aechmea*. subg. *Podaechmea*. a. *A. luedmanniana* (K. Koch) Mez, b. *A. mexicana* Baker; c-d. *A.* subg. *Lamproccocus*. c. *A. racinae* L.B. Sm., d. *A. fulgens* Brongn.; e-f. *A.* subg. *Aechmea*. e. *A. mertensii* (G.Mey.) Schult. & Schult.f., f. *A. cephaloides* J.A.Siqueira & Leme; g-h. *A.* subg. *Ortigiesia.* g. *A. gracilis* Lindm., h. *A. recurvata* (Klotzsch) L.B.Sm.; i-j. *A.* subg. *Platyaechmea*. i. *A. chantinii* (Carrière) Baker, j. *A. distichanta* Lem.; k-l. *A.* subg. *Pothuava.* k. *A. pineliana* (Brongn. ex Planch.) Baker, l. *A. nudicaulis* (L.) Griseb.; m-n. *A.* subg. *Macrochordion*. m. *A. bromeliifolia*, n. *A. maasii* Gouda & W. Till. Fotos: a-b. www.fcbs.org; e. Dirce Komura (gentilmente cedida); c, d, f, g, h, I, j, k, l, m, n. J.R. Maciel

O resultado da ampla variação aceita dentro de *Aechmea* é a evidência de que o grupo é claramente não monofilético e engloba um grande número de outros gêneros (Aguirre-Santoro *et al.* 2015, 2016, Butcher & Gouda cont. updated, Evans *et al.* 2015, Faria *et al.* 2004, Heller *et al.* 2015, Horres *et al.*, 2000, 2007, Louzada *et al.* 2014, Sass & Specht 2010, Schulte *et al.*, 2005, 2009, Schulte and Zizka, 2008, Silvestro *et al.* 2014). Mesmo assim, o conceito morfológico de *Aechmea* vem sendo aplicado em diversas floras regionais, revisões e estudos filogenéticos (Aguirre-Santoro *et al.* 2015, 2016, Aguirre-Santoro & Betancur 2008, Evans *et* *al.* 2015, Goetze *et al.* 2016, Heller *et al.* 2015, Leme & Siqueira-Filho 2006, Martinelli *et al.* 2008, Martins *et al.* 2007, Sass & Specht 2010, Sousa & Wanderley 2001).

Tradicionalmente, os estudos taxonômicos vêm tentando organizar a grande variação morfológica verificada em *Aechmea* num sistema de classificação infragenérico que por vezes classifica o gênero em seções e/ou em subgêneros. A classificação mais aceita (Smith & Downs 1979) reconhece para *Aechmea* oito subgêneros baseados em caracteres da inflorescência e ocorrência de estruturas florais como tubo do hipanto e apêndices petalíneos. Os subgêneros reconhecidos são: *Aechmea*, *Podoaechmea*, *Lamprococcus*, *Ortigiesia*, *Platyaechmea*, *Pothuava*, *Macrochordion* e *Chevaliera* (Figs. 4-6). No entanto, a delimitação desses subgêneros não é clara devido à plasticidade dos caracters utilizados, o que pode ser facilmente constatado na chave taxonômica apresentada por Smith & Downs (1979).

Nesse sistema de classificação, o subgênero *Chevaliera* é um dos poucos que apresenta uma delimitação morfológica bem estabelecida, baseada na presença de inflorescências simples, estrobiliformes ou raramente digitadas, comumente perenes, brácteas florais coriáceas ou lígneas, flores distribuídas polísticamente, sépalas livres ou conadas e pétalas com apêndices reduzidos ou ausentes (Smith & Downs 1979).

Chevaliera foi proposto pela primeira vez por Charles Gaudichaud-Beaupré em 1844 como um gênero de Bromeliaceae. O nome foi dado em homenagem ao botânico francês François Fulgis Chevalier. Gaudichaud faleceu antes que pudesse concluir sua obra que descreveria espécies coletadas em uma viagem ao redor do mundo, deixando uma série de ilustrações sem descrições. Como foram apresentadas duas espécies de *Chevaliera* entre essas ilustrações (*C. sphaerocephala* e *C. ornata*), a publicação foi considerada inválida para o gênero (Figura 5). Posteriormente, Beer (1856) validou a publicação de *Chevaliera* ao descrever as duas espécies ilustradas por Gaudichaud, mas na publicação não foi estabelecido o typus do gênero.

Em 1879, Baker reconheceu *Chevaliera* como a seção III de nove seções de *Aechmea*. Sob *A.* sect. *Chevaliera*, Baker posicionou quatro espécies: *A. veitchii*, *A. sphaerocephala*, *A. ornata* e *A. maria-reginae.* Ele caracterizou a seção *Chevaliera* como plantas com inflorescências simples e espiciformes, ovários comprimidos e quase achatados na parte próxima à ráquis da inflorescência. Já no seu *Handbook of the Bromeliaceae*, Baker (1889) tratou *Chevaliera* como um subgênero com inflorescências em espigas estrobiliformes densas e simples, cada flor subentendida por uma bráctea grande e coriácea e com ovários achatados no lado em direção à ráquis. Dessa vez, Baker transferiu *A. ornata* e *A. maria-reginae* para o subg. *Pothuava* e reconheceu no subg. *Chevaliera* nove espécies da Floresta Atlântica, Amazônica e da América Central.

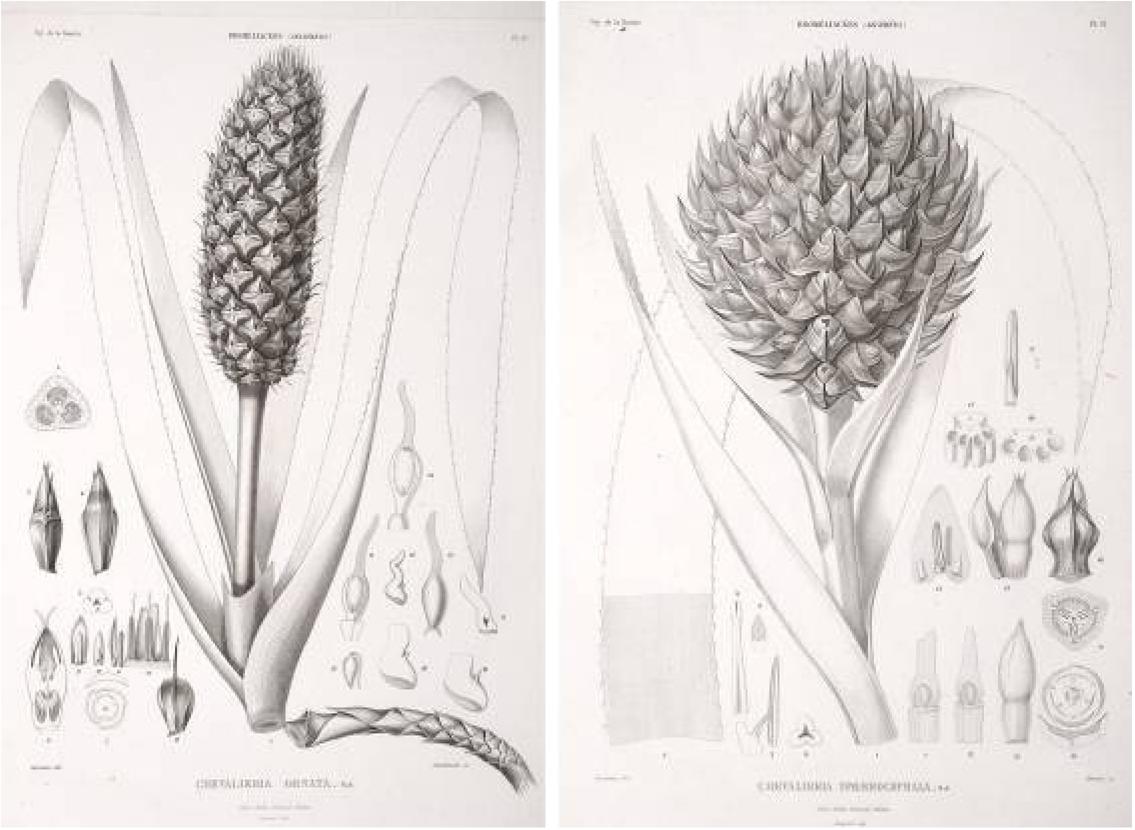

Figura 2.5. Pranchas de *Botanique du voyage autour du monde* de Gaudichaud (1844). Estas pranchas ilustram as duas primeiras espécies atribuídas a *Chevaliera*. *Chevaliera ornata* (=*A. ornata*) foi transferida por Baker para o subg. *Pothuava* e mantida assim por Smith & Downs (1979), mas posteriomente reposicionada para o subg. *Chevaliera* por Sousa (2004). *Chevaliera sphaerocephala* (=*A. sphaerocephala*) é a espécie typus do subgênero.

Delimitação muito parecida de *Aechmea* e do sub. *Chevaliera* foi apresentada por Smith & Downs (1979) que estabeleceram *Aechmea sphaerocephala* Baker como espécie typus. Porém é necessário ressaltar que Smith & Kress (1989, 1990) elevaram *Chevaliera* novamente à condição de gênero sem aparentes justificativas morfológicas ou taxonômicas. Essa decisão não foi seguida pelas posteriores revisões e estudos taxonômicos de *Chevaliera* (Canela *et al.* 2003, Silva 2003, Sousa 2004) que vem mantendo a delimitação e categorização de Smith & Downs (1979).

Sousa (2004) ampliou *A.* subg. *Chevaliera* incluindo espécies que antes pertenciam ao subgênero *Pothuava* e reconhecendo 21 espécies na sua revisão taxonômica. Nos últimos anos, novos táxons foram descritos para *A.* subg. *Chevaliera* (Leme 2010, Leme & Kollman 2009, 2011, Leme *et al.* 2014, Sousa & Wanderley 2014) levando a atual circunscrição que engloba 28 espécies (Figura 6, Tabela 1).

Figura 2.6. Espécies de *A.* subg. *Chevaliera*. As inflorescências compactas e estrobiliformes do Subg. *Chevaliera* são as características mais típicas do grupo. Mesmo volumosas e grandes as inflorescências em geral são insertas nas rosetas e pendentes devido ao peso. Esses aspectos permitem identificar no campo que uma planta pertence ao Subg. *Chevaliera* e não aos Subg. *Pothuava* e *Macrochordion*, que também possuem inflorescências estrobilifomes, mas em geral eretas e exsertas acima da roseta. Espécies na prancha: a. *A. alopecurus* Mez; b. *A. castanea* L.B. Sm.; c. *A. depressa* L.B. Sm.; d. *A. digitata* L.B. Sm. & W. Read; e. *A. fernandae* (E. Morren) Baker; f. *A. gustavoi* J.A. Siqueira & Leme. g. *A. heterosepala* Leme; h. *A. multiflora* L.B. Sm.; i. *A. muricata* (Arruda) L.B. Sm.; j. *A. nigribracteata* J.R. Maciel, Louzada & Alves; k. *A. perforata* L.B. Sm.; l. *A. rodriguesiana* L.B. Sm.; m. *A. saxicola* L.B. Sm.; n. *A. serragrandensis* Leme & J.A. Siqueira; o. *A. sphaerocephala* Baker. Fotos: a-n. J.R. Maciel; o. www.fcbs.org

Tabela 2.1. Comparação taxonômica entre os principais tratamentos incluindo espécies de *A.* subg. *Chevaliera*. Em destaque as espécies andino-amazônicas e da América Central. A terceira coluna contém uma lista de espécies que foram descritas recentemente e que foram atribuídas ao subg. *Chevaliera* de forma inequívoca (*) ou com ressalvas (**). [1] *A. crocophylla* é sinônimo de *A. pectinata* Baker do subg. *Pothuava*; [2] *A. lateralis* é sinônimo de *Disteganthus lateralis* (L.B. Sm.) Gouda.

Baker 1889	**Smith & Downs 1979**	**Sousa 2004**	**Espécies publicadas recentemente**
A. crocophylla Baker[1]			*A. aguadocensis* Leme & Kollmann *
A. fernandae (E. Morren) Baker	*A. fernandae* (E. Morren) Baker	*A. fernandae* (E. Morren) Baker	*A. heterosepala* Leme *
A. schomburgkii (Carriere) Baker	(=*A. fernandae*)	(=*A. fernandae*)	*A. mira* Leme & H.Luther **
A. germinyana Baker	*A. germinyana* Baker	(=*A. veitchii*)	*A. nigribracteata* J.R. Maciel, Louzada & Alves *
A. magdalenae André	*A. magdalenae* André	*A. magdalenae* André	*A. paratiensis* Leme & Fraga **
A. sphaerocephala Baker	*A. sphaerocephala* Baker	*A. sphaerocephala* Baker	*A. recurvipetala* Leme & Kollmann *
A. gigantea Baker	(=*A. sphaerocephala*)	(=*A. sphaerocephala*)	*A. timida* Leme *
A. stephanophora E. Morren	*A. muricata* (Arruda) L.B. Sm.	*A. muricata* (Arruda) L.B. Sm.	
A. veitchii Baker	*A. veitchii* Baker	*A. veitchii* Baker	
	A. cariocae L.B. Sm.	*A. cariocae* L.B. Sm.	
	A. castanea L.B. Sm.	*A. castanea* L.B. Sm.	
	A. conifera L.B. Sm.	*A. conifera* L.B. Sm.	
	A. depressa L.B. Sm.	*A. depressa* L.B. Sm.	
	A. digitata L.B. Sm. & R.W. Read	*A. digitata* L.B. Sm. & R.W. Read	
	A. hostilis E. Pereira	*A. hostilis* E. Pereira	
	A. lateralis L.B. Sm.[2]		
	A. leucolepis L.B. Sm.	*A. leucolepis* L.B. Sm.	
	A. multiflora L.B. Sm.	*A. multiflora* L.B. Sm.	
	A. pallida L.B. Sm.	táxon excluído	
	A. perforata L.B. Sm.	*A. perforata* L.B. Sm.	
	A. rodriguesiana L.B. Sm.	*A. rodriguesiana* L.B. Sm.	
	A. rubiginosa Mez	(=*A. fernandae*)	
	A. saxicola L.B. Sm.	*A. saxicola* L.B. Sm.	
	A. strobilacea L.B. Sm.	*A. strobilacea* L.B. Sm.	
		A. alopecurus Mez	
		A. gustavoi J.A. Siquera & Leme	
		A. ornata Baker	
		A. prasinata G. Sousa & Wanderley	

Essas espécies ocorrem na América Central, Andes, Amazônia e Floresta Atlântica, conferindo ao subgênero uma distribuição disjunta entre o nordeste e o leste da América do Sul, padrão de distribuição geográfica que levou o grupo a ser objeto de nossos estudos (Figura 7). O centro de diversidade do subg. *Chevaliera* é a Floresta Atlântica no leste do Brasil, onde são encontradas 24 espécies (Canella *et al.* 2003, Leme 2010, Leme & Kollman 2009, Leme & Kollman 2011, Leme *et al.* 2014, Silva 2003, Smith & Downs 1979, Sousa 2004, Sousa & Wanderley 2014).

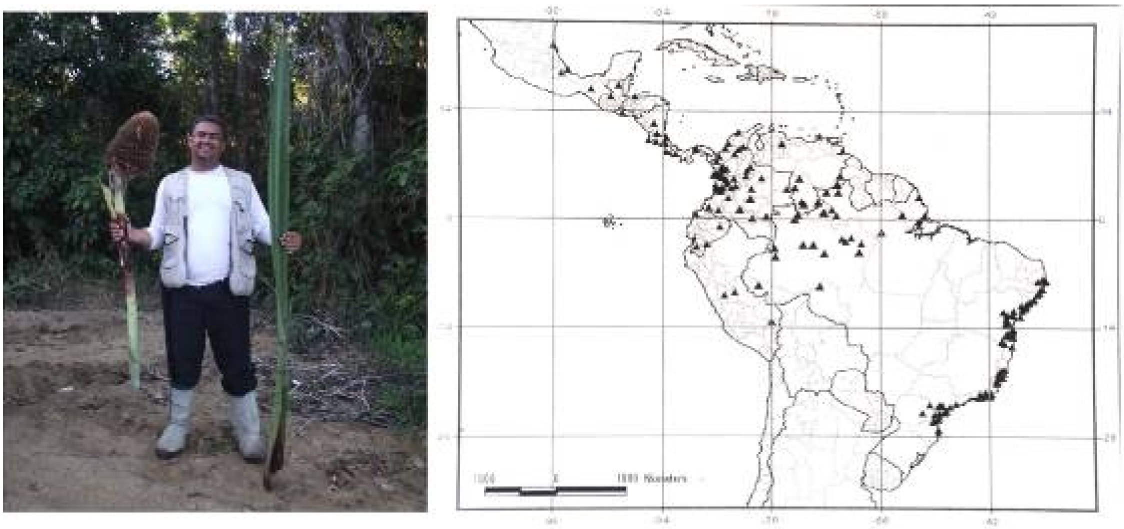

Figura 2.7. Aspectos morfológicos e distribuição do subg. *Chevaliera*. As espécies do Subg. *Chevaliera* possuem grande volume corporal. As rosetas são formadas por folhas muito longas e as inflorescências são robustas. A distribuição do subgênero é disjunta entre a Floresta Atlântica e Amazônica e algumas espécies também são encontradas na América Central, baseada na circunscrição de Smith & Downs (1971) e Sousa (2004). Mapa retirado de Sousa (2004); foto: Débora Cavalcanti.

Embora haja um claro padrão morfológico de espécies com grandes rosetas e inflorescências compactas e multifloridas (Figura 7), Silva (2003) apresentou uma crítica ao conceito de *A.* subg. *Chevaliera* de Smith & Downs com base em dados morfológicos. Segundo Silva (2003), as espécies andino-amazônicas e as espécies atlânticas apresentam distinções morfológicas que justificariam o grupo não ser natural. Além do apontamento de Silva (2003) é possível observar nas chaves identificação de Smith & Downs (1979) e Sousa (2004) dois grupos morfologicamente distintos separados pela margem da bráctea floral inteira e dentada ou serreada. Nesse último se enquadram as espécies do complexo *A. multiflora* (Canela *et al.* 2003).

Como a evolução de Bromelioideae apresenta indícios consistentes de conservação geográfica (Sass & Specht 2010), a hipótese levantada por Silva (2003) e o monofiletismo do complexo *A. multiflora* (Canela *et al.* 2003) se tornam relevantes para serem testados com ferramentas filogenéticas. No entanto, até então os estudos moleculares tem feito uma amostragem muito limitada para qualquer conclusão consistente sobre o monofiletismo do subgênero *Chevaliera* e de seus possíveis arranjos infragenéricos. Isto não permite esclarecer o significado evolutivo de seu padrão de distribuição disjunto entre a Floresta Amazônica e Atlântica (Aguirre-Santoro *et al.* 2015, 2016, Evans *et al.* 2015, Faria *et al.* 2004, Horres *et al.*, 2000, 2007, Sass & Specht 2010, Schulte *et al.*, 2005, 2009; Schulte & Zizka, 2008, Silvestro *et al.* 2014, Sass & Specht 2010).

A natureza dos padrões de disjunção está constantemente sendo questionada em Bromelioideae, já que as evidências sugerem que gêneros ou subgêneros com padrões de distribuição disjuntos não são monofiléticos (Aguirre-Santoro *et al.* 2015, Sass & Specht 2010). Por outro lado, em nível específico é possível encontrar diversos exemplos de distribuição disjunta entre as Florestas Atlântica e Amazônica, como são os casos de *Aechmea mertensii* e *A. aquilega* (Leme & Siqueira-Filho 2006, Smith & Downs 1979). A estabilidade dos conceitos morfológicos dessas duas espécies depõe em favor da efetividade dessas disjunções (Leme & Siqueira-Filho 2006, Smith & Downs 1979).

Smith & Downs (1979) reconheceram duas categorias infraespecíficas para *A. aquilega*. Posteriomente essas subespécies foram elevadas a categoria de espécie por Leme & Siqueira-Filho (2006). Mesmo com essas alterações, o conceito de *A. aquilega* mais restrito, proposto por Leme & Siqueira-Filho (2006) e seguido aqui, prevê uma distribuição geográfica com um núcleo no Norte da América do Sul, outro na costa leste do Nordeste do Brasil, e entre esses dois, algumas populações isoladas em florestas submontanas do estado do Ceará.

Aechmea mertensii é a única espécie no gênero que apresenta uma bráctea floral que envolve todo o ovário (Smith & Downs 1979), aspecto morfológico que confere a estabilidade para reconhecer dois pólos de distribuição bem distintos: um na bacia amazônica e outro na Floresta Atlântica desde a Paraíba até algumas populações reduzidas e isoladas no sul da Bahia. Porém, em campo é possível visualizar um padrão morfológico onde em algumas populações as plantas são robustas e com longas inflorescências e em outras as plantas apresentam inflorescências depauperadas e rosetas com poucas folhas. Essas diferenças morfológicas são provocadas pelas distintas associações específicas que a planta estabelece com formigas (Carrias *et al.* 2012, Céreghino *et al.* 2011).

2.3 Contextualização geográfica

A Floresta Atlântica é um dos principais hotspots de diversidade biológica e é também um dos mais ameaçados devido ao seu histórico de ocupação humana e drástica redução de sua área original (Myers *et al.* 2000, Mittermeier *et al.* 2004, Ribeiro *et al.* 2009). Similarmente, a Floresta Atlântica é o centro de diversidade e o hábitat para um elevado número de espécies em risco de extinção da família Bromeliaceae (BFG 2015, Martinelli *et al.* 2008). E na Floresta Atlântica, a família Bromeliaceae figura entre as mais ricas em espécies (Stehmann *et al.* 2009).

A grande variação latitudinal e altitudinal encontrada na Floresta Atlântica permitem a diversificação de hábitats dentro de um domínio caracterizado por uma cobertura florestal úmida (Thomas & Barbosa 2008, Figura 8). Dessa forma, padrões espaciais de riqueza e endemismo podem ser encontrados ao longo da extensão geográfica do ecossistema, o que permitiu Prance (1987) identificar uma série de centros de endemismos. Evidências utilizando as ferramentas mais diversas e distintos grupos biológicos confirmam a existência desses padrões e atestam suas origens históricas (Carnaval & Moritz 2008, Carnaval *et al.* 2009, 2014).

Dois desses centros de endemismos tem significativa relevância para entender os padrões espaciais e os processos de diversificação de Bromeliaceae na Floresta Atlântica. O primeiro é o sul da Bahia, que reúne o terceiro maior número de Bromélias na Floresta Atlântica conforme definido por Martinelli *et al.* (2008). O segundo é o Centro de Endemismo Pernambuco-CEP que apresenta uma riqueza menos expressiva, mas um elevado número de endemismos (Leme & Siqueira-Filho 2006, Figura 8). Ambos foram objetos de nossos estudos.

O CEP, principalmente, foi objeto do estudo da primeira e segunda parte do projeto. Originalmente, Prance (1987) delimitou o CEP como compreendendo a Floresta Atlântica dos estados de Alagoas e Pernambuco. Mas em textos atuais, o CEP é entendido como a extensão original da Floresta Atlântica ao Norte do Rio São Francisco, entre os estados do Rio

Grande do Norte e Alagoas (Roda 2003). Diversos grupos biológicos como aves, mamíferos, anfíbios, répteis, borboletas e plantas de diversas famílias possuem taxas de endemismos significativos nessa área da Floresta Atlântica (Brown 1982, Leme & Siqueira-Filho 2006, Martinelli et al. 2008, Müller 1972, 1973, Roda 2003).

Essa região é tida como uma das mais fragmentadas e com a maior redução da cobertura original em toda a Floresta Atlântica (Ribeiro *et al.* 2009). Atualmente, a maioria dos fragmentos existentes se caracteriza por variar entre 10 e 300 hectares de extensão, sendo considerados criticamente pequenos para manutenção de vários processos ecológicos e para abrigar espécies com requerimentos ambientais mais complexos (Ribeiro *et al.* 2009). Algumas dessas espécies são da família Bromeliaceae e foram profundamente impactadas pela perda de habitat na região (Siqueira-Filho & Tabarelli 2006).

Mesmo diante do cenário de destruição e da ameaça de extinção de diversas espécies, é impressionante o que os avanços recentes nos estudos da biodiversidade da região têm revelado. Diversas novas espécies foram recentemente publicadas em levantamentos feitos em distintos grupos biológicos (Amorim & Alves 2012, 2015, Carnaval & Peixoto 2004, Chautems *et al.* 2005, Costa-Lima & Alves 2013, Gregório *et al.* 2014, Leme & Siqueira-Filho 2006, Pessoa & Alves 2015, Pessoa *et al.* 2014a, 2014b). Particularmente a família Bromeliaceae teve um expressivo número de descobertas de novos táxons na área (Leme & Scharf 2011, Leme & Siqueira-Filho 2001, 2006). Além disso, recentes levantamentos florísticos revelam uma riqueza de espécies inesperada para o complexo mosaico de pequenas ilhas de vegetação da região. Esses estudos mostram índices de riqueza similares aos de regiões com extensos fragmentos contínuos de Floresta Atlântica (Alves *et al.* 2013, Alves-Araújo *et al.* 2008, Amorim *et al.* 2009, Coelho & Amorim 2014, Melo *et al.* 2011, 2016, Leitman *et al.* 2014).

Outro aspecto da história natural do CEP que despertou o interesse para nossos estudos foram sua conexões biogeográficas. Muitos autores têm relatado padrões de distribuição disjunta entre a Floresta Atlântica ao Norte do Rio São Francisco e a Floresta Amazônica para espécies ou grupos supraespecíficos (Andrade-Lima 1953, 1966, 1982, Batalha-Filho *et al.* 2012, Bigarella *et al.* 1975, Cavalcanti & Tabarelli 2004, Ducke & Black 1954, Oliveira-Filho & Ratter 1995, Rizzini 1963, Santos *et al.* 2007, Siqueira-Filho & Leme 2006).

2.4 Contextualização histórica

A contextualização dos principais eventos climáticos e geológicos ocorridos na história recente da Floresta Atlântica é de fundamental importância para compreender as conclusões dos capítulos a seguir. Devem ser destacados como relevantes para a compreensão dos processos evolutivos na região: o último pulso tectônico da Serra do Mar ao longo do Plioceno, as flutuações climáticas pleistocênicas e as transgressões marinhas ocorridas ao longo do Pleistoceno (Fiaschi & Pirani 2009).

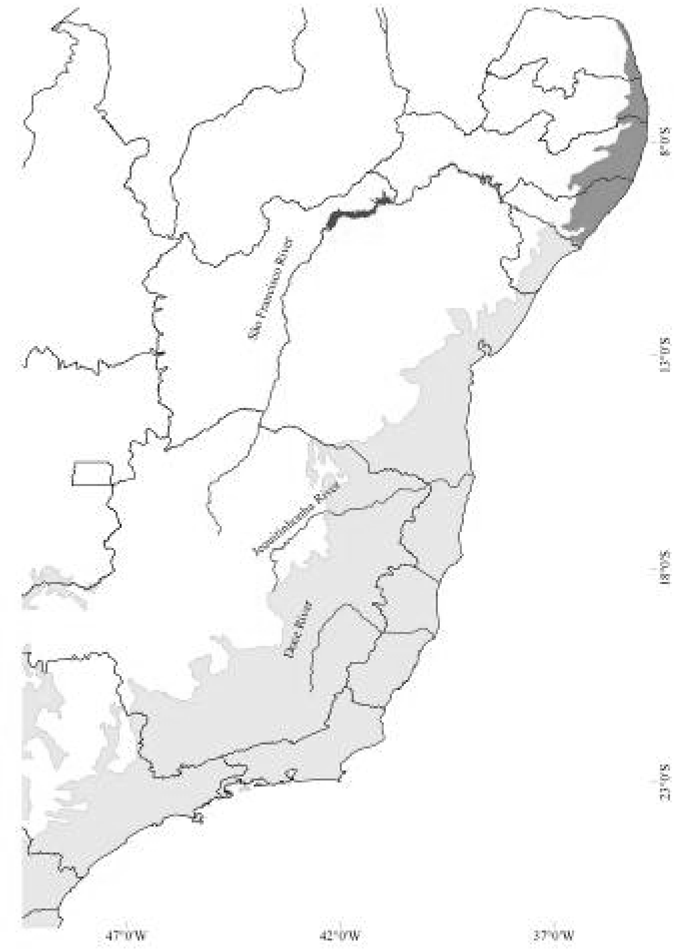

Figura 2.8. Floresta Atlântica ao longo da costa leste do Brasil (toda a área sombreada), seus principais rios e em destaque o Centro de Endemismo Pernambuco-CEP (escuro). A figura mostra a área original de floresta que cobria a região. Os rios mostrados na figura ajudam a delimitar as regiões da Floresta Atlântica com composições florísticas e espécies endêmicas diferentes entre si. Também há evidências de que sejam ou foram barreiras geográficas para diversos grupos biológicos. O Rio São Francisco é o limite sul do CEP, por isso, também a região é chamada de Floresta Atlântica ao Norte do Rio São Francisco.

Mesmo assim, os ciclos de soerguimento dos Andes desde o Mioceno vêm sendo propostos como o principal marco histórico que explicaria vários processos de especiação na América do Sul (Antonelli *et al.* 2009, Antonelli & Sanmartín 2011). Gentry (1982) sugere que diversos grupos com alta diversidade na região neotropical têm distribuição andina e por isso a especiação desses grupos foi influenciada pela tectônica da região. Com o aumento das hipóteses filogenéticas e com os avanços da biogeografia cladística, a hipótese de Gentry está sendo confirmada em um grande número de exemplos (Jabaily & Sytsma 2013, Lohmann *et al.* 2013, Roncal *et al.* 2013, Sarkinen *et al.* 2012, Wagner *et al.* 2013, Zapata 2013). O soerguimento do Andes alterou a dinâmica atmosférica na América do Sul proporcionando mudanças climáticas locais que trouxeram impacto para ambientes não andinos como demonstrado por Ehlers & Poulsen (2009).

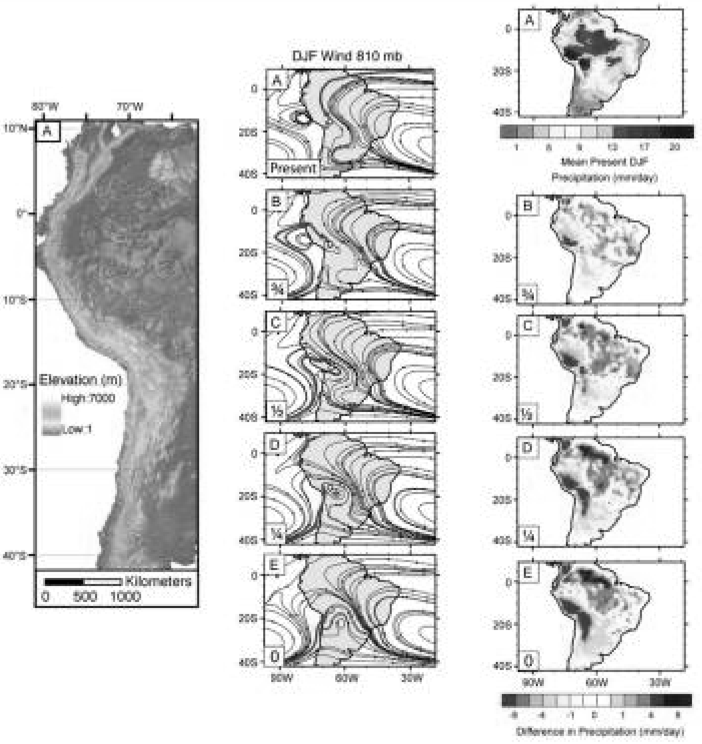

Figura 2.9. Impactos do soerguimento dos Andes. O soerguimento dos Andes abriu novos habitats na costa oeste da América do Sul e deu origem à Amazônia. Mas, além disso, também proporcionou mudanças na circulação de ventos e no regime pluviométrico da região. É isso que os mapas ao lado mostram (retirados de Ehlers & Poulsen 2009). No primeiro mapa é observada a localização e extensão dos Andes, a maior cadeia de montanhas do mundo. A primeira sequência de mapas mostra o modelo de circulação de ventos na América do Sul nas condições atuais (A), com ¾ da cordilheira (B), com ½ da cordilheira (C), com ¼ da cordilheira (D) e sem a cordilheira (E). A segunda sequência dos mapas mostra os modelos de regimes pluviométricos nos mesmos cenários.

Por outro lado, é provável que eventos diretamente relacionados aos ambientes da Floresta Atlântica tenham sido mais significativos para a diversificação local. Um deles foi o último pulso tectônico que ocorreu entre 5 e 2.5 milhões de anos (Plioceno) no sudeste do Brasil ao longo da costa do Rio de Janeiro, São Paulo, Paraná, Santa Catarina e Rio Grande do Sul dando origem ao atual relevo da Serra do Mar (Almeida 1976, Almeida & Carneiro 1998). Esse último ciclo de formação da Serra do Mar é evocado para explicar processos de diversificação na Floresta Atlântica em distintos grupos biológicos (Mata *et al.* 2009, Perret *et al.* 2006, 2013, Turcheto-Zolet *et al.* 2013).

A importância do último pulso tectônico da Serra do Mar também se estende à família Bromeliaceae. Givnish *et al.* (2011, 2014), tem reiteradamente se referido a esse evento como o mais significativo para explicar a riqueza e endemismo de gêneros da família na Floresta Atlântica. Os dados de Silvestro *et al.* (2014) mostram a relação entre o tempo da aquisição do hábito tanque em Bromelioideae e a formação do relevo atual da Serra do Mar, confirmando observações anteriores de Schulte *et al.* (2005, 2009).

Sabe-se que vários ciclos ao longo dos últimos 10Ma influenciaram o clima com expansões e retrações das geleiras, o que provocou mudanças significativas na dinâmica de massas vegetacionais e na distribuição das espécies (Araújo & Rahbek, 2006, Dynesius & Jansson 2000). O Plioceno (5 até 2.5 milhões de anos) viu uma acentuação na tendência global na redução de temperaturas (Zachos *et al.* 2001). Mas é no Pleistoceno (2.5 milhões até 10.000 anos) que o registro de diversos ciclos de mudanças climáticas se torna mais preciso. Essas mudanças climáticas também são consideradas como possíveis influenciadoras dos processos de diversificação em vários grupos, como Bromeliaceae (Silvestro *et al.* 2014) e em especial Bromelioideae que tem idade estimada de 7 milhões de anos.

Vários estudos paleopalinológicos e geológicos registram os efeitos das mudanças climáticas para os biomas brasileiros e em especial para a Floresta Atlântica (Auler *et al.* 2004, Behling 1998, Behling *et al.* 2000, Ledru *et al.* 1996, 1998, Mayewski *et al.* 2004, Oliveira *et al.* 1999, Pessenda *et al.* 2005, Salgado-Labouriau *et al.* 1998, Wang *et al.* 2004). As mudanças climáticas possibilitariam a redução do isolamento entre a Floresta Atlântica e a Amazônica estabelecendo corredores através das formações vegetacionais secas e mais abertas da América do Sul, como postulam diversos autores (Andrade-Lima 1953, 1966, Bigarella *et al.* 1975, Ducke & Black 1954, Rizzini 1963).

As mudanças climáticas também influenciaram a dinâmica poulacional e de colonização da Floresta Atlântica em *Eugenia uniflora*, por exemplo (Turchetto-Zolet *et al.* 2016). Carnaval & Moritz (2008) e Carnaval *et al.* (2009) demonstraram que as mudanças climáticas foram as forças responsáveis pelos processos que originaram determinados refúgios na Floresta Atlântica. Esses refúgios coincidem com padrões de riqueza genética em grupos de animais e plantas na região (Carnaval & Moritz 2008, Grazziotin *et al.* 2006, Turchetto-Zolet *et al.* 2012). Uma das constatações de Carnaval & Moritz (2008) e Carnaval *et al.* (2009) é que, associado às mudancas climáticas, os principais rios da costa leste do

Brasil atuaram como barreiras geográficas, destacando-se os rios São Francisco, Jequitinhonha e Doce.

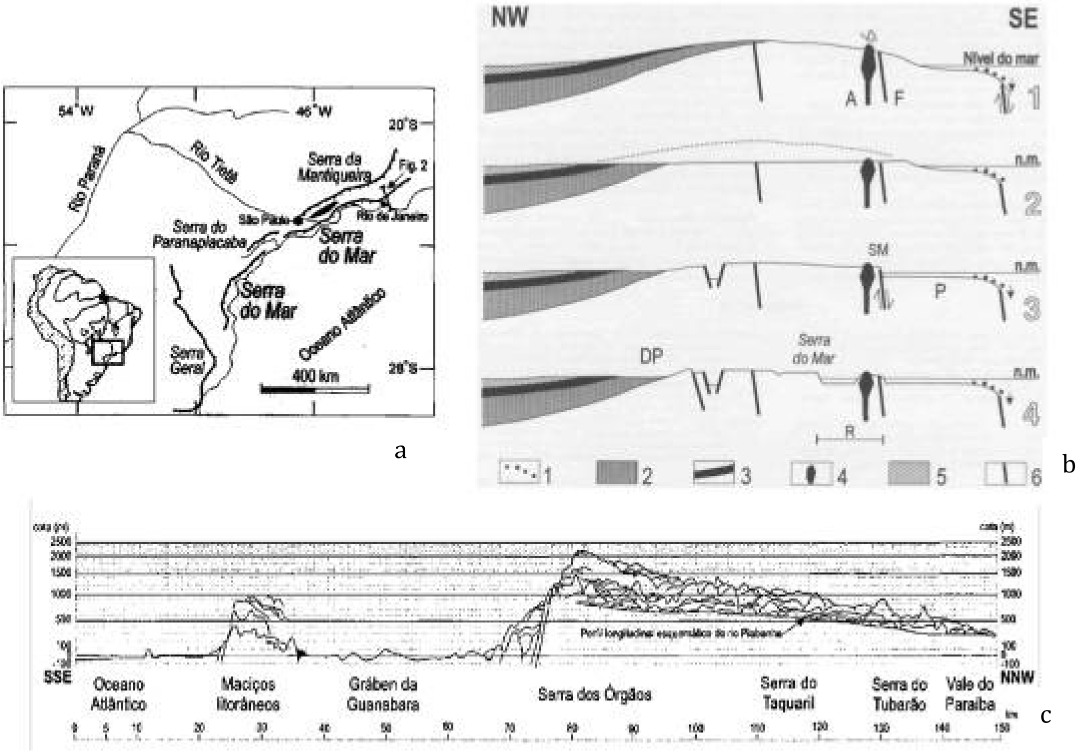

Figura 2.10. Posição (a), sequência evolutiva (b) e corte esquemático (c) da Serra do Mar.

Embora a função desses rios como barreiras geográficas para plantas possa ser questionada com base nas suas conformações modernas (Turchetto-Zolet *et al.* 2012), os distintos eventos de mudanças no nível do mar deixam claro o potencial para barreiras geográficas pretéritas que os maiores rios da costa leste brasileira apresentam (Haq *et al.* 1987, Miller *et al.* 2005). Transgressões marinhas foram registradas diretamente nos deltas dos rios São Franscisco, Jequitinhonha e Doce ao longo de todo o Plio-Pleistoceno (Arai 2006, Dominguez *et al.* 1981, 1987, Dominguez & Martin 1982, Rossetti *et al.* 20013). Os dados dos terraços costeiros do Nordeste do Brasil mostram que desde o Pleistoceno tardio, a região tem experimentado variações que vão de 2 metros abaixo até 12 metros acima do nível do mar atual (Barreto *et al.* 2002, Bezerra *et al.* 2003, Oliveira *et al.* 1999, Suguio *et al.* 2011).

Não é difícil entender que essas mudanças no nível do mar podem ter acarretado mudanças nos cursos e nas margens dos rios, sobretudo em áreas mais próximas à costa onde se insere a Floresta Atlântica, o habitat predominante das espécies que serão estudadas aqui. Tais mudanças podem ter criado isolamento necessário para o início de processos de especiação. Essa hipótese tem base nas evidências das mudanças nos deltas desses rios (Arai 2006, Dominguez *et al.* 1981, 1987, Dominguez & Martin 1982, Rossetti *et al.* 20013).

Outro conjunto de evidências que sustenta o papel dos rios da costa leste brasileira como barreira geográfica vem dos recentes estudos filogeográficos na região. Menezes *et al.* (2016) apontam os rios São Francisco e Jequitinhonha como barreiras que explicam a divergência genética entre os distintos grupos de *Pilosocereus* (Cactaceae). Cazé *et al.* (2016) demonstraram que *Passiflora contracta* (Passifloraceae) tem uma estruturação genética compatível com o Rio Jequitinhonha e Rio Doce como antigas barreiras geográficas. Uma grande transgressão marinha na depresssão La Plata-Paraguai separou as raposas do gênero *Lycalopex* em linhagens do leste e do oeste da América do Sul, dando origem à diversificação do grupo na região (Tchaicka *et al.* 2016). Uma revisão ampla discutindo o papel desses rios como eventuais barreiras para outros grupos biológicos na costa leste do Brasil é feita por Carnaval & Moritz (2009), Carnaval *et al.* (2014) e Turchetto-Zolet *et al.* (2012).

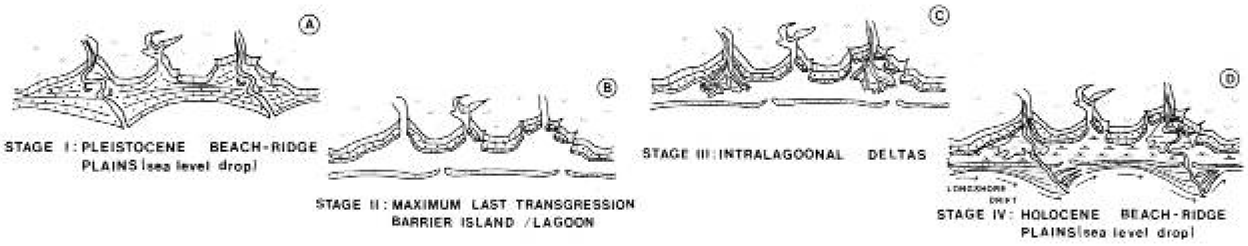

Figura 2.11. Sequência evolutiva proposta por Dominguez *et al.* (1987) para os deltas dos principais rios da costa leste do Brasil.
Conforme observado nessa sequência, as transgressões marinhas ocasionaram a mudança completa dos habitats costeiros, como esses onde são encontradas espécies de *Aechmea*. É esperado que essas transgressões também tenham afetado ambientes mais afastados da costa.

É interessante notar que Heller *et al.* (2015) demonstraram em seus resultados, sem especificar ou discorrer muito, a importância do rio Jequitinhonha como limite para a distribuição das espécies do complexo *Gravisia*. Em nenhum trabalho anterior esse rio havia sido citado ou os estudos de distribuição o haviam apontado como uma possível barreira para grupos de Bromeliaceae.

Por fim, em muitos casos, quando analisados individualmente, as influências desses eventos nos processos de especiação podem revelar padrões conflitantes e incoerentes. No entanto, interpretando-os como três forças sinérgicas, esses processos podem lançar luz na compreensão da história evolutiva dos grupos da Floresta Atlântica e, consequentemente, da região. Principalmente por que os três eventos ocorreram quase simultaneamente e interagiram entre si para a formação moderna da paisagem e da biodiversidade nessa porção da América do Sul.

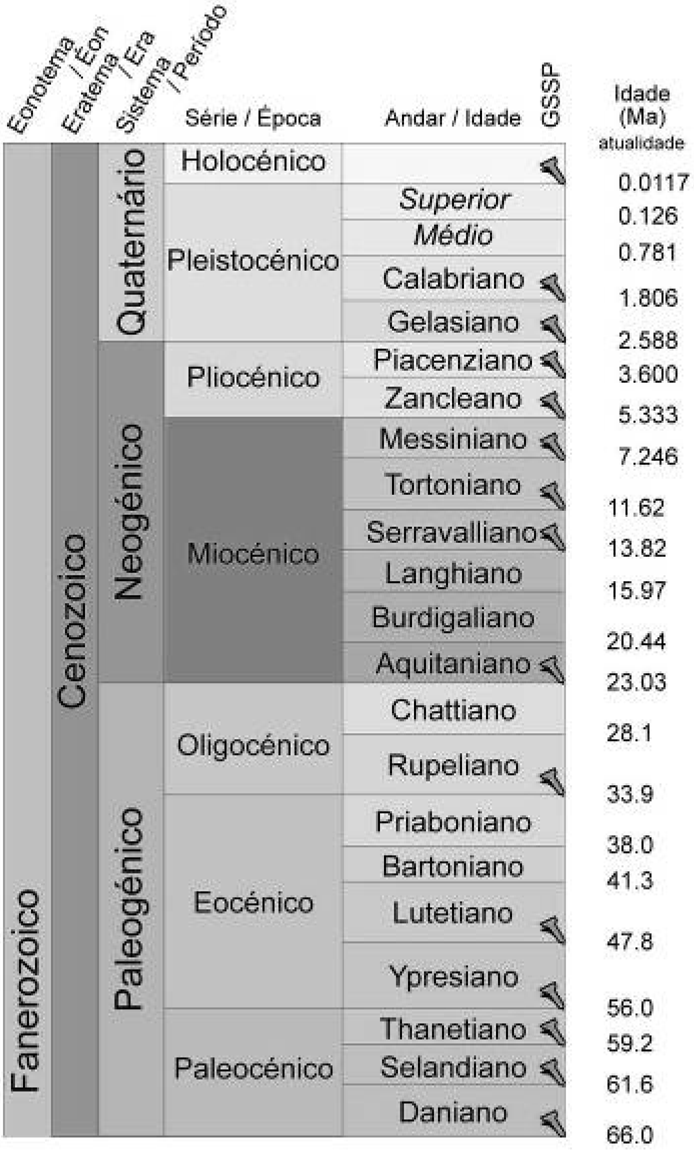

Figura 2.12. Sequêcia cronoestratigráfica internacional da Sociedade Internacional de Estratigrafia versão 2012. A figura foi reduzida para o Cenozoico, era dos principais eventos descritos e que influenciaram a diversificação em Bromeliaceae.

3 *Aechmea nigribracteata* (Bromeliaceae), a new species from southern Bahia, Brazil

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Rafael Batista Louzada

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Abstract

Herein is described and illustrated a new *Aechmea* species. *Aechmea nigribracteata* grows in southern Bahia (Brazil), a region recognised as highly diverse in bromeliads. *Aechmea nigribracteata* belongs to *Aechmea* subg. *Chevaliera* and has completely dentate, blackish floral bracts and petals with two crenate-laciniate ligules.

Keywords

Atlantic Forest, Bromelioideae, Neotropics, Poales, northeastern Brazil

Introduction

Aechmea includes about 288 species classified into eight subgenera, occurring from Mexico to southern Brazil, Uruguay and northern Argentina (Butcher & Gouda cont. upd., Forzza *et al.* cont. upd., Smith & Downs 1979). In the Brazilian Atlantic Forest, the genus is particularly rich and is represented by 140 species (Martinelli *et al.* 2008, Forzza *et al.* cont. upd.).

Within *Aechmea*, the species with large leaves, rosettes clustered in dense clumps, strobiliform inflorescence, flowers subtended by stiff coriaceous floral bracts, and petals with ligules or callosites are traditionally classified into the *Aechmea* subg. *Chevaliera* (Smith & Downs 1979). In the most updated taxonomic revision, Sousa (2004) presented a treatment of *Aechmea* subg. *Chevaliera* comprising 21 species. However, in recent years this number has increased due the description of eight new species (Leme & Siqueira-Filho 2006, Leme 2009, Leme & Kollmann 2009, Leme 2010, Leme *et al.* 2010, Leme & Kollmann 2011, Leme *et al.* 2014). The general difficulties in sampling species of *A.* subg.*Chevaliera* due to their huge rosettes, massive inflorescences, large spines and often epiphytic habits (above 10 meters high) have left many species poorly studied and poorly sampled while other species are probably still waiting for a formal description (Leme & Siqueira-Filho 2006, Sousa 2004, Canela *et al.* 2003).

In this paper we describe, illustrate, and provide conservation and ecological information on a new species of *Aechmea* found in southern Bahia, northeastern Brazil.

Taxonomy

Aechmea nigribracteata J.R. Maciel, Louzada & M. Alves, *sp. nov.* (Fig. 1-2)

Type:—BRAZIL. Bahia: Una, Entrada no Km 49 da BA-001, 15°13’19”S, 39°01’45”W, 31 May 2014 (fl., fr.), *J.R. Maciel*, *L. Daneu*, *D. Cavalcanti* & *B.S. Amorim 1950* (holotype UFP!, isotype FR!).

Aechmea nigribracteata is morphologically related to *A. depressa* L.B. Sm (1941: 54) as shown by huge rosettes, leaves with 150-230 cm long and wider leaf blade, but differs from that species by its central axis elongated (vs. compressed), inflorescence 24-30 cm long (vs. 11-14 cm long), floral bracts blackish (vs. reddish), lanceolate (vs. oblong), wholly dentate (vs. serrate in apical portion) and anthers narrowly bilobed at the base (vs. entire at the base).

Plants terrestrial or epiphytic herbs, shortly caulescent, flowering 70–80 cm tall, forming a funnelform or crateriform rosette. *Leaves* 12–25 in number, green, rigid-coriaceous, 150–230 cm long; *leaf sheaths* 25–35 × 20–30 cm, oblong, ample, contrasting in colour of the leaf blades, pale to dark brown, stiff-coriaceous, densely lepidote on both surfaces, with sub-adpressed and hyaline trichomes, margins entire, membranaceous; *leaf blades* 125–200 × 10–15 cm, green with brown to black apex, linear oblong, erect, stiff-coriaceous, channelled, densely lepidote on both sides of sub-adpressed and hyaline trichomes, apex attenuate then acuminate, margins densely serrulate; *prickles* antrorse, green to pale brown, 4–7 mm long, subtriangular. *Inflorescences* simple, spicate, strobiliform; fertile part of the inflorescence 24–30 cm long, 25–26 cm diam., globose; central axis elongated, dilated, 8–12 cm wide; peduncle 35–60 cm long, 4.5–5 cm diam.; *peduncle bracts* 44–50 × 5–6.5 cm, erect, sparsely lepidote, imbricate, rigid-coriaceous, oblong-lanceolate, green to castaneous nearly throughout, black at the base, margins serrulate, apex acuminate; *floral bracts* 63–70 × 11–13 mm, much exceeding the sepals, straight or nearly so, densely imbricate, stiff-coriaceous throughout when completely developed or membranaceous at the base during the first stage of development, slightly carinate, lanceolate, acute, navicular, abaxially glabrescent, blackish, margins wholly dentate, prickles 2–2.5 mm long. *Flowers* 6–7 cm long, patent or spreading, pedicels 3–5 mm long; *sepals* 28–35 × 6–8 mm, incurved, carinate, free, sparsely lepidote on both surfaces, castaneous at the base and green toward the apex, narrowly triangular, chartaceous, asymmetric, margins entire, apex mucronate, spines 0.8–2 mm long; *petals* 33–35 × 3–5 mm, free, erect, spathulate, fleshy, green, apex acute, corolla tubular-erect; *appendages* 2, crenate-laciniate, inserted at the base. *Stamens* about equal in length the pistil, included; filaments straight, 18–20 mm long, free; *anthers* 10–12 mm long, sub-basifixed, narrowly bilobed at the base. *Ovary* 19–21 mm long, trigonous; *epigynous tube* 8–10 mm long. *Style* stout; *stigma* conduplicate-spiral, lobes with lacerate margins. *Fruits* 6–8 cm long, cylindrical, green.

Etymology:—The name *Aechmea nigribracteata* refers to blackish floral bracts that also have entirely dark dentate margins. This combination of character states is unique among *Aechmea* subg. *Chevaliera* species.

Distribution and habitat:—*Aechmea nigribracteata* is only known from a restrict area of Atlantic coastal forest (Una region) in southern Bahia state, northeastern Brazil. This is an area particularly diverse in bromeliads species (Fontoura & Santos 2010), where five species of *Aechmea* subg. *Chevaliera* have been recorded (Fontoura & Santos 2010, Leme 2010, Sousa 2004) and recently recollected. These species are *Aechmea conifera* Smith (1941: 53), *A. depressa* Smith (1941: 54), *A. gustavoi* Siqueira & Leme (2001: 147), *A. multiflora* Smith (1937: 4) and *A. perforata* Smith (1941: 55). *Aechmea nigribracteata* grows as an epiphyte on the lower and stronger branches of trees or can be found as a terrestrial plant in sandy soils in coastal shrubby vegetation (locally called "Restinga") where it forms dense clumps (Fig. 2d). The region has an average of 1,800 mm rainfall a year and the driest months are between December and March (Fontoura & Santos 2010).

Phenology:—*Aechmea nigribracteata* was collected flowering and fruiting between May and July.

Conservation status:—The species is considered critically endangered based in criteria B1 (extent of occurrence less than 100 km^2) (IUCN 2013).

Comments:—The strobiliform inflorescence, rigid floral bracts, and petals with ligules lead us to conclude that *Aechmea nigribracteata* belongs to *Aechmea* subg. *Chevaliera* (Figs. 1–2). Within this subgnenus *A. nigribracteata* is related to species of the *A. multiflora* complex (Canela *et al.* 2003) where its morphologically closer is *Aechmea depressa* Smith (1941: 54) due to its huge rosettes, leaves with 150-230 cm long and wider leaf blade. However *A. nigibracteata* differs from *A. depressa* by its central axis elongated (vs. compressed), inflorescence 24-30 cm long (vs. 11-14 cm long), and floral bracts blackish (vs. reddish), lanceolate (vs. oblong), wholly dentate (vs. serrate in apical portion) and anthers narrowly bilobed at the base (vs. entire at the base).

The morphological relationships of *A. nigribracteata* with other species from *A. multiflora* complex is expressed in the taxonomic key below.

Identification key to species of *Aechmea multiflora* complex

1. Central axis compressed .... *A. depressa*

- Central axis elongated and compressed just in early stages of development 2

2. Floral bracts lanceolate, blackish, margins wholly dentate, prickles 2–2.5 mm long, anthers narrowly bilobed at the base .... *A. nigribracteata*

- Floral bracts oblong to spathulate, greenish to reddish, margins minutely serrulate or serrate up to 1/3, prickles ca. 1 mm long, anthers entire at the base 3

3. Floral bracts spathulate .... *A. multiflora*

- Floral bracts ovate .... *A. saxicola*

Additional specimens examined (paratypes):—BRAZIL. Bahia: Una, Arredores da REBIO Una, 15°13’19”S, 39°01’45”W, 8 December 2013 (fr.), *J.R. Maciel et al. 1839* (UFP!; RB!); *ib.,* Fazenda Nossa Senhora das Graças, 26 July 2000 (fr.), *J. Jardim et al. 3062* (CEPEC!; NY not seen; RB!).

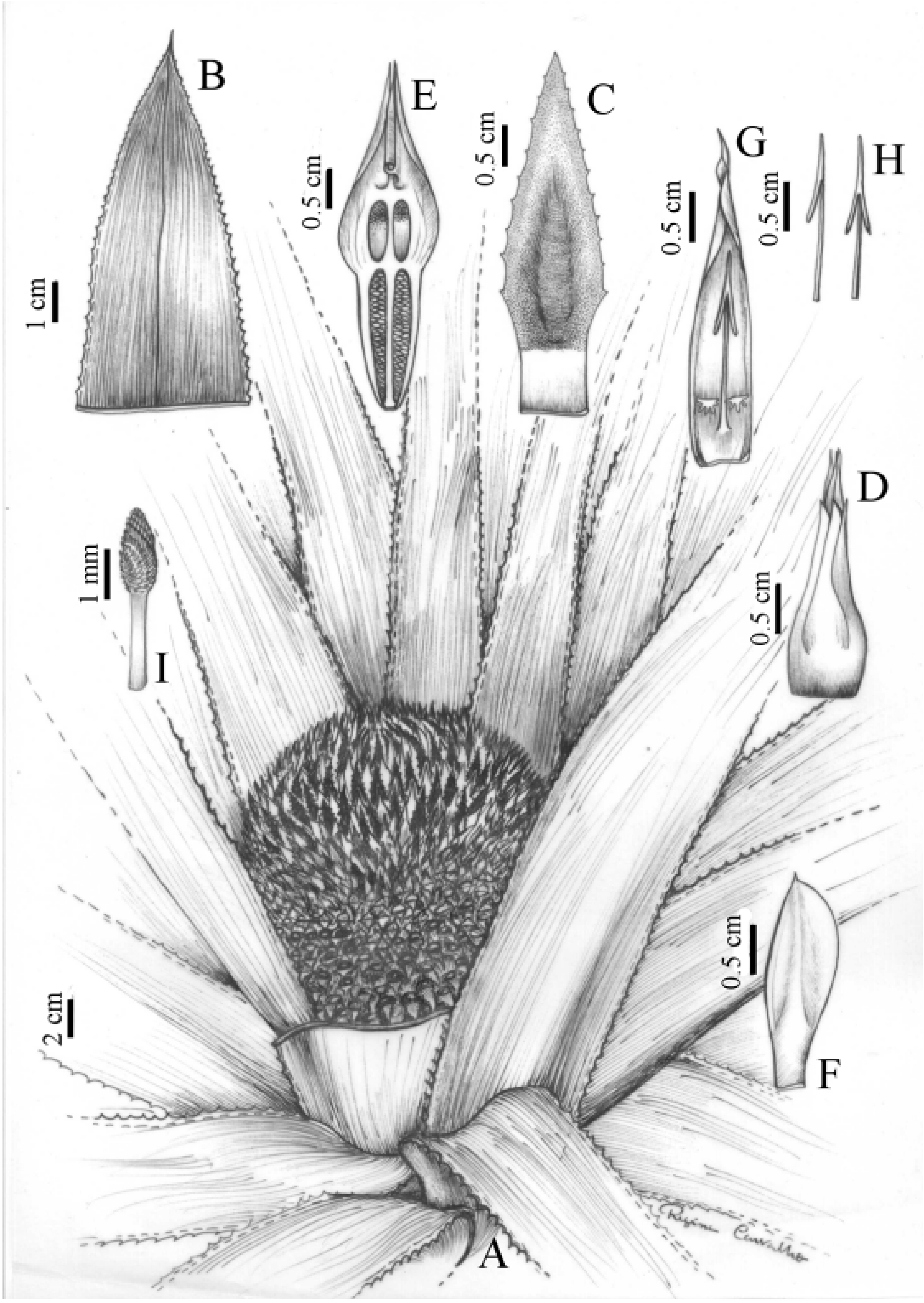

Figure 3.1. A—I. *Aechmea nigribracteata* (*J.R. Maciel et al. 1950*). A. Habit, B. Leaf, C. Floral bract, D. Flower, E. Longitudinal view of flower, F. Sepal (adaxial view), G. Petal (abaxial view), H. Stamen, I. Stigma. (Drawn from the holotype by Regina Carvalho).

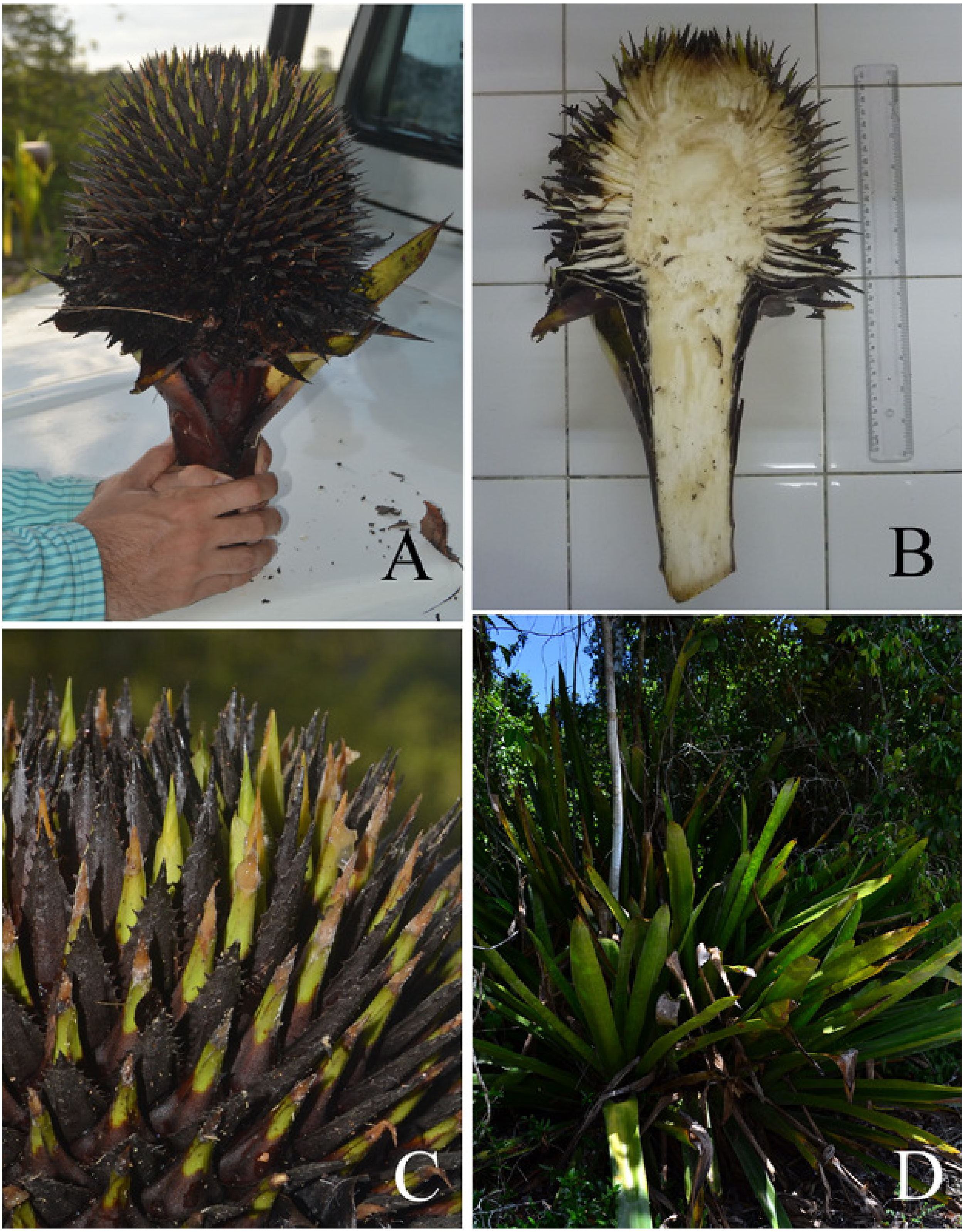

Figure 3.2. A—D. *Aechmea nigribracteata* (*J.R. Maciel et al. 1950*). A. Inflorescence, B. Longitudinal section of inflorescence, central axis and peduncle details, C. Floral bracts and flower details, D. Habit. (Photos: J.R. Maciel).

4 Searching for the gigantic bromeliads of Northeastern Brazil

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Georg Zizka

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Aechmea Ruiz & Pavon is one of the most representative genera of Bromeliaceae - Bromelioideae with over 288 species distributed in eight subgenera (Smith & Downs 1979, Luther 2012). It is distributed from Mexico to southern Brazil, Uruguay, and northern Argentina.

The genus is particularly highly diversified in Brazil where around 180 species are found, of which 150 are considered endemic to the country. In the Brazilian Atlantic Coastal Rainforest, a well known area of plant diversity and endemism, almost 140 species have already been registered (Martinelli *et al.* 2008, Forzza *et al.* 2014).

According to a recent study (Sass & Specht 2010), *Aechmea*, as a whole, is considered an unnatural genus. Furthermore, the relationships among the recognized subgenera are still unknown and far away from a better understanding. The results of this study suggest that *Aechmea* subg. *Chevaliera* (Gaudich. ex Beer) Baker possibly has multiple origins. Nevertheless, the circumscription and delimitation used by them for *Aechmea* subg.*Chevaliera* differs from Sousa (2004) and Sousa *et al.* (2008), who performed the most up-to-date taxonomic review of the group. Their data indicate that the species of *A*. subgen. *Chevaliera* from eastern Brazil are closely related. Indeed, it is clear that the sampling performed until now has not been enough to provide good support for any inference about the systematics and evolution of the subgenus and allied groups.

Aechmea subg. *Chevaliera* is a small group within the big and morphologically diverse genus *Aechmea* and comprises around 25 species (Sousa 2004). Previously known under the genus *Chevaliera*, these species are easily recognised by their large proportions and aggressive spines. The rosette of some individuals can reach up to 3 m in diameter. When they cluster as a clone, a common condition, or as more than one individual, a dense and impenetrable mass of sharp and long leaves results. Their beauty is usually associated with a big, compact and heavy inflorescence which holds hundreds of small and colourful flowers in a spiral arrangement and colourful bract spines (Sousa *et al.* 2008). The blooming period of one inflorescence can last for more than 15 months as observed in one cultivated specimen of *A. sphaerocephala* (Zizka 1990).

They grow in rainforests of Central and South America, such as the Amazon Forest and the Brazilian Atlantic Rainforest. However, most of the Brazilian species are microendemic to a narrow portion of the Atlantic Rainforest, and are known for the general sparsity and small size of their populations (Sousa 2004). It is possible that similar cases of narrow endemism can also be found in the species from central and northern South America. They are often found in very humid, dense and well preserved forests formed of tall trees, especially ones from the Pernambuco-wood family (Fabaceae), the Brazilian-nut family (Lecythidaceae) and the caimito family (Sapotaceae), among others. As enormous and unbelievably heavy epiphytes, they need strong branches on big trees to support them, although several species grow as terrestrials in the understorey too. As an example of their gigantism, one single mature specimen of some of the species can weight 25–30 kg, support in its rosette tank around one liter of water, while the inflorescence alone can weigh 4–5 kg, and one leaf can be up to 3 m long!

Because of their astonishing and fascinating biological condition, the species of *Aechmea* subg. *Chevaliera* are among the least collected and less known bromeliads. Usually, few samples are available in herbarium collections and they are, in general, seldom included in the living collections of the most important botanical gardens in the world.

The Atlantic Forest in the Brazilian Northeastern (Map 1) houses almost half of the species of *Aechmea* subg. *Chevaliera*. Some of them are included in the Brazilian Red List (Martinelli & Moraes 2013) as threatened species and with a high risk of extinction because of the loss of habitat in fragmented forests combined with their naturally few populations. *Aechmea muricata* (Arruda) L.B. Sm. exemplifies this scenario. It occurs along the Atlantic Rainforest (Map 1) in the states of Rio Grande do Norte – RN, Pernambuco – PE and Alagoas – AL (Magalhaes *et al.* 2014). Less than ten populations have been recorded in an area with no more than 200 km maximum distance between the northernmost and southernmost ones. Recently, a new population of this species was found in the northern part of the state of Pernambuco (Igarassu municipality) and close to the site where the British botanist George Ramage made an earlier collection in 1887 (typus of *A. stephanophora* E. Morren (BM), a synonym of *A. muricata*).

The Atlantic Rainforest in the state of Bahia – BA (Map 1) is one of the hot-spots for plant diversity in the world (Thomas *et al.* 2008), particularly along the southern part. This region plays an important role in terms of diversity and conservation of several plant families but especially bromeliads and orchids (Siqueira-Filho & Leme 2006).

The Biological Reserve of Una, in southern Bahia -BA (Map 1), is historically one of the best collected sites of the Brazilian Atlantic Forest (Amorim *et al.* 2008), and especially rich in Bromeliaceae. Four species of *Aechmea* subg. *Chevaliera* are recorded growing sympatrically in this area: *A. conifera* L.B. Sm., *A. depressa* L.B. Sm., *A. gustavoi* J.A. Siqueira & Leme and *A. perforata* L.B. Sm. (Fig.1). They grow in sandy or organic-rich soil or also as epiphytes on the canopy trees. The impressive and unusual number of sympatric species of *Aechmea* subg. *Chevaliera* at this site seems clearly related to the natural biological diversity of the area but also due to the forest's well preserved condition, humidity and the fact that it creates a continuous area of forest.

Some of the species of *Aechmea* subg. *Chevaliera* found in the Biological Reserve of Una are considered rare and narrow-endemics, such as *Aechmea gustavoi* which is known from only three small populations in the states of Pernambuco and Bahia.

Nevertheless, during very recent surveying for gigantic bromeliads, another fascinating site was found in the state of Bahia. In this new site, we were able to find striking diversity and an impressive number of individuals of three species of *Aechmea* subg. *Chevaliera*: *A. digitata* L.B. Sm. (Fig. 2), *A. multiflora* L.B. Sm. (Fig. 3) and *A. perforata* L.B. Sm. (Fig. 1).

The Boa Nova National Park (Map 1, Fig. 7) is located in Boa Nova municipality and around 120 km from the coast and 150 km from Una Biological Reserve. It is con- sidered an ecotone zone (transition zone) between the Atlantic Rainforest, which is a humid and dense forest along the coast, and an inland, semi-arid and savannah-type of vegetation, locally called "Caatinga". The preserved area is part of the inland limits of the Atlantic Rainforest. The landscape is a mosaic of forest combined with exposed rocky outcrops. The forest has distinct zones which can be humid or drier – depending on the position of the slopes – and holds a high diversity of vines and epiphytes.

Individuals of all three species were found in the drier forests of the National Park, which is locally known as "Mata de Cipó" because of the abundance of woody vines. The forest has a lower canopy (8–15 m) and an impressive number of climbing plants. Specimens of *Aechmea* subg. *Chevaliera* were found on the ground and also as epiphytes on 4–6 m tall trees, which is distinctly different from the scenario found in more humid forest not far from there.

Aechmea multiflora (Fig. 3, 6) and *Aechmea perforata* (Fig. 1) are the most common species in northeastern Brazilian Atlantic Rainforest, wherein several populations have been geo-referenced since 2012. However, *Aechmea digitata* (Fig. 2), easily recognised by the peculiar shape and size of the dark-brown inflorescence (Sousa *et al.* 2008), was previously known from only three localities, all with small populations.

Aechmea muricata and *A. multiflora* (Fig. 6) are two species of the subgenus clearly related to vegetation of savannah-like physiognomy but occasionally they are also found in dry forests along the coast. These plants are usually recorded from coastal shrubby dune vegetation (locally called "Restinga") on sandy and sometimes salty soil. This ecosystem is one of the most threatened in Brazil because of the real estate market and construction of beach resorts.

Many species of *Aechmea* subg. *Chevaliera* are poorly known morphologically; their descriptions are based on one to a few samples from sometimes one single locality (Smith & Downs 1979, Sousa 2004), and often no examples are recorded as being in cultivation.

Among them is *Aechmea conifera* L.B. Sm., which is a good example of how poorly known the species are in this group of gigantic bromeliads. It is known from a few samples collected in the state of Bahia (Map 1) with no flowers recorded or described. It is sympatric with two other species that have similar leaves and habit and have been described recently: *Aechmea serragrandensis* Leme & J.A. Siqueira and *Aechmea recurvipetala* Leme & L. Kollmann.

In spite of their beauty and size, we still need to make a considerable effort to better understand the morphology and systematic relationships of this group as well as develop effective actions for their conservation. Field work and search for new populations have been intensified, resulting in a range of new samples for herbarium and ecological studies, molecular analyses and living collections.

No doubt, there are still lots of forest fragments in northeastern Brazil to search and many populations of these peculiar and gigantic bromeliads to be found. New findings will allow us to provide good samples for research projects and to be cultivated in botanical gardens.

Figure 4.1. *Aechmea perforata* at Boa Nova National Park, Bahia (Foto by J.R. Maciel).

Figure 4.2. Top left: *A. digitata* at Boa Nova (Foto by J.R. Maciel); top right: *A. multiflora* at Boa Nova (Foto by J.R. Maciel); bottom: *A. multiflora* at county of Entre Rios, state of Bahia (Foto by A. Popovkin).

Figure 4.3. Top: *A. multiflora* as a terrestrial and gigantic bromeliad in vegetation of coastal savannah-like physiognomy (“restingas”) between states of Sergipe and Bahia (Foto by M. Alves); bottom: general view of “mata de cipó” at Boa Nova where three species of *A.* subg. *Chevaliera* were recorded (Foto by J.R. Maciel).

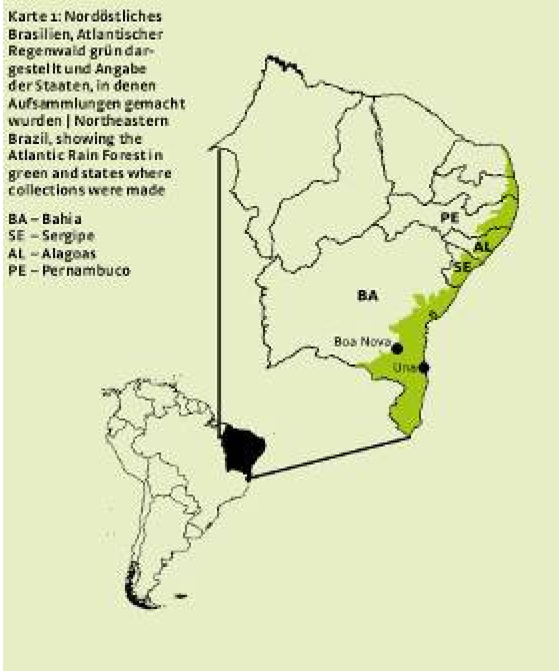

Figure 4.4. Top: *A. multiflora*, rainforest county of Entre Rios, state of Bahia. (Foto by A. Popovkin); bottom: map of cited areas.

5 *Aechmea* Ruiz & Pavón from the northern portion of the Atlantic Forest

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Abstract

Herein we present a taxonomic synopsis of *Aechmea* species from Alagoas, Pernambuco, Paraíba, Rio Grande do Norte and Ceará states. The lack of a taxonomic key for identification of species, the high rate of endemism and the recent novelties published within *Aechmea* from this region motivated this work. Samplings were conducted in areas of all states studied between 2010 and 2014. Morphological descriptions were written using on terminology stated in the literature and DELTA EDITOR 1.04 software. We identified 27 species in the study areas while two names were excluded from the species list compiled from the literature. The subgenus *Aechmea* was the most representative with 20 species. Of particular importance was the Gravisia complex, represented by ten of the 14 species that form this informal taxonomic group. Pernambuco and Alagoas were the most species-rich compared to the other states. For each species found in the study area, we present identification keys, comments on the taxonomic relationships, habitat information and geographical distribution.

Keywords

Bromeliaceae, Poales, taxonomy, morphology.

Introduction

Aechmea Ruiz & Pavon comprises nearly 288 species distributed in eight subgenera and is one of the most representative genera of subfamily Bromelioideae (Forzza *et al.* 2014, Smith & Downs 1979). Its species occur from Mexico to southern Brazil, Uruguay and northern Argentina (Butcher & Gouda cont. upd., Forzza *et al.* 2014, Smith & Downs 1979). In the Atlantic Forest of Brazil, 140 species have been cited (Martinelli *et al.* 2008, Forzza *et al.* 2014) which represents more than 50% of the species richness of *Aechmea*.

However, all this diversity is classified under an unnatural concept (Givnish *et al.* 2014, 2011, Sass & Specht 2010, Schulte *et al.* 2009, Horres *et al.* 2007, Givnish *et al.* 2007, Schulte *et al.* 2005), reflecting the traditional difficulties in classifying and establishing a precise definition of the genus (Faria *et al.* 2010, Wendt 1997, Smith & Downs 1979). While relationships among lineages within *Aechmea* are still unclear, the delimitation proposed by Smith & Downs (1979) has been used in taxonomic studies (Butcher & Gouda cont. upd., Forzza *et al.* 2014, Aguirre-Santoro & Betancur 2008, Martinelli *et al.* 2008, Martins *et al.* 2007).

In the northern portion of the Atlantic Forest, Sousa & Wanderley (2001) recorded ten species of *Aechmea* for the state of Pernambuco and later, Leme & Siqueira-Filho (2006) found 23 species in the states of Pernambuco and Alagoas. Martinelli *et al.* (2008) recognized Pernambuco and Alagoas as a region with high diversity and endemism of Bromeliaceae within the Atlantic Forest.

North of the São Francisco River, the Atlantic Forest fragments have not yet received enough attention concerning their diversity of bromeliads. These forest remnants exhibit a range of edaphic, geomorphological and altitudinal aspects (Ferraz & Rodal 2008). Sometimes these remnants can be found inserted in a semiarid matrix and are locally known as "brejos de altitude" (Thomas & Barbosa 2008). Although they are not recognized as part of the Atlantic Forest (Thomas & Barbosa 2008) we have included them in our study area. In this region, recent discoveries have expanded the geographical distribution of species (Magalhães *et al.* 2014) and new taxa have been described (Leme & Scharf 2011). Furthermore, recent advances in our knowledge of *Aechmea* phylogeny have indicated the role of biogeography on the systematics of the genus (Sass & Specht 2010) highlighting the importance of regional taxonomic studies.

In this work, we studied *Aechmea* species from the northern part of the Atlantic Forest (Alagoas, Pernambuco, Paraíba, Rio Grande do Norte and Ceará states) and provide identification keys as well as geographical and ecological information for the species.

Material and Methods

Field work was performed from December 2010 to July 2014 in montane, submontane and lowland Atlantic Forest fragments from Alagoas, Ceará, Paraíba, Pernambuco and Rio Grande do Norte states. Voucher specimens were deposited at UFP herbarium and duplicates sent to RB and NY. Collections at ALCB, ASE, CEPEC, EAC, HRB, HUEFS, IAN, INPA, IPA, JPB, MAC, MBML, MIRR, MPEG, NY, PEUFR, RB, UFP, UFRN, UFRR, US and VIES were also analyzed. To confirm species identification, protologs and specimen types were consulted in the herbaria cited above or online.

Morphological descriptions were conducted using DELTA Editor 1.04 software, following a morphological list of characters adapted from Gouda (1998), and terminology was also based in Siqueira-Filho & Leme (2006) and Smith & Downs (1979). The morphological descriptions of the species was ommited and its was characterized based in short diagnoses.

Results and Discussion

No specimens were found to confirm the occurrence of *A. marauensis* Leme cited to Alagoas, Pernambuco and Paraiba (Forzza *et al.* 2014). *Aechmea conifera* L.B. Smith was excluded because the samples cited by Sousa & Wanderley (2001) belong to *A. serragrandensis* Leme & J.A. Siqueira-Filho. Thus, *A. conifera* and *A. marauensis* are now restricted to Bahia.

We documented 27 species of *Aechmea* in Alagoas (17 spp), Pernambuco (19 spp), Paraíba (12 spp), Rio Grande do Norte (3 spp) and Ceará (4 spp) states. Species richness decreases from south to north, reflecting on a local scale the same pattern discussed by Martinelli *et al.* (2008) for the Atlantic Forest.

Among the 27 species recorded here, *Aechmea* subg. *Aechmea* is represented by 20 species, *A*. subg. *Chevaliera* by four, and *Aechmea* subg. *Lamprococcus*, *A.* subg. *Macrochordion* and *A*. subg. *Pothuava* by one species each.

The *Gravisia* species complex is the richest informal taxonomic group in the study area with 10 of the 14 species recognized as belonging to this complex by Leme & Siqueira-Filho (2006) and Read & Luther (1991). The *Aechmea lingulata* complex is represented in the area by four species. This taxonomic complex combines 21 species distributed in the Caatinga and Atlantic Forest of Brazil and the Caribbean (Leme & Siqueira-Filho 2006).

Key to the Species of *Aechmea* from the northern Atlantic Forest

1. Leaf blade margins entire .... 18. *A. marginalis*

1. Leaf blade margins dentate or serrulate

  2. Leaf blades variegated .... 2. *A. atrovittata*

  2. Leaf blades green on both surfaces or adaxially green and abaxially vinaceous

    3. Inflorescences simple

      4. Floral bracts absent; inflorescence axis wholly exposed .... 22. *A. nudicaulis*

      4. Floral bracts present; inflorescence axis completely hidden by bracts

        5. Leaves shorter or nearly as long as the inflorescence, 20-60 cm long

        .... 3. *A. bromeliifolia var. bromeliifolia*

        5. Leaves much longer than the inflorescence, 65-220 cm long

          6. Inflorescences 11-15 cm long, fertile part 7.5 cm long ....14. *A. gustavoi*

          6. Inflorescence 60-80 cm long, fertile part 11-25 cm long

            7. Floral bracts with margins densely serrulate .... 20. *A. multiflora*

            7. Floral bracts with margins entire

8. Inflorescences glaucous; floral bracts 1.9-2.8 cm × 1-1.4 cm 21. *A. muricata*

8. Inflorescences yellow; floral bracts 7-7.5 cm × 3.8-4.5 cm

.... 25. *A. serragrandensis*

3. Inflorescences compound

9. Floral bracts ≥ 1 cm long

10. Inflorescence 10-12 branched

11. Primary bracts as long as or longer than the basal branches, erect, suberect or reflexed

12. Primary bracts suberect to erect; floral bracts 1.2-1.4 cm long; pedicels 4-5 mm long... 5. *A. catendensis*

12. Primary bracts reflexed; floral bracts 1.5-2 cm long; pedicels 1-2.5 mm long .... 9. *A. emmerichiae*

11. Primary bracts distinctly shorter than the basal branches, divergent

13. Leaf blade apex attenuate, acute; primary bracts ovate-lanceolate; floral bracts much shorter than the internodes .... 10. *A. eurycorymbus*

13. Leaf blade apex truncate, pungent; primary bracts ovate; floral bracts slightly longer than the internodes ....13. *A. guainumbiorum*

10. Inflorescence 4-8 branched

14. Peduncle bracts green; branches spreading; rachis partly exposed, sepals yellow .... 6. *A. cephaloides*

14. Peduncle bracts red or orange; branches erect; rachis hidden, sepals orange

15. Inflorescence orange; fertile part 19-25 cm long; peduncle bracts orange; primary bracts divergent with the branches ..... 1. *A. aquilega*

15. Inflorescence yellow; fertile part 8-16 cm long; peduncle bracts red; primary bracts erect

16. Fertile part of inflorescence 8 cm long; primary bracts yellow .... 15. *A. lactifera*

16. Fertile part of inflorescence 12-16 cm long; primary bracts red .... 7. *A. chrysocoma*

9. Floral bracts < 1 cm long or absent

17. Flowers pedicellate

18. Peduncle bracts divergent, imbricate; primary bracts ovate, apex pungent .... 8. *A. costantinii*

18. Peduncle bracts erect, remote; primary bracts elliptic, apex acute

19. Terrestrial or rupicolous; leaves 33-65 cm long; leaf blade laxly serrulate; inflorescence pinkish; primary bracts red; sepals elliptical 16. *A. leptantha*

19. Epiphytic; leaves 70-110 cm long; leaf blade laxly dentate; inflorescence red; primary bracts yellow; sepals oblong .... 27. *A. werdermannii*

17. Flowers sessile

20. Inflorescence branched only at basal portion, red; leaf blades adaxially green and abaxially vinaceous .... 12. *A. fulgens*

20. Inflorescence branched from base to top, yellow, red, green or white; leaf blades green

21. Flowering plant 20-50 cm tall, forming a tubular to narrowly funnelform rosette with 6-8 leaves; inflorescence 30-40 cm long, fertile part 5.5-16 cm long; branches 1.5-2 cm long .... 19. *A. mertensii*

21. Flowering plant 60-170 cm tall, forming a tubular, crateriform or infudibuliform rosette with 8-20 leaves; inflorescence 53-120 cm long, fertile part 15-70 cm long; branches 5-26 cm long

22. Fertile part of inflorescence 50-70 cm long; with 80-100 branches .... 4. *A. castelnavii*

22. Fertile part of inflorescence 15-54 cm long; with 4-28 branches

23. Primary bracts as long as the branches or exceeding them, pink or red .... 26. *A. tomentosa*

23. Primary bracts reduced or shorter than the axillary branches, green

24. Blade prickles 1.5-3 mm long; inflorescence branches 15-26 cm long .... 23. *A. patentissima*

24. Blade prickles 0.5-2 mm long; inflorescence branches 5-12 cm long

25. Inflorescence with 20-22 branches .... 24. *A. pernambucentris*

25. Inflorescence with 6-16 branches

26. Leaf sheath 16-21 cm long; leaf blade 62-110 × 3.5-5 cm, margins laxly to subdensely serrulate; inflorescence green to red .... 11. *A. froesii*

26. Leaf sheath 11-13 cm long; leaf blade 39-70 × 8-10 cm, margins densely serrulate; inflorescence whitish ……………………………………………………………………… 17. *A. maranguapensis*

Aechmea Ruiz & Pavon

Terricolous, rupicolous or epiphytic plants, short- or long-caulescent, forming a tubular, narrowly funnelform, funnelform, broadly funnelform, crateriform or utriculate rosette. Leaves much shorter than the inflorescence to much exceeding the inflorescence; sheaths broadly ovate to elliptical; blades lanceolate to ligulate, green on both surfaces, adaxially variegated or abaxially vinaceous, erect, arching or recurving, glabrous to densely lepidote, apex attenuate, rounded, truncate, obtuse or emarginate, acute to pungent, margins entire to densely serrulate, prickles antrorse, straight or retrorse. Inflorescences simple or compound, capitate, globose, ovoid, ellipsoid, subcylindrical or paniculate, brown, whitish, pinkish, yellow, green, vinaceous, orange, red or glaucous; peduncle bracts remotely to densely imbricate, orange, red, pink, brown, glaucous, green or castaneous; primary bracts erect to divergent with the branches or reflexed, remotely to densely-imbricate, linear-lanceolate to ovate, entire to serrulate, shorter than the secondary peduncle to exceeding the branches, yellow, red, green, pink or orange; erect, spreading or curved; rachis hidden to wholly exposed; floral bracts ample to absent, much shorter than the internodes to exceeding the internodes remotely to very densely imbricate, membranaceous, chartaceous, stiff-chartaceous, coriaceous or stiff-coriaceous, glabrous to very densely lepidote, orange, white, green, red, brown, pink, glaucous or yellow. Flowers contiguous to spreading to a right angle with the rachis, sessile to long-pedicellate; sepals obovate to ovate-lanceolate, membranaceous to coriaceous, apex rounded to pungent, glabrous to densely lepidote, pink, white, green, yellow, orange or lilac.

1. ***Aechmea aquilega*** (Salisb.) Griseb., Fl. Brit. W.I. 592. 1864. (Figure 1a)

Selected specimens: ALAGOAS: Campo Alegre, 27.XII.2000, *I. Bayma 522* (MAC); CEARÁ: Guaramiranga, 22.IV.2013, *J.R. Maciel et al. 1709* (UFP); PARAÍBA: Mamanguape, 05°56’01”S, 35°05’56”W, 01.V.2005, *R.A. Pontes & P. Gadelha-Neto 216* (JPB, RB) PERNAMBUCO:

Jaboatão dos Guararapes, Engenho Comporta, 12.VII.2005, *J.A. Siqueira-Filho et al. 1512* (UFP); RIO GRANDE DO NORTE: São Miguel do Gostoso, 08.VIII.2013, *J.R. Maciel* & *T. Capistrano 1775* (UFP).

This species occurs from the Caribbean to Brazil, in the Amazon and Atlantic Forest or in dry lands of the Caatinga. In the study area it is cited to Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Sergipe and Alagoas (Forzza *et al.* 2014, Leme & Siqueira-Filho 2006, Read & Luther 1991). It grows in open areas as an epiphytic or terrestrial plant, but it is also tolerant of shady habitats. It can be differentiated from other species of *Aechmea* in the study area by its orange inflorescences with fertile part around 20 cm long, peduncle bracts orange and primary bracts divergent with the branches. Moreover, its leaves are as long as the inflorescence, primary bracts are reflexed and longer than the branches. It belongs to the *Gravisia* complex (Read & Luther 1991) and due to its morphological variation in inflorescence and habit many taxa have been described and later recognized as synonyms (Leme & Siqueira-Filho 2006, Sousa & Wanderley 2000, Read & Luther 1991, Smith & Downs 1979).

2. ***Aechmea atrovittata*** Leme & J.A.Siqueira, Fragm. Mata Atlântica do Nordeste. 228. 2006. (Figure 1b-c).

Specimens examined: ALAGOAS: Paripueira, Sítio Laranjeiras, 04.I.2001, *J.A. Siqueira-Filho & A.Frassy s.n.* (UFP-isotype); ibidem, 31.I.2012, *J.A. Siqueira-Filho et al. 2746* (HVASF).

Endemic to the state of Alagoas and known only from the type locality. It grows as an epiphyte in the lowland Atlantic Forest. Leme & Siqueira-Filho (2006) highlighted the heavily impacted conditions of its habitat in Alagoas, where the only known population is recorded and put it under risk of extinction. It can be differentiated from other species in this study by its variegated leaves, long caulescent growth form and fasciculated inflorescence. It is morphologically related to *A. disjuncta* (L.B. Sm.) Leme & J.A. Siqueira and cited under the complex *A. fosteriana* by Leme & Siqueira-Filho (2006).

3. ***Aechmea bromeliifolia*** var. ***bromeliifolia*** (Rudge) Baker, in Bentham & Hooker f. Gen. Pl. 3(2): 664. 1883. (Figure 1d-e).

Selected specimens: CEARÁ: Barbalha, Floresta Nacional do Araripe, 16.XII.2000, *I. Costa 117* (EAC); Guaramiranga, Serra do Baturité, 22.VI.2013, *J.R. Maciel et al. 1708* (UFP); PARAÍBA: Areia, Campus II da UFPB, 20.VII.2005, *R. Pontes 327* (JPB).

It occurs from Central America to northwestern South America and Brazil (Faria *et al.* 2010). In the study area it is found in Ceará and Paraíba. It grows as an epiphytic or terrestrial plant in Cerrado, Caatinga, Atlantic and Amazonian Forests and in coastal sandy soils (Faria *et al.* 2010). It can be characterized by its leaves shorter or nearly as long as the inflorescence which differentiates this species from *A.* subg. *Chevaliera*. Moreover *A. bromeliifolia* has densely lepidote floral bracts and white or brown inflorescences. It belongs to *A.* subg. *Macrochordion* (Baker) de Vrieese and two varieties are accepted by Faria *et al.* (2010): *A. bromeliifolia* var. *albobracteata* Philcox and *A. bromeliifolia* var. *bromeliifolia*, the latter of which is found in the study area based on its known geographical distribution and pink peduncle bracts.

4. ***Aechmea castelnavii*** Baker, Handb. Bromel. 39. 1889. (Figure 1f).

Selected specimens: CEARÁ: Aquiraz, Rio Pacoti, 15.X.1935, *F. Drouet 2616* (US); Itapipoca, Serra dos Picos, 13.I.2006, *D. Lima s.n.* (EAC-49556); Viçosa do Ceará, Serra das Flores, 4.VIII.2005, *L.Lima-Verde et al. 3401* (EAC).

This species occurs from Costa Rica to Bolivia and Brazil (Smith & Downs 1979), where it grows in the Atlantic and Amazonian Forests (Forzza *et al.* 2014, Smith & Downs 1979) as an epiphyte in open or shaded places. In the study area, it is recorded only from Ceará state. It has a very long pinkish inflorescence, with up to 80-100 branches. These characters are unique among other species in this study.

5. ***Aechmea catendensis*** J.A.Siqueira & Leme, Fragm. Mata Atlântica do Nordeste. 205. 2006. (Figure 1g).

Selected specimens: ALAGOAS: Ibateguara, Engenho Coimbra, 09.IX.2002, *M.A. Oliveira & A. Grilo 1096* (UFP), Matriz de Camaragibe, Serra da Curitiba, 26.X.2005, *R. Lyra-Lemos 9107* (MAC); PERNAMBUCO: Jaqueira, Serra do Urubu, 08. IX.2000, *J.A. Siqueira-Filho 1090* (UFP-holotype); Maraial, Engenho Curtume, 23.XII.2007, *M. Sobral-Leite 609* (UFP).

Endemic to Pernambuco and Alagoas, occurring in a very restricted area. It is a terricolous or rupicolous plant, growing in open areas of rocky outcrops within the Atlantic Forest. Leme & Siqueira-Filho (2006) suggested it as part of the *Gravisia* complex. It is morphologically related to *A. emmerichiae* but can be distinguished by the suberect to erect primary bracts (vs. reflexed in *A. emmerichiae*); 1.2–1.4 cm long floral bracts (vs. 1.5–2 cm long) and 3-3.2 cm long flowers (vs. 3.5-4 cm long).

6. *Aechmea cephaloides* J.A.Siqueira & Leme, Fragm. Mata Atlântica do Nordeste. 202. 2006. (Figure 2a).

Selected specimens: PERNAMBUCO: Caruaru, Parque Municipal Prof. Vasconcelos Sobrinho, 9.II.2000, *J.A. Siqueira-Filho et al. 1013* (UFP); Lagoa dos Gatos, Sítio Veloso, 6.VI.1999, *J.A. Siqueira-Filho et al. 939* (UFP-isotype); Taquaritinga do Norte, Mata da Torre de Microondas, 3.II.2005, *J.A. Siqueira-Filho et al. 1458* (UFP),.

Endemic to the state of Pernambuco. It grows as a terrestrial plant in shaded Atlantic Forest (Leme & Siqueira-Filho 2006). Among the taxa of the *Gravisia* complex, it has a more massive inflorescence and larger rosette. Its inflorescence is globose due to the very congested apical branches and the basal branches are patents with ascendant flowers . It also has crateriform rosettes and inflorescences shorter than the leaves. The combination of characters makes it very different from the others.

7. *Aechmea chrysocoma* Baker, Handb. Bromel. 44. 1889. (Figure 2b).

Selected specimens: ALAGOAS: Marechal Deodoro, 20.II.1999, *I. Bayma & C. Barros 192* (MAC); PARAÍBA: Maturéia, 27.IX.1997, *M.F. Agra 4286* (JPB); PERNAMBUCO: Goiana, Estação Experimental do IPA, 27.II.1996, *G. Sousa 177* (UFP).

Endemic to the northeastern São Francisco River area, where it occurs in Paraiba, Pernambuco and Alagoas states. It grows as an epiphytic or terrestrial plant in shaded places from the Atlantic Forest. It has a yellow inflorescence with a 12-16 cm long fertile part, red peduncle bracts and red and erect primary bracts. This name was revalidated by Leme & Siqueira-Filho (2006) and the species also belongs to the *Gravisia* complex. Originally, it was described by Baker (1889), then accepted as a variety under *A. aquilega* by Smith & Downs (1979) and finally as synonymous with *A. aquilega* by Read & Luther (1991).

However, it is clear that the *Gravisia* complex requires new approaches for a better taxonomic delimitation of the taxa within this informal group.

8. ***Aechmea costantinii*** (Mez) L.B.Sm., Phytologia 19: 281. 1970. (Figure 2c).

Selected specimens: ALAGOAS: Ibateguara, Engenho Coimbra, 01.VIII.2003, *J.A. Siqueira Filho et al. 1390* (UFP); PARAÍBA: Areia, Reserva Ecológica Estadual Mata do Pau Ferro, 15.VI.1999, *G. Baracho 836* (UFP); PERNAMBUCO: Bezerros, Reserva de Serra Negra de Bezerros, 4.III.1996, *G. Sousa et al. 181* (UFP).

Endemic to the northeastern São Francisco River area. Epiphytic in shaded and open areas in submontane and montane Atlantic Forest from Paraiba, Pernambuco and Alagoas (Leme & Siqueira-Filho 2006). *Aechmea costantinii* is differentiated by the minute floral bracts and pungent primary bracts, yellow inflorescence and flowers, 4–4.5 cm long pedicels and densely lepidote sepals. Sousa & Wanderley (2000) cited *A. stelligera* to Pernambuco which was later synonymized with *A. costantinii (*Leme & Siqueira-Filho 2006).

9. ***Aechmea emmerichiae*** Leme, Bradea 4(39): 309. 1987. (Figure 2d).

Selected specimens: PARAÍBA: Maturéia, Parque Estadual do Pico do Jabre, 15.IV.2005, *R. Pontes & E.A. Rocha 197* (JPB, RB); *Ibidem*, 8.XII.2004, *R. Pontes & N.T. Lima 148* (JPB, RB).

Endemic to northeastern Brazil, where it occurs in Bahia and Paraíba. In the study area it occurs in Paraíba state (Leme & Siqueira-Filho 2006). It grows in rocky outcrops in montane areas of the Atlantic Forest and in open areas. It is considered part of the *Gravisia* complex (Read & Luther 1991) and closely related to *A. eurycorymbus* and *A. aquilega*. It differs by its inflorescence with 10-12 branches, primary bracts as long as or exceeding the basal branches and 1.5–2 cm long floral bracts.

10. ***Aechmea eurycorymbus*** Harms, Notizbl. Bot. Gart. Berlin-Dahlem 12: 528. 1935. (Figure 2e-f).

Selected specimens: ALAGOAS: Quebrangulo, Reserva Biológica de Pedra Talhada, 12.IV.1994, *A.C. Cervi et al. 7416* (NY); PARAÍBA: Campina Grande, 9.X.1948, *M.B. Foster 2408* (RB, US); PERNAMBUCO: Ibimirim, 25.II.1961, *M. Mee s.n.* (RB, US-2580048), Triunfo, Lagoa do Mariano, 19.IX.1995, *L.P. Félix et al. s.n.* (HST-7785, HUEFS).

Endemic to the northeastern São Francisco River area. It occurs in Paraíba, Pernambuco and Alagoas as a terrestrial plant in shaded places of the lowland Atlantic Forest. It is morphologically related to *A. emmerichiae* and *A. guainumbiorum*, but can be differentiated by its attenuate and acute leaf blade apices and floral bracts, laxly imbricate peduncle bracts, ovate-lanceolate primary bracts and floral bracts shorter than the internodes. Leme & Siqueira-Filho (2006) and Sousa & Wanderley (2000) also emphasized how unclear the taxonomic limits between *A. eurycorymbus* and *A. werdermanii* are. Some of the diagnostic characters used by Leme & Siqueira-Filho (2006) to recognize both taxa overlap. The main morphological characters to differentiate both species are the length of the floral bracts (1.7-2.5 cm long in *A. eurycorymbus vs.* 0.6-0.8 cm long in *A. werdermanii*) and pollen morphology (finely reticulated exine and dense walls *vs.* broadly reticulated exine and not dense walls) (Leme & Siqueira-Filho 2006).

11. ***Aechmea froesii*** (L.B.Sm.) Leme & J.A.Siqueira, Fragm. Mata Atlântica do Nordeste. 225. 2006. (Figure 3a).

Selected specimens: ALAGOAS: Ibateguara, Engenho Coimbra, 17.XII.2002, *J.A. Siqueira-Filho 1314* (UFP, HVASF); Murici, Fazenda Bananeira, 17.III.2005, *J.A. Siqueira-Filho 1474* (UFP); PERNAMBUCO: Ipojuca, Engenho de Pindeirama, 11.XII.1997, *S. Tavares 60* (UFP); Sirinhaém, Mata da Laranja, 14.XII.2004, *J.A. Siqueira-Filho 1444* (UFP).

Endemic to northeastern Brazil, this species occurs from Pernambuco to Bahia along the Atlantic Forest. In the study area it occurs in Pernambuco and Alagoas. It grows as an epiphytic or terrestrial plant in open or shaded areas. It belongs to the *Aechmea lingulata* complex (Leme & Siqueira-Filho 2006) and can be differentiated from the others by its green to red inflorescences with 6–9(14) branches. It often has red inflorescences but this is variable within populations. Smith & Downs (1979) recognized it as a variety of *A. lingulata* while Sousa & Wanderley (2000) accepted no infraspecific taxa under *A. lingulata*. However, Leme & Siqueira-Filho (2006) proposed a new combination which is followed here.

12. ***Aechmea fulgens*** Brongn., Ann. Sci. Nat., Bot. ser. 2, 15: 371. 1841. (Figure 3b).

Selected specimens: ALAGOAS: Ibateguara, Coimbra, 25.I.2003, *M. Oliveira 1240* (UFP); PERNAMBUCO: Jaqueira, RPPN Frei Caneca, 28.IV.2014, *J.R. Maciel et al. 1909* (UFP); PARAÍBA: Natuba, Mata da antena da Telemar, 15.V.2005, *R. Pontes 246* (JPB).

Endemic to the northeastern São Francisco River area. It occurs as a terrestrial and sometimes epiphytic plant in shaded places in the Atlantic Forest in Paraíba, Pernambuco and Alagoas states. Among the caulescent species in this study, it can be differentiated by its green or adaxially green and abaxially vinaceous leaves, branched and red inflorescence, sessile flowers and lilac sepals. Smith & Downs (1979) proposed two varieties based on the chromatic pattern of the leaves, which were recognized neither by Sousa & Wanderley (2000) nor Leme & Siqueira-Filho (2006).

13. *Aechmea guainumbiorum* J.A.Siqueira & Leme, Fragm. Mata Atlântica do Nordeste. 207. 2006. (Figure 3c).

Selected specimens: PERNAMBUCO: Maraial, Engenho Curtume, 2.XI.2001, *J.A. Siqueira-Filho 1184* (UFP-holotype); *Ibidem*, 24.X.2006, *M.Sobral-Leite 235* (UFP) .

Endemic to the state of Pernambuco. Rupicolous in exposed rock outcrops in submontane Atlantic Forest at 500-700 m altitude. Closely related to *A. eurycorymbus*, from which it differs by its truncate and pungent leaf blade apex, the remote basal-most peduncle bracts and the imbricate uppermost peduncle bracts; ovate primary bracts and floral bracts slightly exceeding the internodes. According to Leme & Siqueira-Filho (2006), this species belongs to the Gravisia complex.

14. *Aechmea gustavoi* J.A.Siqueira & Leme, Selbyana 22(2): 147. 2001. (Figure 3d-e).

Specimens examined: PERNAMBUCO, Jaqueira, Serra do Urubu, 08.IX.2000, *J.A. Siqueira-Filho 1091* (UFP-holotype); *Ibidem*, 29.IV.2014, *J.R. Maciel et al. 1929* (UFP).

Endemic to northeastern Brazil and occuring in Bahia and Pernambuco, in submontane Atlantic Forest at 500 to 600 m altitude. In the study area it is restricted to Pernambuco. It is an epiphyte of canopy trees at 10 m above the ground and in shaded areas. It is very distinctive due to its capitate inflorescence and the short fertile portion wholly inserted in the rosette. Leme & Siqueira-Filho (2006) related this inflorescence pattern to species of *Neoregelia* subg. *Protoregelia*, but morphological characters leave no doubt of its systematic position. Sousa (2004) and Leme & Siqueira-Filho (2006) indicated more populations in the states of Pernambuco and Alagoas, however the species has not yet been collected in these areas.

15. *Aechmea lactifera* Leme & J.A.Siqueira, Fragm. Mata Atlântica do Nordeste. 199. 2006. (Figure 3f-g).

Selected specimens: ALAGOAS: Maceió, XI.2000, *R. Menescal s.n.* (CEPEC); PERNAMBUCO: Ipojuca, Fazenda Merepe, 13.I.1997, *J.A. Siqueira-Filho 796* (UFP-holotype); *Idem*, Mata do Cupe, 26.V.2013, *J.R. Maciel et al. 1734* (UFP).

Endemic to the northeastern São Francisco River area, it occurs in Pernambuco and Alagoas states. Epiphytic or terrestrial plants in shaded areas in lowland Atlantic Forest. It is morphologically related to *A. chrysocoma*, but is differentiated by the shorter fertile part of inflorescence (8 cm *vs.* 12-16 cm long) and yellow primary bracts (vs red). A dense, milky mucilage can be found on the inflorescence during anthesis which resembles latex. Siqueira-Filho & Leme (2006) stressed this character as a main feature to distinguish this species but it cannot be used with herbarium specimens which lack this data on the label. Furthermore, *A. lactifera* is not the only species which has this milky mucilage; it has also been recorded in *A. chrysocoma* and *A. aquilega* during fieldtrips.

16. *Aechmea leptantha* (Harms) Leme & J.A.Siqueira, Fragm. Mata Atlântica do Nordeste. 213. 2006. (Figure 3h-i).

Selected specimens: ALAGOAS: São José da Laje, Usina Serra Grande, 27.II.2002, *M. Oliveira 780* (IPA); PARAÍBA: Mamanguape, Reserva Biológica Guaribas, 21.VII.2010, *R. Pontes 470* (JPB); PERNAMBUCO: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, 29.VI.2014, *J.R. Maciel et al. 1925* (UFP).

Endemic to northeastern Brazil from Paraiba to Sergipe. In the study area it occurs in Paraíba, Pernambuco and Alagoas. Rupicolous in exposed rock outcrops in the Atlantic Forest and Caatinga. The combination of a pinkish, large and lax inflorescence with pedicellate flowers and red primary bracts is unique among the studied species. Leme & Siqueira-Filho (2006) placed this taxon under *Aechmea* (previously described as *Portea leptantha* Harms) based on morphological evidence, but recently Sass & Specht (2010) have confirmed its affinity to *Portea* species based on molecular evidence. Herein we follow Forzza *et al.* (2014) and Leme & Siqueira-Filho (2006), who used morphological characters to place this species under *Aechmea*.

17. ***Aechmea maranguapensis*** Leme & Scharf, Bromelie 2011(2): 59. 2011. (Figure 4a).

Selected specimens: CEARÁ: Maranguape, Serra do Maranguape, 24.IV.2013, *J.R. Maciel et al. 1727* (UFP); *Ibidem*, 26.XI.1955, *D. Andrade-Lima & G. Black s.n.* (EAC-1536); Pacoti, Sítio Olho D'Água dos Tangarás, 2.XI.1996, *L. Lima-Verde 155* (EAC).

Endemic to the state of Ceará and growing as an epiphytic or rupicolous plant in Serra de Maranguape above 700 m alt. Leme & Sharf (2011) related it to *A. pernambucentris* and *A. sulbahianensis* Leme, Amorim & J.A. Siqueira. However, based on the studied specimens, it seems to be morphologically related to *A. froesii* in the *A. lingulata* complex due to its little-branched inflorescence. However, it can be differentiated by its lilac flowers that are purplish at the apex, white inflorescence, shorter sheaths and shorter and wider leaf blade.

18. ***Aechmea marginalis*** Leme & J.A.Siqueira, Selbyana 22(2): 149. 2001. (Figure 4b).

Specimen examined: ALAGOAS: Ibateguara, II.2001, *J.S. Medeiros & A. Frassy s.n.* (HB-holotype).

Endemic to the state of Alagoas and restricted to a small area of lowland Atlantic Forest where grows as an epipyte. It has a capitate but branched yellow inflorescence and green bracts. However, the main character to recognize it is the entire leaf blade margin, uncommon among species from the area.

19. ***Aechmea mertensii*** (G. Mey.) Schult. & Schult. f. in Roemer & Schultes, Syst. Veg., ed. 15 bis 7(2): 1272. 1830. (Figure 4c).

Selected specimens: ALAGOAS: Ibateguara, Engenho Coimbra, 25.I.2003, *M. Oliveira & A. Grillo 1246* (UFP); PARAIBA: Mamanguape, Reserva Biológica Guaribas, 26.VIII.2010, *R.A. Pontes & J.R. Lima 559* (JPB); PERNAMBUCO: Ipojuca, Oiteiro de Nossa Senhora do Ó, 01.VI.2013, *J.R. Maciel et al. 2013* (UFP).

It is cited from Colombia, Peru and Brazil (Smith & Downs 1979), where it occurs in the Amazon and Atlantic Forest. In the study area it is found from Paraíba to Alagoas. It is epiphytic, often growing in lighted areas and associated with *Anthurium gracile* Lindl. (Araceae) and ant gardens formed among the roots of both species. It reaches 20-50 cm tall while blooming, with a tubular to narrowly funnelform rosette and few leaves (6-8). The inflorescence is short-branched, with sessile and yellow flowers. A floral bract enfolding most of the ovary is a unique condition among the species studied here. Sousa & Wanderley (2000) indicated that the specimens from the Amazon Forest are often more robust.

20. *Aechmea multiflora* L.B.Sm., Contr. Gray Herb. 117: 4, pl. 1, figs. 1–3. 1937. (Figure 4d-e).

Selected specimens: ALAGOAS: Coruripe, Usina Guaxuma, 31.X.2004, *J.A. Siqueira-Filho et al. 1436* (UFP); Feliz Deserto, s.l., 4.XI.1979, *D. Andrade-Lima 79-8772* (IPA); Maragogi, s.l., 11.X.1980, *D. Andrade-Lima 80-8813* (IPA).

Endemic to Brazil, distributed from Alagoas to Bahia state. In the study area it was recorded only for Alagoas. It is a common species in lowland coastal forest ("restinga") where it grows as a terrestrial plant in sandy soils and shaded places or as an epiphyte. It can be recognized by its massive, globose and red inflorescence with, densely serrulate, red floral bracts. The fruits are edible with a sweet flavor. Canela *et al.* (2003) pointed out that the inflorescence of *A. multiflora* elongates after anthesis which differentiates it from *A. depressa* L.B. Sm.. Leme & Siqueira (2001) described *A. frassyi* as related to *A. multiflora* but later the same authors synonymized it (Leme & Siqueira 2006).

21. *Aechmea muricata* (Arruda) L.B.Sm., Phytologia 8: 12. 1961. (Figure 4f-g)

Selected specimens: ALAGOAS: Paripueira, Sítio Laranjeiras, 04.I.2001, *J.A. Siqueira-Filho & A. Frassy 1147* (UFP); PERNAMBUCO: Cabo de Santo Agostinho, Mata da Pólvora, 01.VI.2013, *J.R. Maciel et al. 1745* (UFP); RIO GRANDE DO NORTE: Baía Formosa, Mata Estrela, 24.III.2013, *R. Magalhães 19* (UFRN).

Endemic to the northeastern São Francisco River area, restricted to Alagoas, Pernambuco and Rio Grande do Norte (Magalhães *et al.* 2014). It grows in open and shaded areas as an epiphytic or terricolous plant in lowland Atlantic Forest. It is common in sandy soils along the coast in "restinga" vegetation. It can be characterized by its green and subcylindrical inflorescence. Leme & Siqueira-Filho (2006) and Sousa & Wanderley (2000) highlighted the heavy impact on and loss of natural populations in urban areas in the state of Pernambuco.

22. *Aechmea nudicaulis* var**. *nordestina*** J.A.Siqueira & Leme, Fragm. Mata Atlântica do Nordeste. 243. 2006. (Figure 5a).

Selected specimens: PARAÍBA: Salgado de São Félix, Sítio Pau D´árco, 16.IV.2005, *R.A. Pontes 164* (RB); Natuba, Fazenda Sr. Gera, 14.V.2005, *R. Pontes 254* (JPB). PERNAMBUCO: Gravatá, Sítio Brejo Velho, 5.II.2005, *J.A. Siqueira-Filho & M. Sobral-Leite 1470* (UFP); Macaparana, Pirauá, 02.II.2004, *J.A. Siqueira-Filho et al. 1454* (UFP-holotype).

Aechmea nudicaulis occurs from Central America to Brazil (Wendt 1997) and *A. nudicaulis* var. *nordestina* is one of the varieties recognized. It is endemic to the montane and submontane northern Atlantic Forest and found in the states of Paraíba and Pernambuco (Leme & Siqueira-Filho 2006). The pale green peduncle bracts, sepals and inflorescence can be used to distinguish this variety (Smith & Downs 1979). In the study area it can be grouped with the plants with long caulescent growth form, but it has green leaves and a simple, pale green inflorescence with the axis fully exposed.

23. *Aechmea patentissima* Baker, J. Bot. 17: 227. 1879. (Figure 5b-d).

Selected specimens: ALAGOAS: União dos Palmares, Faz. Sto. Antonio, 29.X.2002, *J.A. Siqueira-Filho 1290* (UFP); PARAÍBA: Mamanguape, REBIO Guaribas, VIII.2013, *J.R. Maciel et al. 1777* (UFP); PERNAMBUCO: Jaqueira, RPPN Frei Caneca, 28.IV.2014, *J.R. Maciel et al. 1903* (UFP); RIO GRANDE DO NORTE: Natal, Parque das Dunas, 21.IX.2012, *E. Tomaz 1*.

In the study area it occurs in Rio Grande do Norte, Paraíba, Pernambuco and Alagoas states, but has a wide distribution in the Atlantic Forest and can also been found in Bahia, Espírito Santo and Rio de Janeiro. It is terrestrial or epiphytic in shaded or open places. It is related to *A. pernambucentris* but can be distinguished by the higher number of inflorescence branches. *A. patentissima* has a longer inflorescence and longer branches than *A. pernambucentris*. Leme & Siqueira-Filho (2006) restored *A. patentissima* to species status unlike Smith & Downs (1979) and Sousa & Wanderley (2000), who placed *A. patentissima* as a variety of *A. lingulata*. Leme & Siqueira-Filho (2006) included this species in the *A. lingulata* complex and related it to *A. lingulatoides* Leme & H. Luther.

24. *Aechmea pernambucentris* J.A.Siqueira & Leme, Fragm. Mata Atlântica do Nordeste. 227. 2006. (Figure 5e).

Selected specimens: PERNAMBUCO: Taquaritinga do Norte, 21.IX.1998, *G. Baracho 761* (UFP-holotype); Idem, Mata da Torre de Microondas, 3.II.2005, *J.A. Siqueira-Filho et al. 1459* (UFP); Jaqueira, Mata da Serra do Quengo, 28.IX.1997, *J. Siqueira-Filho & M. Campelo 736* (UFP).

Endemic to the northeastern São Francisco River area and restricted to montane forests of Pernambuco state. It is epiphytic in shaded forest above 700 m altitude. The inflorescence is highly-branched which resembles *A. patentissima*, but the fertile portion of the inflorescence and branches are shorter. It belongs to the *Aechmea lingulata* complex (Siqueira-Filho & Leme 2006) with *A. froesii*, *A. maranguapensis* and *A. patentissima*.

25. ***Aechmea serragrandensis*** Leme & J.A.Siqueira, Fragm. Mata Atlântica do Nordeste. 241. 2006.

(Figure 5f).

Selected specimens: ALAGOAS: Ibateguara, Engenho Coimbra, 02.VI.2005, *J.A. Siqueira-Filho et al. 1500* (UFP-holotype); Maceió, Serra da Saudinha, 1.IV.2005, *A. Costa 169* (MAC); Porto Calvo, Propriedade Eixo, 30.VIII.1969, *D. Andrade-Lima 69-5589* (IPA).

Endemic to the state of Alagoas and with a very restricted distribution, where it grows as an epiphyte in shaded areas in the lowland Atlantic Forest. It is very distinctive due to its ovoid or ellipsoid inflorescence with yellow and entire floral bracts. The plants support a big rosette and massive inflorescences. Despite the poor morphological knowledge of *A. conifera* (Sousa 2004), Leme & Siqueira-Filho (2006) described *A. serragrandensis* by comparing it to *A. conifera*. The authors cited *A. Lima 69-5589* as a paratype, which was used by Sousa (2004) to recognize *A. conifera* in the state of Alagoas. Thereby, we excluded recognition of the species *A. conifera* from the study area.

26. ***Aechmea tomentosa*** Mez, Monogr. Phan. 9: 229. 1896. (Figure 5g).

Selected specimens: ALAGOAS: Porto Calvo, Eng. Oriente, 14.VIII.1960, *D. Andrade-Lima 60-3512* (IPA); Flexeiras, Serra das Águas Belas, 02.XI.2002, *W.W. Thomas et al. 13187* (CEPEC, NY); PERNAMBUCO: Ipojuca, Oiteiro de Nossa Senhora do Ó, 01.VI.2013, *J.R. Maciel et al. 1744* (UFP); Sirinhaém, Engenho do Anjo, 15.XII.2004, *J.A. Siqueira-Filho et al. 1445* (UFP).

Endemic to the northeastern São Francisco River area. It occurs as a terrestrial plant in sandy soil of the lowland Atlantic Forest along the coast of the states of Alagoas and Pernambuco. It grows in shaded areas and is seldom found in open habitats. It has small floral bracts and sessile flowers. It is distinguished by being the only species in the area with cinereous inflorescences, entire and red peduncle bracts and primary bracts and sepals with a 0.5-0.8 mm long spine. Sousa & Wanderley (2000) and Leme & Siqueira-Filho (2006) used the peduncle and flower indument, primary bract shape, branch arrangement and flower length to distinguish this taxon from *A. costantinii* (=*A. stelligera*) and *A. werdermanii*.

27. *Aechmea werdermannii* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 12: 529. 1935. (Figure 5h).

Selected specimens: ALAGOAS: Maceió, s.l., II.2004, *E. Leme 4984* (HB); PARAÍBA: São João do Tigre, Quati, 24.V.2006, *R.A. Pontes 355* (JPB); PERNAMBUCO: Floresta, Reserva Biológica de Serra Negra, 27.I.2006, *J.A. Siqueira-Filho 1550* (UFP).

Endemic to the northeastern São Francisco River area. Epiphytic in montane and submontane Atlantic Forest from Paraiba, Pernambuco and Alagoas. It grows in shaded places. The species is morphologically similar to *A. leptantha* and *A. eurycorymbus* but differs by its habit (epiphytic) with longer leaves (70-110 cm) and red inflorescences. Although it was not included by Read & Luther (1991) under the *Gravisia* complex, Leme & Siqueira-Filho (2006) suggested its relationship.

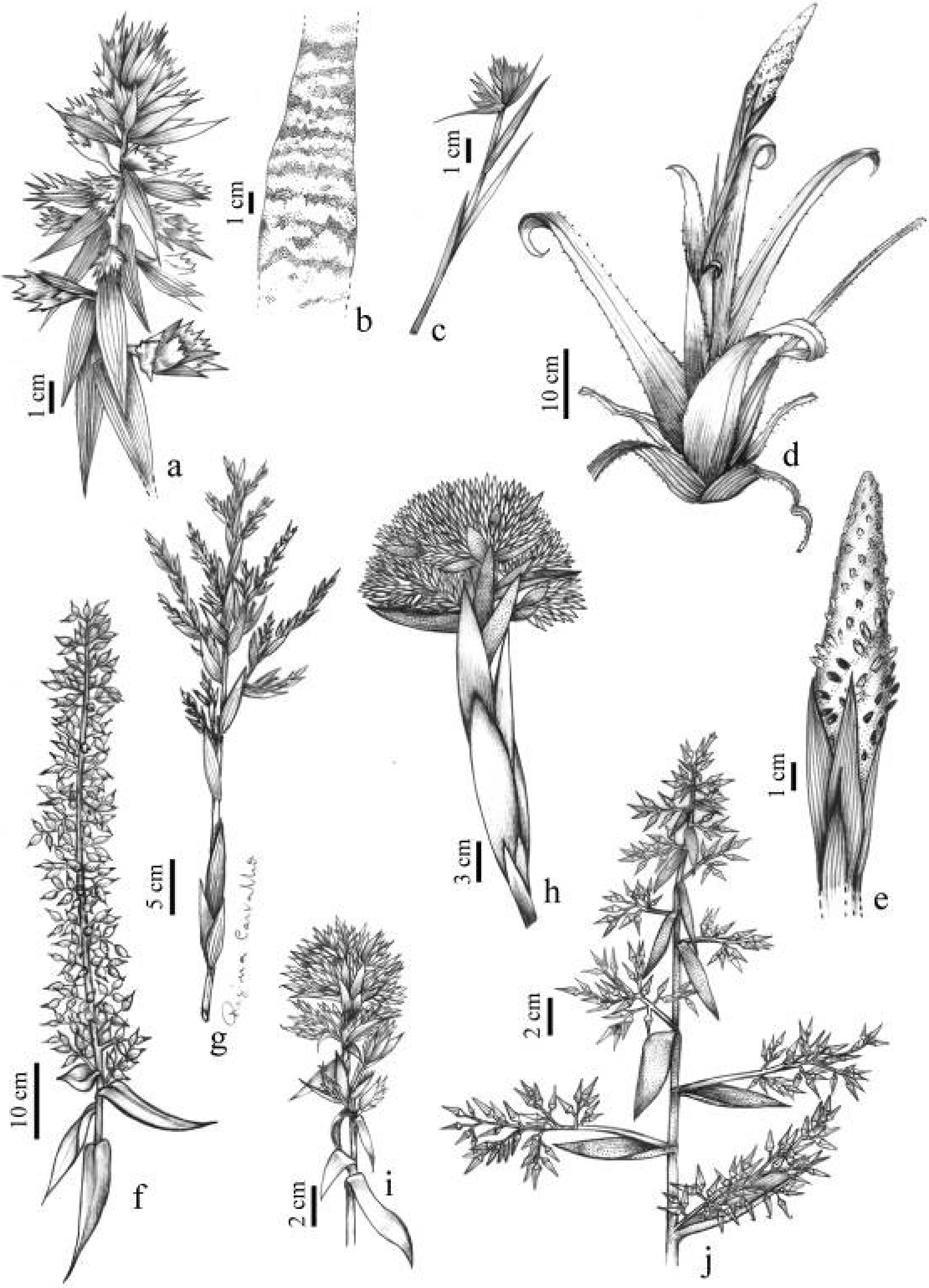

Figure 5.1. Species of the *Aechmea*. a. *A. aquilega* – fertile part of inflorescence. b-c. *A. atrovittata* – b. leaf blade – c. inflorescence. d-e. *A. bromeliifolia* var. *bromeliifolia* – d. fertile part of inflorescence – e. habit. f. *A. castelnavii* – fertile part of inflorescence. g. *A. catendensis* – inflorescence. h. *A. cephaloides* – inflorescence. i. *A. chrysocoma* – fertile part of inflorescence. j. *A. costantinii* – portion of inflorescence.

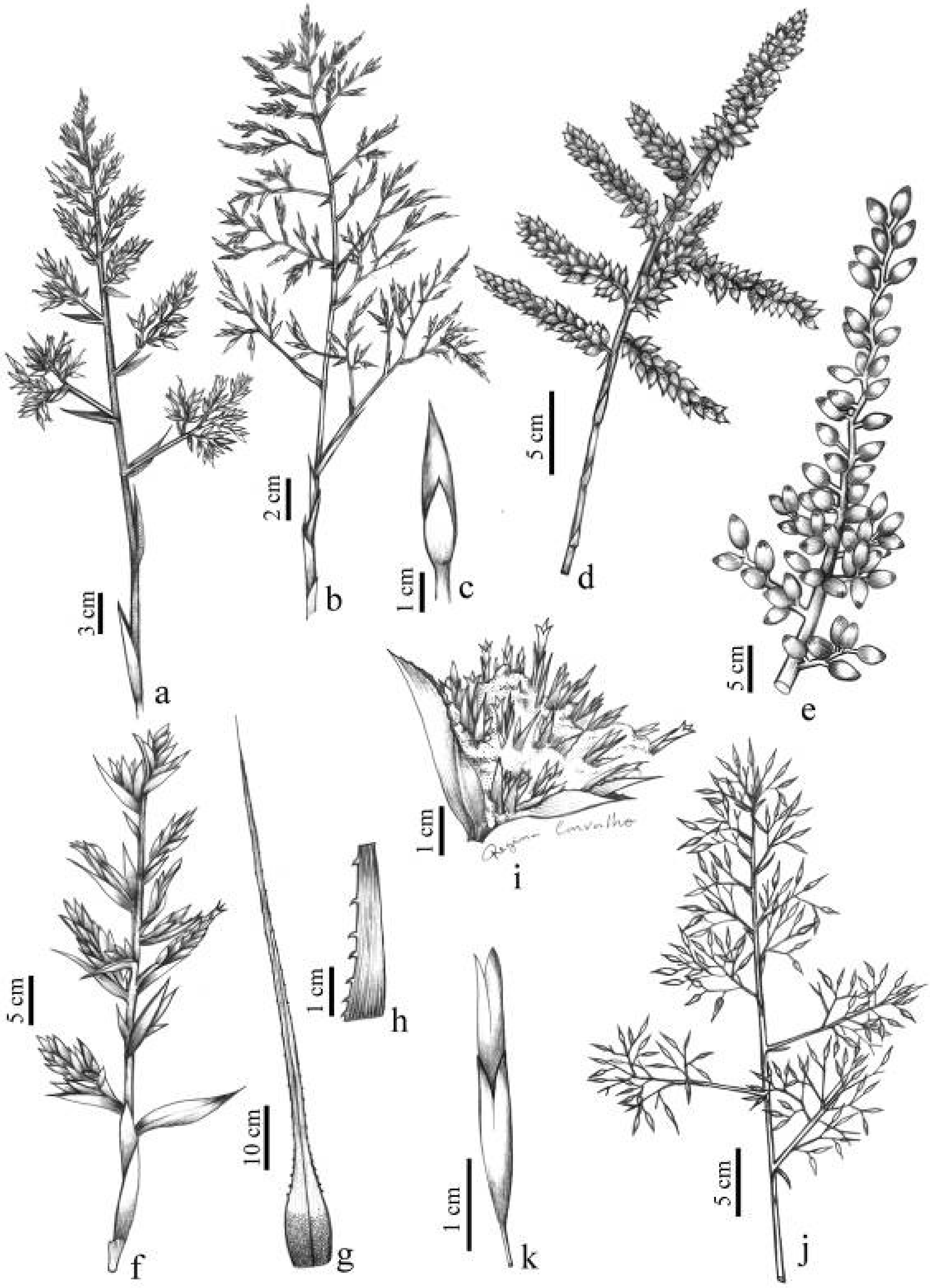

Figure 5.2. Species of the *Aechmea*. a. *A. emmerichiae* – inflorescence. b-c. *A. eurycorymbus* – b. inflorescence – c. floral bract view. d. *A. froesii* – inflorescence. e. *A. fulgens* – fertile part of inflorescence. f. *A. guainumbiorum* – inflorescence. g-h. *A. gustavoi* – g. leave – h. leaf margin detail. i. *A. lactifera* – i. fascicle of the infloresence. j-k. *A. leptantha* – j. fertile part of inflorescence – k. flower.

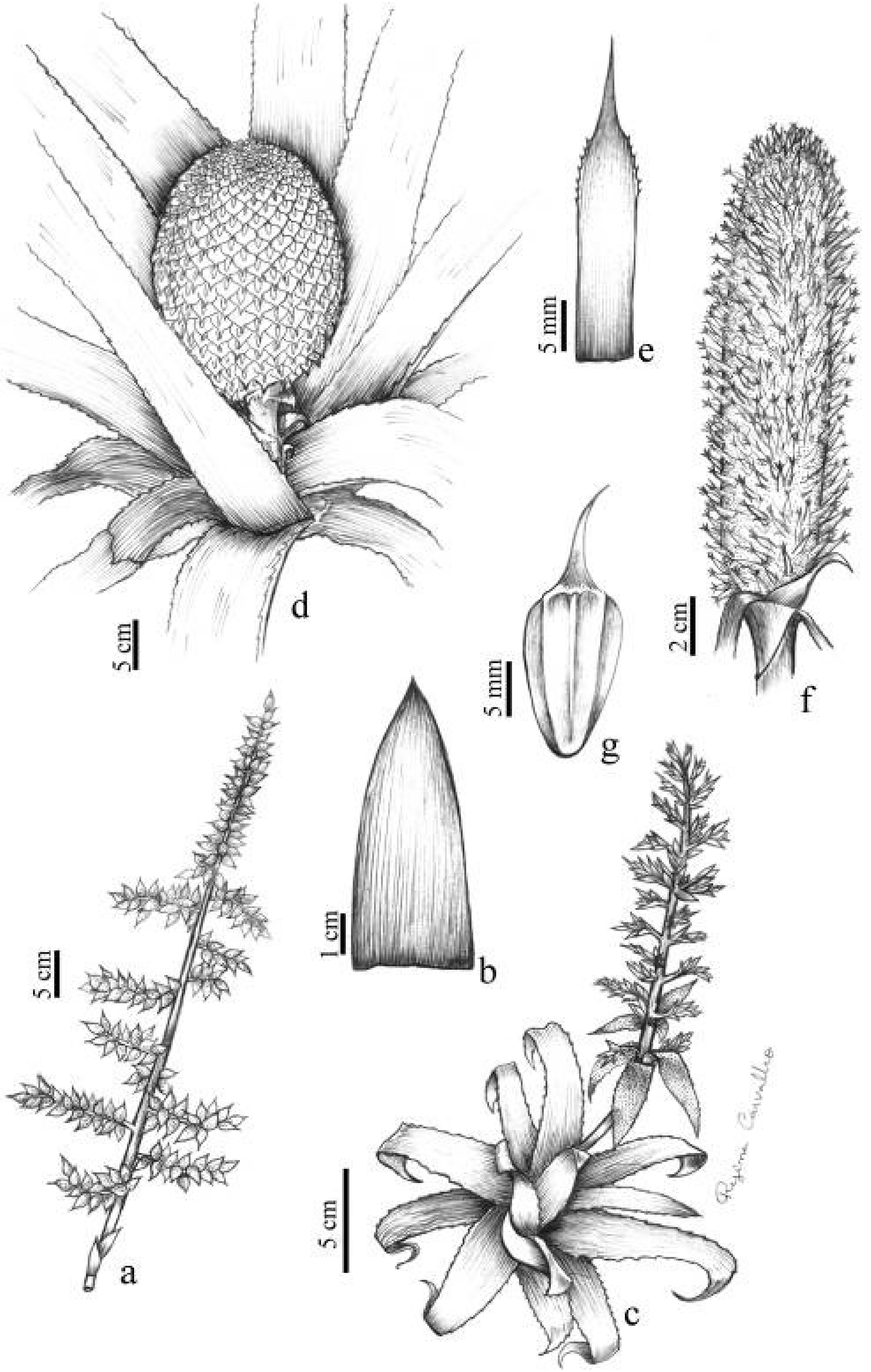

Figure 5.3. Species of the *Aechmea*. a. *A. maranguapensis* – inflorescence. b. *A. marginalis* – part of the leaf blade. c. *A. mertensii* – habit. d-e. *A. multiflora* – d. habit – e. floral bract. f-g. *A. muricata* – f. fertile part of inflorescence – g. floral bract.

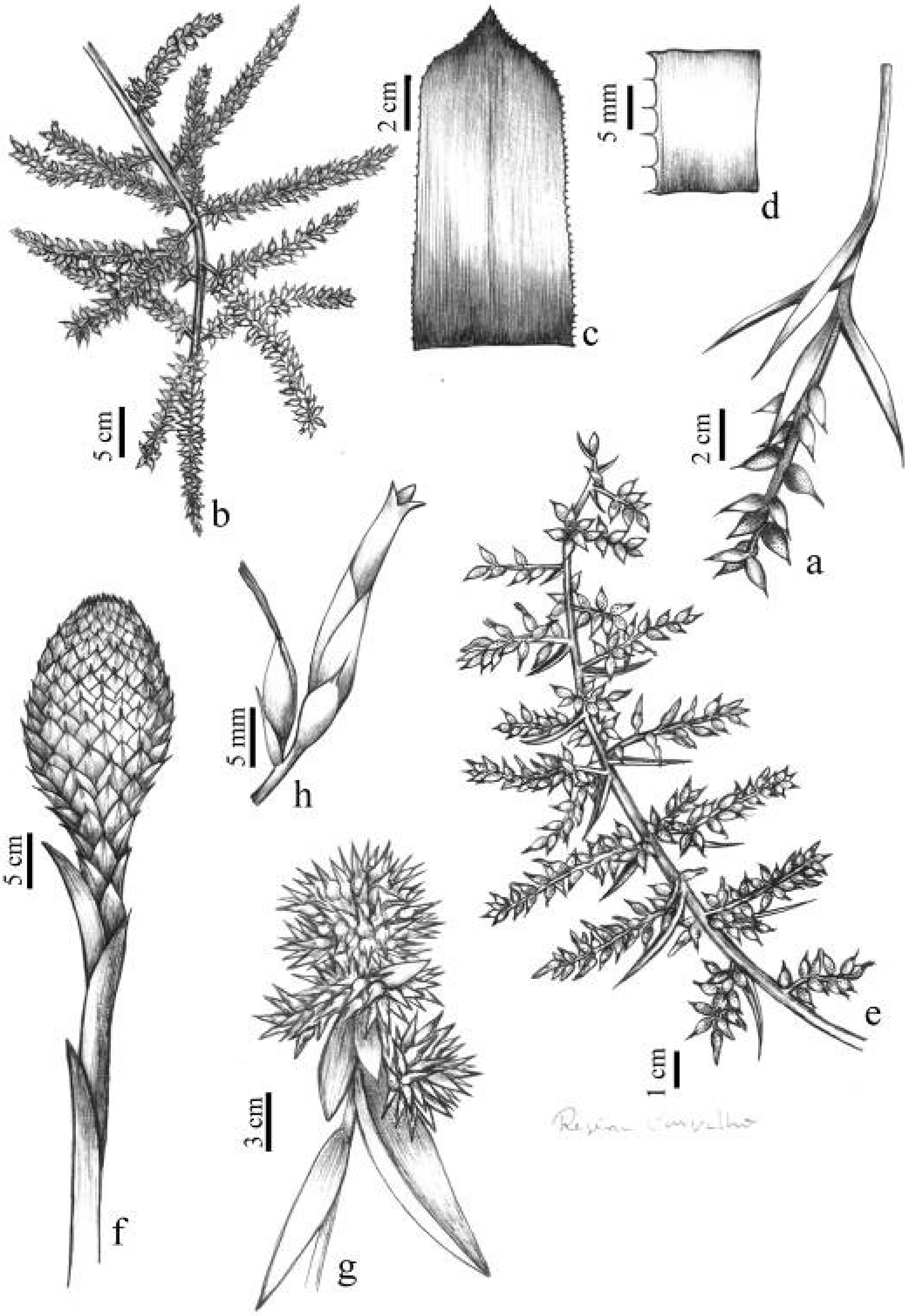

Figure 5.4. Species of the *Aechmea*. a. *A. nudicaulis* var. *nordestina* – inflorescence. b-d. *A. patentissima* – inflorescence – c. portion of leaf blade – d. margin detail. e. *A. pernambucentris* – f. *A. serragrandensis* – inflorescence. g. *A. tomentosa* – fertile part of inflorescence. h. *A. werdermanii* – flower.

List of examined material

Albuquerque, N. 205(19), 499(19); **Amorim, B.** 819(16), 1122(19); **Andrade-Lima, D. & Black, G.** EAC-1536(17); **Andrade-Lima, D.** 13(26), 38(26), 54-1895(16), 55-2135(21), 57-2738(12), 57-2764(23), 57-2767(19), 57-2769(23), 58-3267(3), 59-3388(26), 59-3395(23), 60-3512(26), 61-3980(16), 63-4177(23), 63-4186(19), 63-4197(21), 65-4318(21), 66-4444(4), 67-4977(12), 69-5541(12), 69-5589(25), 70-5875(3), 72-8224(1), 72-8273(23), 79-8772(20), 80-8813(20); **Baracho, G. & Siqueira-Filho, J.** 590/579(1); **Baracho, G.** 476(12), 517(12), 527(8), 584(23), 588(26), 687(23), 730(23), 738(21), 761(24), 836(8), 837(23); **Barbosa, M.** 2478(26); **Barbosa, V.** 182(16); **Barreto, R.** 82-64(16); **Barros, C. *et al.*** 106(1); **Barros, R. *et al.*** HST-7820(12); **Bayma, I. & Barros, C.** 192(7); **Bayma, I.** 522(1); **Benko-Iseppon, A. *et al.*** 1698(16), 1699(16), 1700(16); **Bogner, J.** 1195(3); **Brasil, R.** 230(23); **Brito, Z.** 18(8); **Cano, O.** 46a(16); **Carvalho, A.** 7078(12), 7130(11), 7131(26), 7131(8), 730(23); **Castro, A.** 2(3), 1981(4); **Cervi, A.** 7416(10); **César, E.** 88(23), 89(23), 124(19), 168(23); **Costa, A.** 8(16), 169(25); **Costa, I.** 117(3), 347(3), EAC-32341(3); **Costa-e-Silva, M.** 2853(16); **Drouet, F.** 2616(4); **Ducke, A.** IAN-2051(1), IAN-115984(1); **Esteves, G. & Lyra-Lemos, R.** 1795(23), 2168(21); **Esteves, G. & Staviski, M.** 1715(1); **Esteves, G.** 2101(19); **Fagundes, J.** 82(16); **Falcão, A.** 868(26); **Félix, L.** 1785(12), 3065(19), 3923(19), 5540(8), 5549(23), 6155(3), 6371(8), 7005(19), EAC-19048(3), EAN-15661(23), HST-17314(12), JPB-15658(19); **Félix, L. *et al.*** 7167(26), HST-7785(10); **Fernandes, A.** EAC-1835(3), EAC-1836(1), EAC-4145(3), EAC-11681(27); **Ferreira, E.** 254(3), 328(3); **Ferreira, P.** 45-68(19); **Fevereiro, V.** 134(8); Fontana, A. 6553(27), 6991(27); **Fortunato, M.** 59(17), 61(17); **Foster, M.** 2406(23), 2408(10); **Freire, J.** 17(23); **Gadelha-Neto, P.** 815(23), 2999(23), RB-418532(12); **García-González, J.** 1224(19); **Girao-e-Silva, W.** EAC-27199(3); **Gomes, L.** 209(19); **Gomes, V. & Xavier, A.** 2109(3); **Gomes, V. *et al.*** 353(1), 712(3); **Guedes, F.** 108(16); **Guedes, M.** ALCB-92995(23); **Krapovickas, A.** 38033(16); **Leite, M.** 236(16), 791(21); **Leme, E. & Siqueira-Filho, J.** 6507(7), 6509(23), 6771(23); **Leme, E.** 3914(17), 5086(20); **Leme, E. *et al.*** 6618(19); **Lima, D.** EAC-49556(4); **Lima, J.** 2141(3); **Lima, R.** 1722(8); **Lima, V.** 96(27), 828(8); **Lima-Verde, L.** 155(17), 1766(3), 1794(3), 3401(4), EAC-15693(3), EAC-21247(3); **Lima-Verde, L. *et al.*** 3444(3); **Lopes, A.** UFP-22481(26), UFP-22482(21), UFP-21755(12); **Luceno, M.** UFP-11463(15); **Luetzelburg, P.** 26461(3), s.n. (Smith & Downs 1979)(3); **Lyra-Lemos, R. & Staviski, M.** 404(19); **Lyra-Lemos, R.** 2736(19), 4629(19), 5300(26), 5979(19), 6316(12), 8026(19), 9107(5); M.Agra, M. 260(19), 4286(7), 4516(7); **Maciel, J. *et al.*** 1708(3), 1709(1), 1727(17),1728(17), 1734(1), 1743(19), 1744(26), 1745(21), 1867(19), 1909(12), 1912(23), 1913(15), 1914(5), 1925(16), 1926(8), 1929(14); **Maciel, J. & Capistrano, T.** 1770(1), 1775(1); **Mariz, G.** 493(23); **Martinelli, G.** 15043(27), 15055(3), 15071(17), 15084(23), 15087(8), 15088(16), 15104(26), 15107(8), 15108(12), 15111(12), 15123(26), 15126(12), 15129(26), 15131(26), 15331(12), 15333(16); **Martinelli, G. *et al.*** 15338(11); **Matias, L.** EAC-27661(17); **Medeiros, J. & Frassy, A.** s.n.(18); **Mee, M.** US-2580028(1), US-2580048(10); **Meiado, M.** 370(16); **Melo, A.** 110(19), 239(19); **Mendonça, E. *et al.*** 46(6); **Menescal, R.** CEPEC-127566(15); **Miranda, C.** 3505(23); **Monteiro, F.** 8(17), 15(17); **Montenegro, P.** 42(19); **Moraes, J.** 862(8), 1239(21), EAN-68(8), EAN-1192(23), EAN-1236(12), EAN-1477(22); **Nojosa, D.** EAC-26148(3); **Nunes, E.** UFP-18569(26); **Oliveira, C.** 265(16); **Oliveira, J.** 03(19),14(26); **Oliveira, M. & Grillo, A.** 1096(5),1246(19); **Oliveira, M.** 898(19), 1238(11), 1240(12), 1246(19), 780(16); **Oliveira, R.** EAC-27280(17); **Oliveira. O.** 1467(23); **Pereira, E.** 868(26); **Pereira, M.** 114(16); **Pereira, R. *et al.*** 766(1); **Pereira, R.** IPA-53614(16); **Pessoa, M.** 98(8); **Pickel, B.** 1281(12), 2233(1), 2298(12), 2488(23), 2992(16), 2995(19), 3059(26), 3457(19), 3536(16), 3657(23); **Pontes, R. & Lima, N.**

131(7); **Pontes, R.** 51(23),84(8), 85(8), 97(23), 98(23), 107(8), 108(8), 110(8), 113(8), 121(23), 132(23), 142(9), 144(9), 145(9), 148(9), 150(9), 156(16), 157(16), 159(16), 162(16), 164(22), 165(22), 166(22), 167(22), 194(9), 195(9), 196(9), 197(9), 198(9), 207(16), 208(16), 210(16), 218(19), 219(19), 220(19), 223(23), 234(10), 244(12), 246(12), 247(12), 249(12), 254(22), 318(8), 327(3), 328(8), 329(8), 332(12), 339(10), 345(10), 346(16), 355(27), 404(8), 415(10), 415(10), 430(27), 470(16), 558(23), 559(19), 577(27), 605(23); **Pontual, I.** 233(26); **Pontual, I.** 66-262(23); PPD 223(23); **Queiroz, E.** 2584(19),2600(7); **Rocha, F.** 156(23); **Rocha, R. *et al.*** 1602(23); **Sacramento, A.** 50(21),454(19); **Segadas-Vianna, F.** rest I-279(23); **Sevilha, A.** 2542(23); **Silva, D.** 24(27); **Silva, J.** 388(5); **Silva, V.** UFP-39360(1); **Siqueira-Filho, J. & Frassy, A.** 8(2); **Siqueira-Filho, J. & Leme, E.** 1218(1); **Siqueira-Filho, J.** 478(26), 483(26), 562(12), 592(16), 595(23), 599(16), 600(12), 608(26), 609(21), 696(3), 724(23), 736(24), 742(8), 773(22), 786(16), 796(15), 804(21), 938(5), 942(8), 943(23), 999(19), 1007(26), 1043(8), 1090(5), 1091(14), 1147(21), 1167(5), 1184(13), 1187(15), 1216(21), 1247(26), 1250(8), 1260(27), 1277(27), 1286(12), 1290(23), 1294(8), 1296(21), 1297(8), 1302(8), 1314(11), 1331(8), 1380(8), 1389(16), 1390(8), 1393(12), 1436(20), 1443(21), 1444(11), 1445(26), 1454(22), 1459(24), 1470(22), 1472(12), 1474(11), 1500(25), 1550(27), 1628(7), 1859(17), 2383(2), 2385(26), 2391(11), 2402(3), 2456(13), 2508(12), 2511(19), 2715(16), 2735(13), 2741(19), 2744(5), 2745(15), 2746(2), 2747(8), 2780(16), 2781(12); **Siqueira-Filho, J. *et al.*** 497(19),939(6), 1013(6), 1426(6), 1446(19), 1458(6), 1479(19), 1501(19), 1512(1); **Sobral-Leite, M.** 235(13), 609(5), 1016(16); **Sousa, G. & Wanderley, M.** 26(19); **Sousa, G.** 60(27), 86(12), 97(12), 126(19), 127(12), 148(24), 149(26), 159(8), 160(8), 164(26), 165(23), 166(23), 168(23), 169(21), 170(8), 171(8), 172(24), 176(7), 177(7), 178(7), 181(8), 182(23); **Staviski, M.** 1601(23); **Staviski, M. *et al.*** 973(19), 1019(23); **Tavares, S.** 60(11), 873(1), 1044(23); **Thomas, W.** 11693(3), 12458(12), 13187(26); **Tomaz, E.** 1(23), 2(23); **Vasconcellos, J.** 207(16), US-2059452(8); **Viana, A.** 255(11), 264(8), 268(16); **Viana, J.** 124(26); **Wedermann, E.** 2931(10); **Xavier, L.** JPB-1(23), JPB-2(16), JPB-5(23), JPB-7(8), JPB-8(16), JPB-9(8), JPB-781(8).

6 Habitat loss affects Wallacean shortfall and potential distribution evaluation

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Abstract

The ecological niche modelling has three basics assumptions: environmental equilibrium, niche conservatism and sampling sufficiency. According sampling sufficiency, the environmental spaces of organisms are always satisfactorily caught by distributional data. However, database and scientific collections have limitation to represent species geographical distribution accurately, which is called Wallacean shortfall. Wallacean shortfall has intuitive effects on ecological niche modelling assumptions, especially the sampling sufficiency. For testing if this assumption is affected by Wallacean shortfall, we made a comparison among environmental spaces of realized and potential distribution from Bioclim and Maxent algorithms for *Aechmea* species from Atlantic Forest. The results suggest that analysis can be incorporated in an evaluation framework by combining available techniques. In this way, the analysis developed here could improve and give more support for decision about models quality. Moreover, we were able to show that population vanishing by deforestation is affecting the knowledge about species environmental spaces in Atlantic Forest. It indicates a new source to Wallacean shortfall never described before.

Keywords

Bromeliaceae, Bromelioideae, *Aechmea*, biogeography, environmental space

Introduction

The ecological niche modelling has three basics assumptions: environmental equilibrium, niche conservatism and sampling sufficiency. As work assumptions, they are not factual, but theoretically conditions expected for all species choosen to model it fundamental niche (Araújo & Peterson 2012). Nevertheless, several studies had been tested the environmental equilibrium and niche conservatism of species and they reveal that many species do not suit these assumption (Araújo *et al.* 2005, Broennimann *et al.* 2007, Gallagher *et al.* 2010, Mandle *et al.* 2009, Munguía *et al.* 2012, Pearman *et al.* 2008, Peterson 2011, Petitpierre *et al.* 2012, Rödder & Lötters 2009, Sánchez-Fernandez *et al.* 2012, Webber *et al.* 2012). However, there is no experimental study testing how sampling insufficiency can affect ecological niche modelling.

More than theoretical, sampling sufficiency seems to be a real problem mainly in regions with high diversity and incipient collection effort, such as Neotropics. Sampling sufficiency does not represent an ideal number of points necessary to run an algorithm, but the quantity and quality of occurrence points necessary to catch an environmental space of species (Pearson *et al.* 2007, Soberón & Nakamura 2009). Sampling sufficiency is related to one of barriers in geographical distribution studies: the Wallacean shortfall. The Wallacean shorfall is the incomplete knowledge about species distribution available in databases and scientific collections (Richardson & Whittaker 2010, Rocchini *et al.* 2011, Whittaker *et al.* 2005). This limitation about geographical distribution of species causes problems in biogeographic studies, which might be supported on inconsistent information. Wallacean shortfall might also affect ecological niche modelling studies, although is unknown how evaluate if a species has or not sampling sufficiency.

According Rocchini *et al.* (2011), there are at least three technical sources to Wallacean shortfall. The first one is the natural complexity of species distribution that sometimes occurs in inaccessible places to men; the second source is the quality of data available in collections and database, which many times are inaccurate about the precise geographical location; and finally, the third one regards to technological limitations to collect distributional data. All these limitations are regarding to difficulties in data collect and storage, but none of them takes into account anthropic impacts which could leave to vanishing of populations and thus species niche information (Rocchini *et al.* 2011).

To test species sampling sufficiency, we created a statistical framework based on comparison between realized and potential environmental spaces. This analysis pursuit evaluates the level of equivalency between environmental spaces. In addition to check the sampling sufficiency, the analyses also verify the functioning of a model by comparison between the environmental spaces from distributional data and model results.

Material and Methods

Biological model and study area

To this study, we selected the genus *Aechmea* Ruiz & Pavon (Bromeliaceae) as biological model. We restricted our sampling to species from Atlantic Forest at North of São Francisco River or Pernambuco Center of Endemism. In this area, *Aechmea*i s represented by 27 species which are widely distributed in Neotropics, distributed along Atlantic Coast, and also restricted to Pernambuco Center of Endemism (Maciel *et al.* 2015, Fig. 1, Table 1). Plants of *Aechmea* are independent from the substrate and without specificity of phorophyte (Benzing 2000). Thus, its patterns of geographical distribution are almost completely limited by abiotic factors. *Aechmea* species are a good model to use bioclimatic variables dueits geographical patterns of distribution and substrate independency.

The region selected is known as a center of endemism and richness of Bromeliaceae species (Martinelli *et al.* 2008). Moreover, recently the area had an extra effort orientated to collection of Bromeliaceae, including several new species described and increased of information about endemic and endangered taxa (Leme & Scharf 2011, Leme & Siqueira-Filho 2001, 2006, Maciel *et al.* 2015, Siqueira-Filho & Leme 2006, Sousa & Wanderley 2000). It reduces the effect of collection effort lack over our analysis.

Occurrence data and variable selection

The information for the database used in this study was gathered from the herbaria ALCB, ASE, CEPEC, EAC, HRB, HUEFS, IAN, INPA, IPA, JPB, MAC, MBML, MIRR, MPEG, NY, PEUFR, RB, UFP, UFRN, UFRR, US and VIES. The taxonomical validation of each sample was based on morphological studies of the *typus* and literature (Leme & Siqueira-Filho 2006, Maciel *et al.* 2015, Smith & Downs 1979). In addition to that, we conducted a field survey between 2010 and 2014 in the Atlantic and Amazon Forests. The collection aimed to confirm the presence of species and increase records in a database of local place names.

For samples with no geo-referenced data, a coordinate was assigned based on a comparison of the descriptions of localities found on the labels of samples and gazetteer databases available on the Internet (http://earth-info.nga.mil/gns/html/, http://www.geonames.org/). Georeferencing tools such as Google Earth were used. Samples without the location indication accurate were discarded.

For this study, we used the bioclimatic and elevation variables of the Worldclim database (Hijmans *et al.* 2005, available at http://worldclim.org). The environmental data for points of species occurrence were sampled and submitted to a correlation analysis. We calculated the Pearson correlation coefficient between the climatic variables and ones with high level of correlation (R^2>0.7) were eliminated. Seven variables were selected: mean annual temperature, temperature seasonality, annual variation in temperature, mean temperature of the hottest quarter, precipitation seasonality, precipitation of the hottest quarter, and precipitation of the coldest quarter.

The study area for the preparation of models and their projection onto distinct AOGCMs of the Mid-Holocene and Last Interglacial was defined by the geographical extension of 95.75ºW, 29.42ºW, 37.42ºS and 16.5ºN. This extension corresponds to the northern and southern limits of distribution of the species selected for the study and covers, in addition to the Atlantic and Amazon Forests, other South American ecosystems.

Modelling

To perform the models, we used Bioclim and Maxent algorithms. These two algorithms represent extremes in complexity. Bioclim produces a bioclimatic envelope that identifies in environmental space the maximum and minimum limits regarding to environmental characteristics recorded to occurrence data. Maxent seeks for regions with high probability of concordance with all data known by avoid restrictions that do not reflect the environmental characteristic of occurrence datain environmental space. Thus, Maxent applies a maximum entropy principle to find a potential distribution of a species.By comparison, Maxent is a more complex algorithm than Bioclim. A recent revision about functioning of both can be found in Hijmans & Elith (2014).

The quality of the models was evaluated by a 3-fold partition, where 66% of the data was used for training and 33% for testing. Therefore, for each species data set there were three partitions and for each partition a model. A total of 500 points were randomly collected in the study area as background data. The same logic of partition into training and testing data was used. We defined the background area based on the distribution limits of species. We are aware that the size of background area has effects on AUC and TSS results (Allouche *et al.* 2006, Giovanelli *et al.* 2010), however the large space delimited is associated to the distribution of species and our intent is project a model in an area comprising the Atlantic and Amazon Forests. Then, we applied a threshold based on TSS values and models with best results selected and converted to binary maps of presence and absence.

Environmental space analysis

The environmental values used in the analysis of environmental spaces were extracted in four different ways to each species: 1) binary maps of Bioclim models; 2) binary mapsof Maxent models; 3) minimum convex polygon based on occurrence points; 4) occurrence data.Each dataset was submitted to an analysis of principal components (PCA) and the two axis of each PCA was used to a kernel analysis. The kernel results of species were used to compare the environmental spaces of among datasets.

To estimate the level of sampling sufficiency we developed the follow relation, where PC is the principal component and K is kernel analysis:

$$S = \frac{pPC_{Li} \cdot pK_{Li}}{rPC_{Li} \cdot rK_{Li}} .$$

Results of this relation were taken to make a correlation analysis between number of points used to models and sampling sufficiency. We realized that species showing graphical equivalency among observed and potential environmental spaces had S-values between 0.8 and 1 (Tab. 1). Thus, we adopted that species with S-values below 0.8 and over 1.1 had sampling insufficiency.

All analysis of this study were performed on statistical environment R (R Core Team 2014). The preparation of layers was performed using the raster package (Hijmans 2005), and the distribution models were calibrated, evaluated and projected on geographical space using function of dismo package (Hijmans & Elith 2014).

Resultados

Datasets of potential and realized distributions were performed to 18 of 27 species of *Aechmea*. Bioclim models often showed lower TSS values (TSS=0.248-1) than Maxent (TSS=0.589-1). A similar pattern was found to AUC (BioclimAUC=0.624-1; MaxentAUC=0.822-1). However, 14 Bioclim partitions showed AUC values below threshold of 0.5, while 23 Maxent partitions had the same tendency.

Ten species show sampling sufficiency in the analysis (Tab. 1). However, among them, five have sufficiency only to Maxent distributions. Sampling sufficiency was found more often in species widely distributed than in endemic species (Fig. 3-4). Additionally, endemic species such *A. catendensis*, *A. chrysocoma*, *A. eurycorymbus*, *A. gustavoi*, *A. nudicaulis* and*A. werdermanii*had its potential occurrence projected to huge extensions in calibration area. This behavior was verified to Maxent models and indicates insufficiency sampling mainly to Maxent environmental spaces.

Sampling sufficiency is not correlated with number of occurrence points used to modelling (Fig. 2). Species with high number of occurrence points, such *A. bromeliifolia* (n=316) and *A. mertensii* (n=346), showed same level of sampling sufficiency than species with less points (Tab. 1). Even though, no species with less than thirty occurrence points shows sampling sufficiency, except for *Aechmea catendensis* (n=8). This species shows equivalency among realized and Bioclim environmental spaces (Tab. 1).

Some endemic species showed huge projections of their potential distribution on Bioclim and Maxent models, however these potential distributions were restricted to its known occurrence area in Atlantic Forest at North of São Francisco River. In these cases, algorithms projected a distribution where nowadays is urban places, where no more native forest remnant exists to host the species. Some of them have sampling sufficiency (eg. *A. fulgens*, Fig. 5) while others not (eg. *A. leptantha*, Fig. 5).

Discussion

A new source to Wallacean shortfall

Our results show that majority of species widely distributed have realized and potential environmental spaces equivalents, which means sampling sufficiency. On another hand, restricted distributed species usually show sampling insufficiency. These results suggest ecological niches were partially surveyed to endemic species in distributional data available in collections and databases.

The debate about difficulties in studies of species geographical distribution has focused on human limitations to collect data. Therefore, all three main causes of Wallacean shortfall are associated to technical limitations, accessibility to the areas and scientific interest to perform collections (Bini *et al.* 2006, Guisan & Thuiller 2005, Kamino *et al.* 2012, Jimenez-Valverde *et al.* 2008, Sóberon & Nakamura 2009, Rocchini *et al.* 2011). These authors had never taken into account any influence of habitat reduction or population extinction over knowledge of species distribution. The way how populations and habitat vanishing might help to create a fragmentary representation of species niche and distribution in occurrence information from scientific collections seems obvious.

Results obtained show clearly how habitats of some species are not completely captured by samples used to modelling distributions. Technical limitations and sampling bias are not the reasons to these results. The selected biological group studied had an intense collect effort in the last decades on region (Siqueira-Filho & Leme 2006, Sousa & Wanderley 2000) which was recently improved too (Maciel *et al.* 2015). New population discovered and descriptions of 15 new species in the region are good evidences of high collection effort in Bromeliaceae (Leme & Scharf 2011, Leme & Siqueira-Filho 2001, 2006, Maciel *et al.* 2015, Magalhães *et al.* 2014). In addition, the Atlantic Forest at North of São Francisco River has an intense collection effort already reported (Sousa-Baena *et al.* (2014). These data is available online in open and free access database of Brazilian scientific collections (Sousa-Baena *et al.* 2014). It reflects recent regional efforts in inventories of all plants living forms, including bromeliads (Barbosa *et al.* 2011, Gomes & Alves 2009, 2010, Melo *et al.* 2011, 2015).

There is no direct relation between the number of points used in models and the sampling sufficiency. Nevertheless, most of species with sampling sufficiency has thirty or more occurrence records on our dataset. Thirty points has been considered a minimum number to good functioning of algorithms such Bioclim and Maxent (Elith *et al.* 2006, Pearson *et al.* 2007, Wisz *et al.* 2008). The lack of correlation between number of points and sampling sufficiency points out that quantity of samples has small influence on the completeness of environmental space representation. Quality and precision of collected point are real agents of improvement in niche species information. Accordingly, Pearson *et al.* (2007), in many cases a low number of occurrence records can be enough to characterize the environmental space occupied by a species. Proosdij *et al.* (2015) suggest that good models can be generated with 3 and 13 occurrence points to simulated environments, while for real data of endemic species an ideal number ranges from 14 to 25 points. A similar pattern was found to restricted distributed species of *Aechmea* in our study. This also explains the lack of correlation between the occurrence number points and sampling sufficiency that was found here.

Endemic species from Atlantic Forest at North of São Francisco River show potential distributions in urban areas with no forest remnants. In addition, the region is recognized by deep fragmentation and reduction of native forest cover with forest remnants often smaller than 200 hectares (Ribeiro *et al.* 2009). Habitat and population vanishing are affecting the quality of information about niche of *Aechmea* species causing sampling insufficiency. Thus, here we propose a new source of Wallacean shortfall to join three others before described (Rocchini *et al.* 2011). This new one is the population vanishing caused by native forest cover reduction of some region. This event hampers the full representation of species distribution rendering impossible catch rightly its environmental space.

One more evaluation tool of ENMs

Our results clearly show a potential tool for evaluate and validate ecological niche models. Verify internally whether models are able to capture originals environmental spaces is an alternative way to evaluate reliability of distributional data used on analysis. This information could support decisions about models choice or species selection.

Improving evaluation process is one of the main targets in ecological niche modelling studies (Araújo & Guisan 2006). The challenge implies in adjusting evaluation and validation tools concerning the specific goals of each study and applies new procedures. According to

Araújo & Guisan (2006), there are examples that a simple verification (ability of models to adjust to training data) can be applied. The sampling sufficiency analysis developed here could be taken as a complementary verification process to other analysis already available. It could help solve problems identified in some procedures.

As an example, the largely used Area Under Curve (AUC) underwent several critiques concerning of its real application in selecting models or thresholds to binary data transformation (Hijmans 2012, Jiménez-Valverde 2012, 2008, Lobo *et al.* 2008, Manel *et al.* 2001, Peterson *et al.* 2007, 2008). The AUC should not take as validation tool if a statistical bias correction in original dataset is not applied, according Hijmans (2012). Jiménez-Valverde (2012) is more emphatic affirming that AUC should not be the only parameter to model verification. Although, AUC is still used in ecological niche modelling studies to verify models effectiveness (Hijmans 2012, Jiménez-Valverde 2012, 2008, Lobo *et al.* 2008). Lobo *et al.* (2008) describe data restriction use in increased resolution of calibrate area as one of the limitation in AUC using to validation and evaluation tool. Giovanelli *et al.* (2010) used this property as explanation of area calibration effects over Bioclim and Maxent algorithms behaviors in restricted distributed species models. Thus, graphics of sampling sufficiency can be combined with AUC to evaluate confidence levels of transferability in studies with huge calibration areas in relation to already known species distribution.

As consequence of AUC limitations, the TSS use (True Skill Statistic) has become much more popular in the last years as a tool to verify models quality. The TSS was suggested by Allouche *et al.* (2006) as more efficient than AUC. Besides TSS, other tools such Kappa and Jacknif based analysis have been proposed as alternative to AUC and to deal with limited data available too (Allouche *et al.* 2006, Pearson *et al.* 2007). Nevertheless, some of these tools are hardly criticized about their usefulness (Allouche *et al.* 2006, Jiménez-Valverde 2012, Lobo *et al.* 2008).

However, all these analyses are based on confusion matrix to ascertain models efficacy, using prediction and commission errors as quality parameters (Fielding & Bell 1997, Jiménez-Valverde 2012, Lobo *et al.* 2008, Pearson *et al.* 2007). It makes the self-evaluation dependent of data used in analysis. In our study, the confusion matrix is not used to evaluate model performance to capture the system provided by occurrence data, although the analysis does not use independent data. Therefore, the graphical evaluation of sampling sufficiency could be applied to improve models evaluation methods because it makes an internal assessment of model functioning. In this way, Araújo & Guisan (2006) had already indicated that as challenge to modelling development.

By using these graphics is possible to know how original data show equilibrium and how algorithms are capturing the system observed in species occurrence records. The modelling user can see in fact algorithm functioning and whether is coherent with environmental space represented in records collected by research. Comparing data of sampling sufficiency with expected levels of models transferability is another possibility of verification based on it. For example, traditionally ecological niche modelling has been used to find new populations of rare species or areas to collect new species (Araújo & Peterson 2012, Bourg *et al.* 2005, Feria *et al.* 2002, Raxworthy *et al.* 2003). By a combined analysis of these sampling sufficiency graphs with models transferability is possible to understand how the geographical projection would represent an environmental space reliable. Thus, high model transferability may be interpreted as habitats availability for a species or simply a noise in analysis caused by high variation in environmental information of original dataset.

Implications for species conservation

Besides the possible application of the presented analysis to make decisions about models selection, there is a clear implication of sampling sufficiency graphs for species conservation. Most of species used in this paper is classified in some criteria of concerning threats of its conservation (Siqueira-Filho & Leme 2006). Our results show the impact of historical reduction of available habitats of these species due the vanishing process of Atlantic Forest original cover. Moreover, these results allow conclude that we are not able to survey the niche of some species because part of its habitat disappeared before it could be collected, since many of these species were just recently described or collected (Leme & Siqueira-Filho 2001, 2006). Thus, this analysis might also provide a quantitative evaluation of habitat loss by a species under a temporal series perspective. Thus it might be a good tool to apply one of the criteria to be evaluated in conservation studies (Moraes & Martinelli 2013).

The fragmented landscape of Atlantic Forest at North of São Francisco River brought in its essence gradual floristic impoverishment as direct consequence of distance reduction between edges and nucleus of its small remnants (Oliveira *et al.* 2008). It causes a populational reduction of many bromeliads species, which have more complex environmental requirements (Benzing 2000). This impoverishment process of bromeliads communities in Atlantic Forest at North of São Francisco River was observed and described in previous researches (Siqueira-Filho & Leme 2006) and confirmed in our field work oriented by our modelling projections of species distributions.

Finally, all results presented here reinforce the importance of developing new methods contextualized in a biological perspective. In this way, a new tool is provided here whilst to contribute to species conservation and to understand evolutionary processes.

Table 6.1. Studied species of *Aechmea* (Bromeliaceae) and their patterns of geographical distribution (widely: WD; atlantic: AF; restricted: RE), number of points used to produce models and sampling sufficiency values of Bioclim and Maxent models.

Species	Distribution	Points	Bioclim	Maxent
A.aquilega (Salisb.) Griseb.	WD	60	0.97	0.97
A.bromeliifolia (Rudge) Baker	WD	316	0.89	0.80
A.castelnavii Baker	WD	30	1.00	0.71
A.catendensis J.A.Siqueira & Leme	RE	8	0.88	0.52
A.chrysocoma Baker	RE	14	1.36	0.45
A.costantinii (Mez) L.B.Sm.	RE	48	1.63	1.69
A.eurycorymbus Harms	RE	10	1.11	0.63
A.froesii (L.B.Sm.) Leme & J.A.Siqueira	AF	44	1.00	1.00
A.fulgens Brongn.	RE	36	0.90	0.90
A.gustavoi J.A.Siqueira & Leme	AF	4	0.56	0.56
A.leptantha (Harms) Leme & J.A.Siqueira	RE	44	0.89	0.62
A.mertensii (G. Mey.) Schult. & Schult. f.	WD	346	0.87	0.90
A.multiflora L.B.Sm.	AF	32	0.85	0.71
A.muricata (Arruda) L.B.Sm.	RE	16	0.62	0.62
A. nudicaulis var. *nordestina* J.A. Siqueira & Leme	RE	8	1.23	1.33
A.patentissima Baker	AF	84	0.60	0.60
A.tomentosa Mez	RE	32	0.85	0.63
A.werdermannii Harms	RE	12	2.90	2.03

Figure 6.1. Patterns of geographical distribution of *Aechmea* species from Atlantic Forest at North of São Francisco River: a-widely distributed; b-Atlantic distribution; c-restricted distribution.

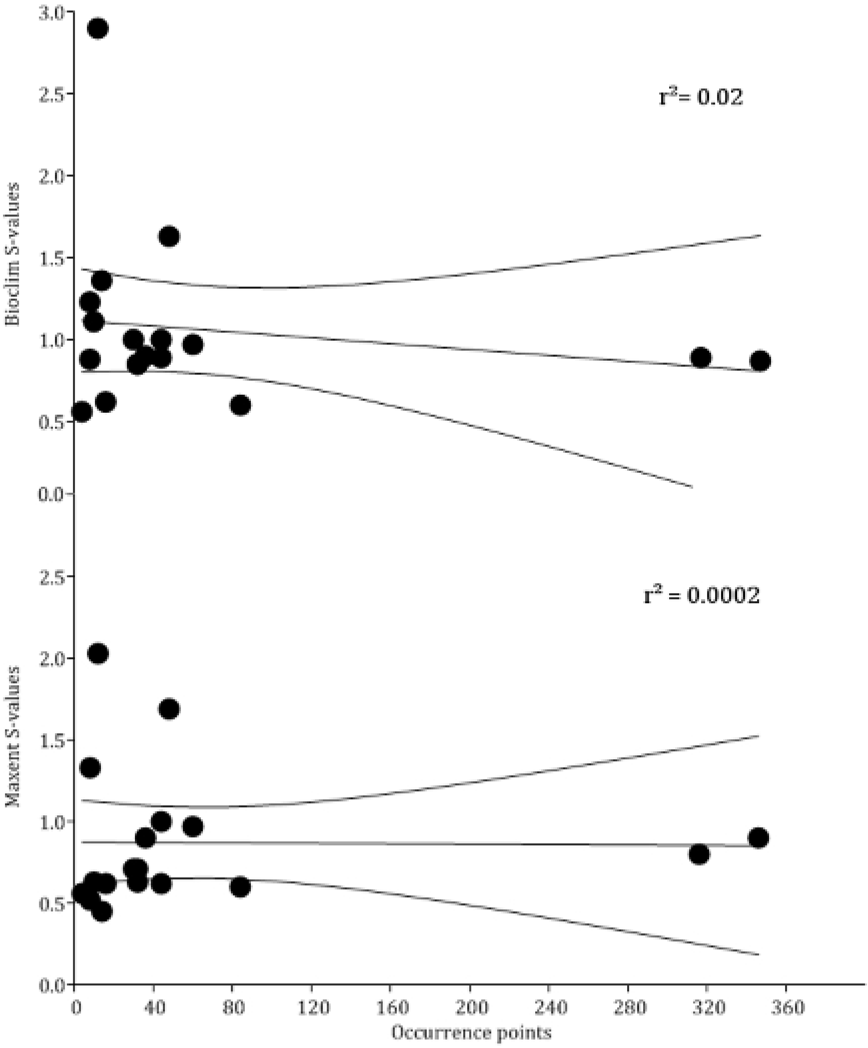

Figure 6.2. Regression analysis showing lack of correlation between numbers of points used to produce models and sampling sufficiency. a-Bioclim model; b-Maxent model.

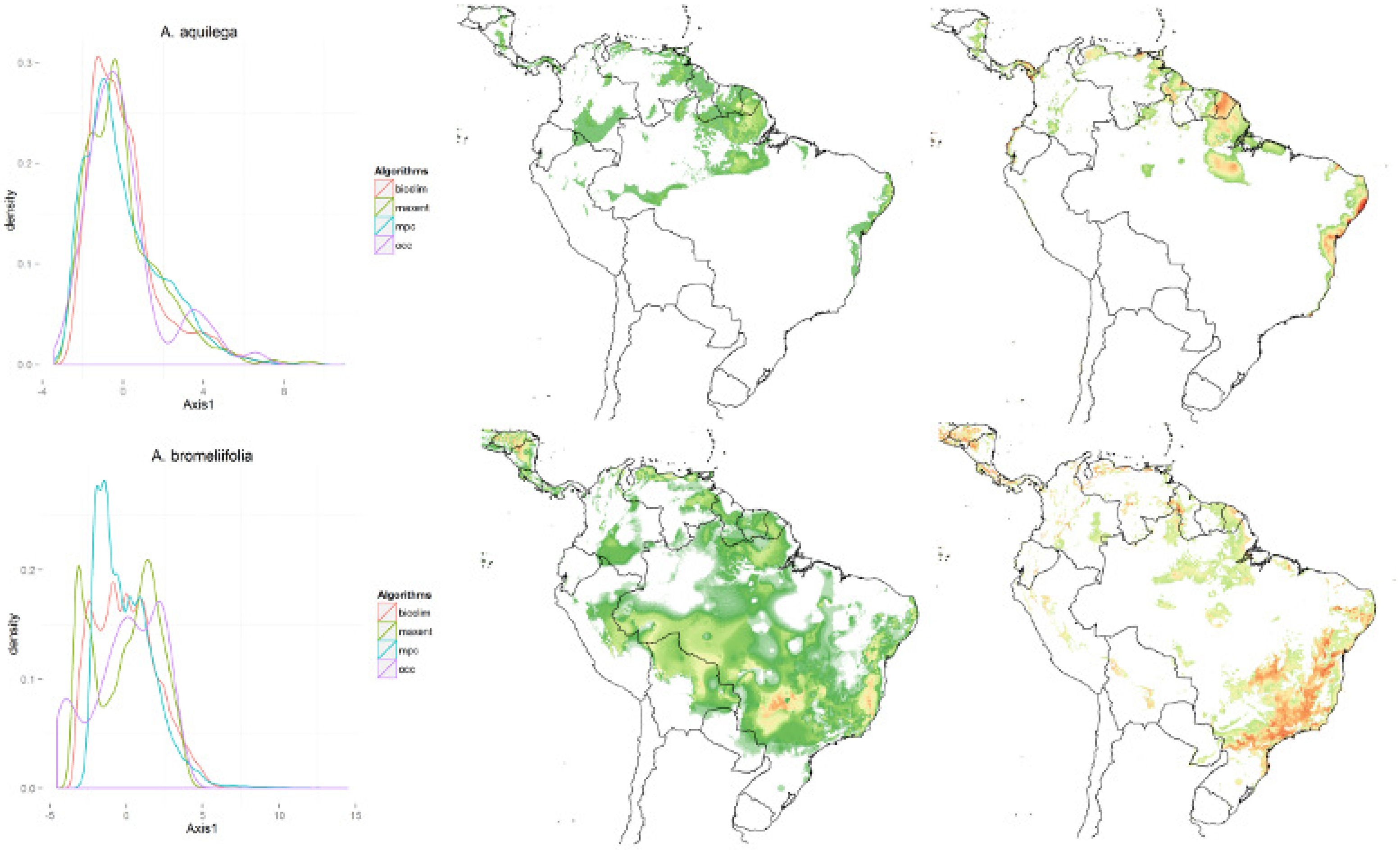

Figure 6.3. Sampling sufficiency graphics and Bioclim and Maxent models of *A. aquilega* and *A. bromeliifolia*, two widely distributed species. Lines in the graphics represent environmental spaces of each dataset. Bioclim – environmental space of Bioclim models; Maxent – environmental space of Maxent models; mpc – environmental space of convex hull; occ – environmental space of occurrence points.

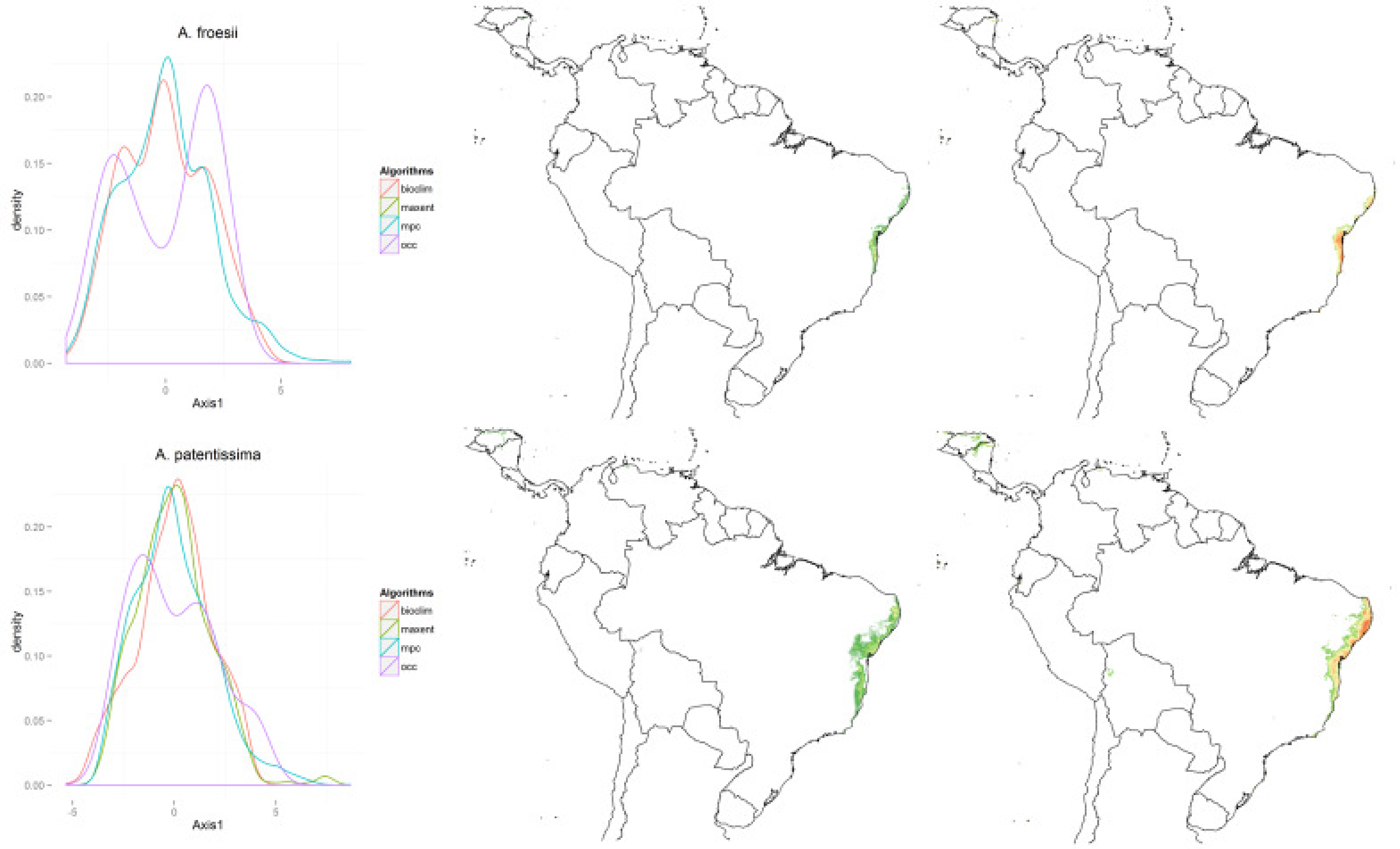

Figure 6.4. Sampling sufficiency graphs and Bioclim and Maxent models of *A. froesii* and *A. patentissima*, two Atlantic distributed species. Lines in the graphs represent environmental spaces of each dataset. Bioclim – environmental space of Bioclim models; Maxent – environmental space of Maxent models; mpc – environmental space of convex hull; occ – environmental space of occurrence points.

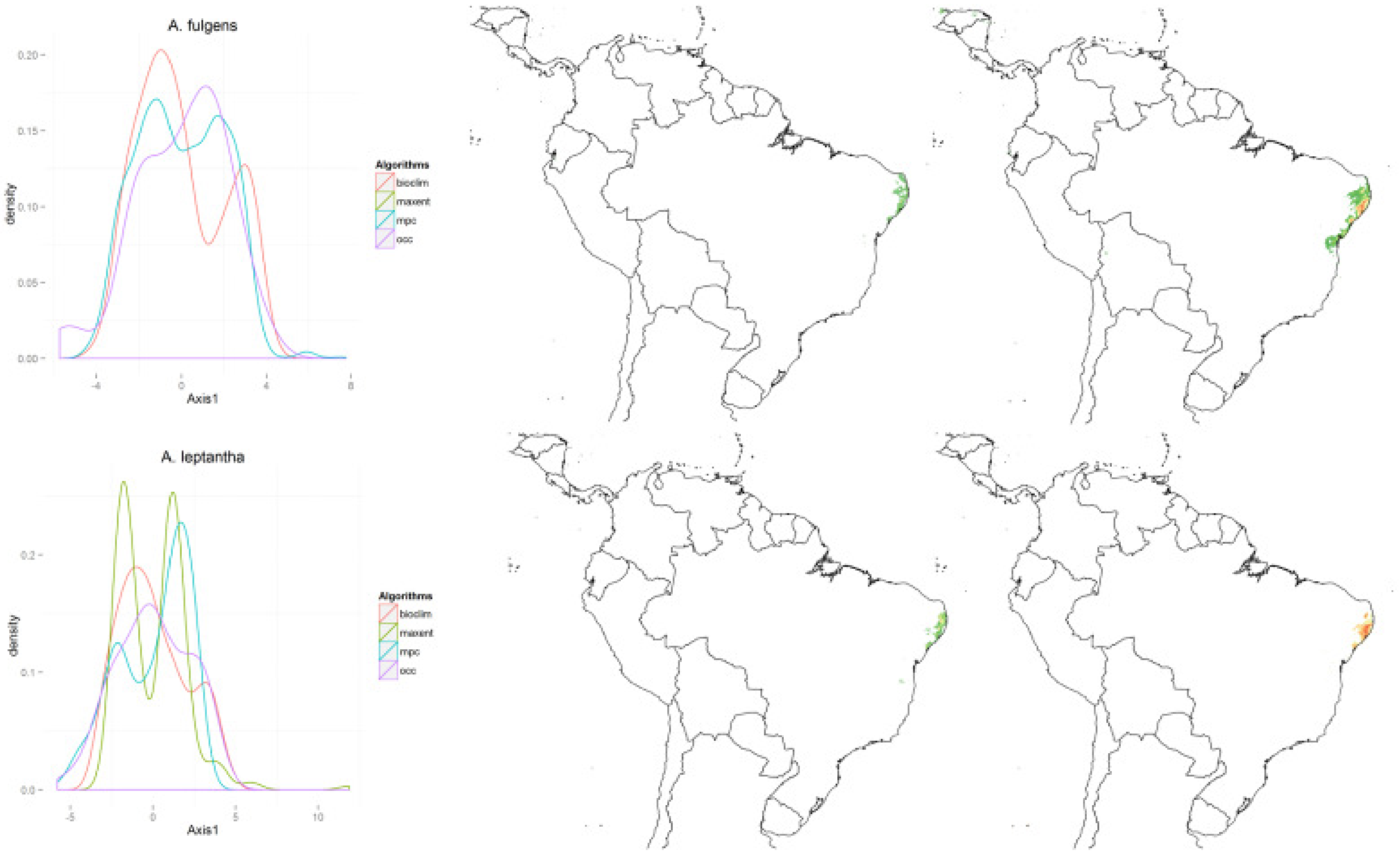

Figure 6.5. Sampling sufficiency graphs and Bioclim and Maxent models of *A. fulgens* and *A. leptantha*, two restrictdistributed species. Lines in the graphs represent environmental spaces of each dataset. Bioclim – environmental space of Bioclim models; Maxent – environmental space of Maxent models; mpc – environmental space of convex hull; occ – environmental space of occurrence points.

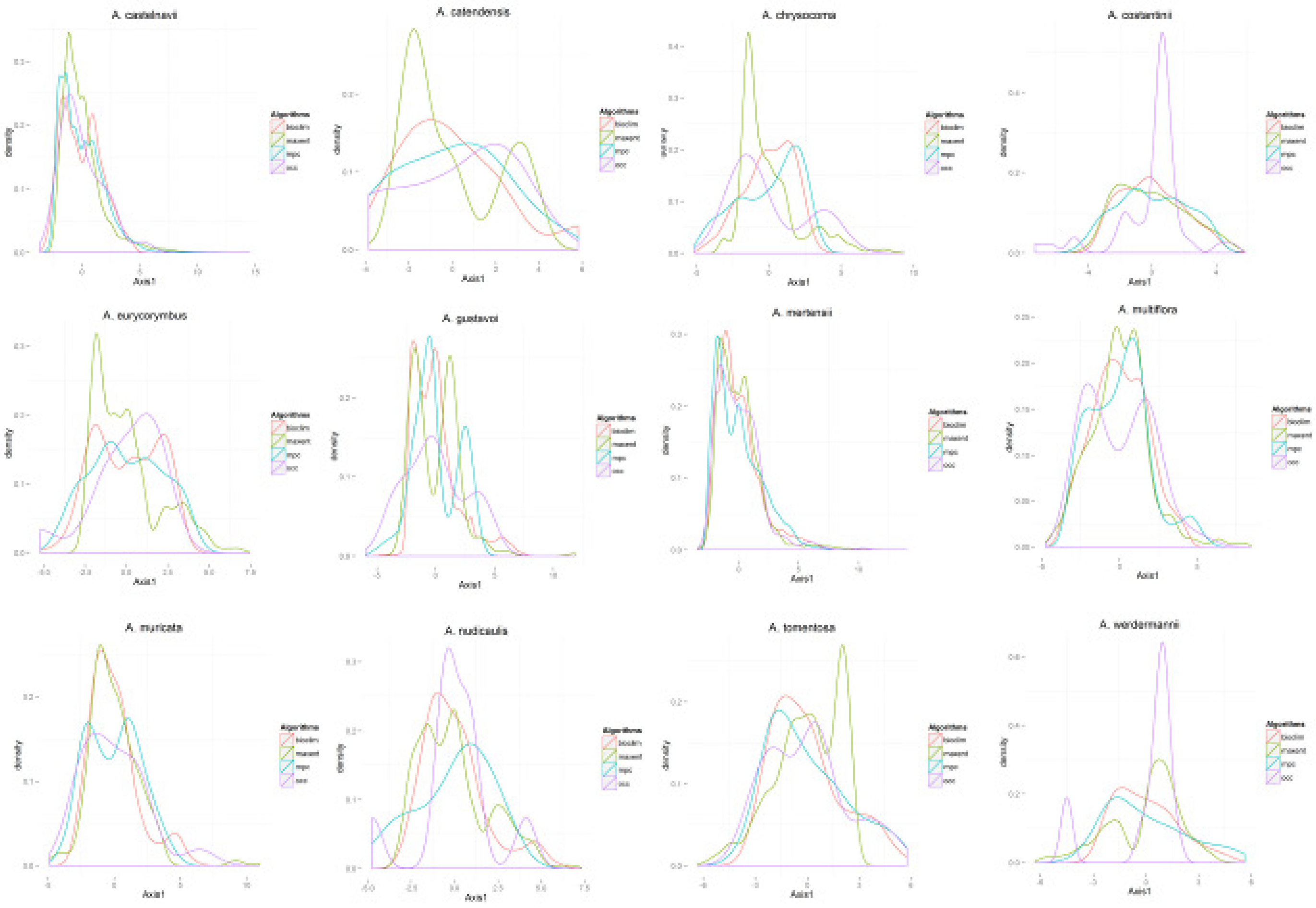

Figure 6.S1. Sampling sufficiency graphics for species of *Aechmea* (Bromeliaceae). Lines in the graphs represent environmental spaces of each dataset. Bioclim – environmental space of Bioclim models; Maxent – environmental space of Maxent models; mpc – environmental space of convex hull; occ – environmental space of occurrence points.

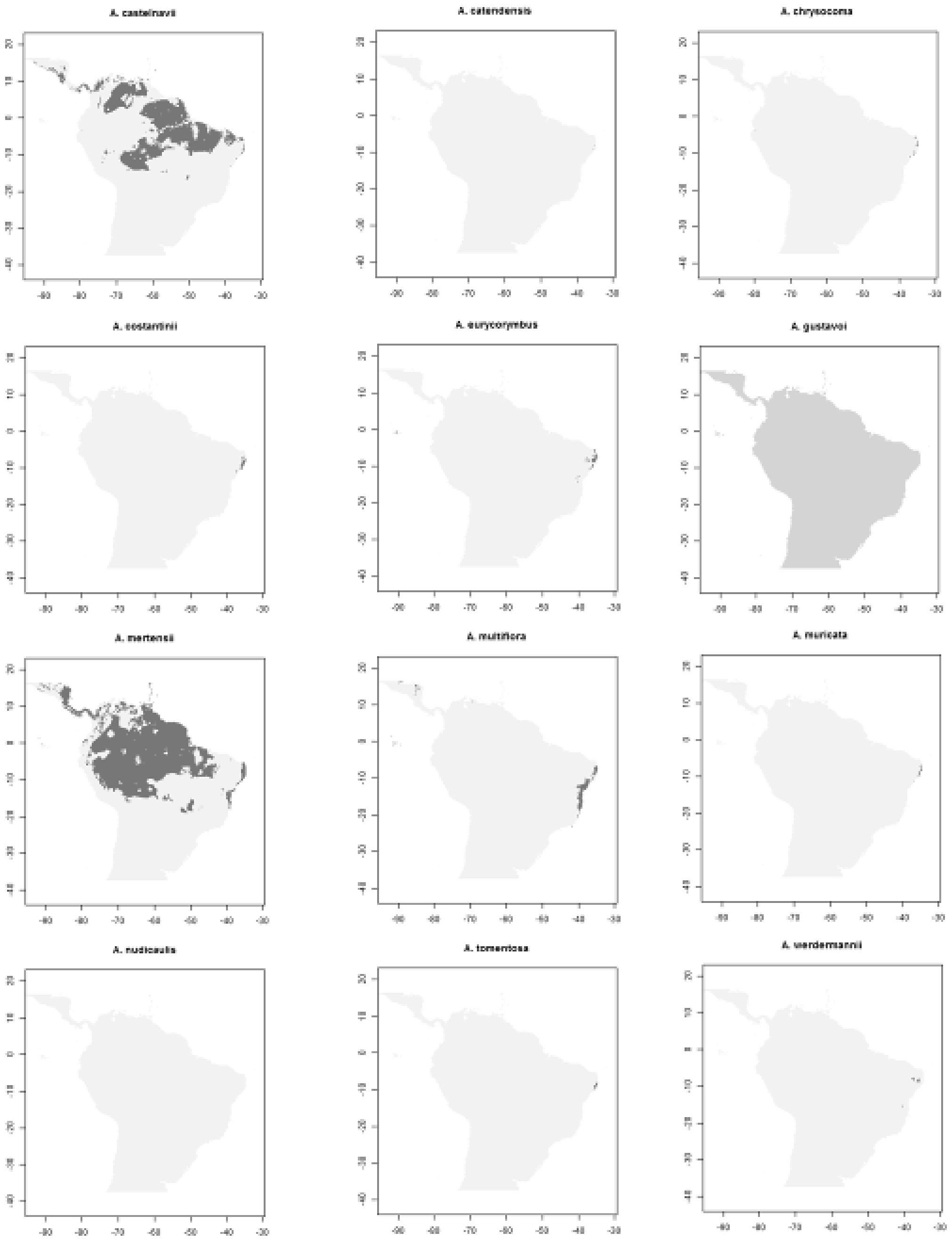

Figure 6.S2. Binary models of Bioclim of other studied species of *Aechmea* (Bromeliaceae). The gray area represents presence of species based in TSS values used to recover environmental information to construct Bioclim dataset.

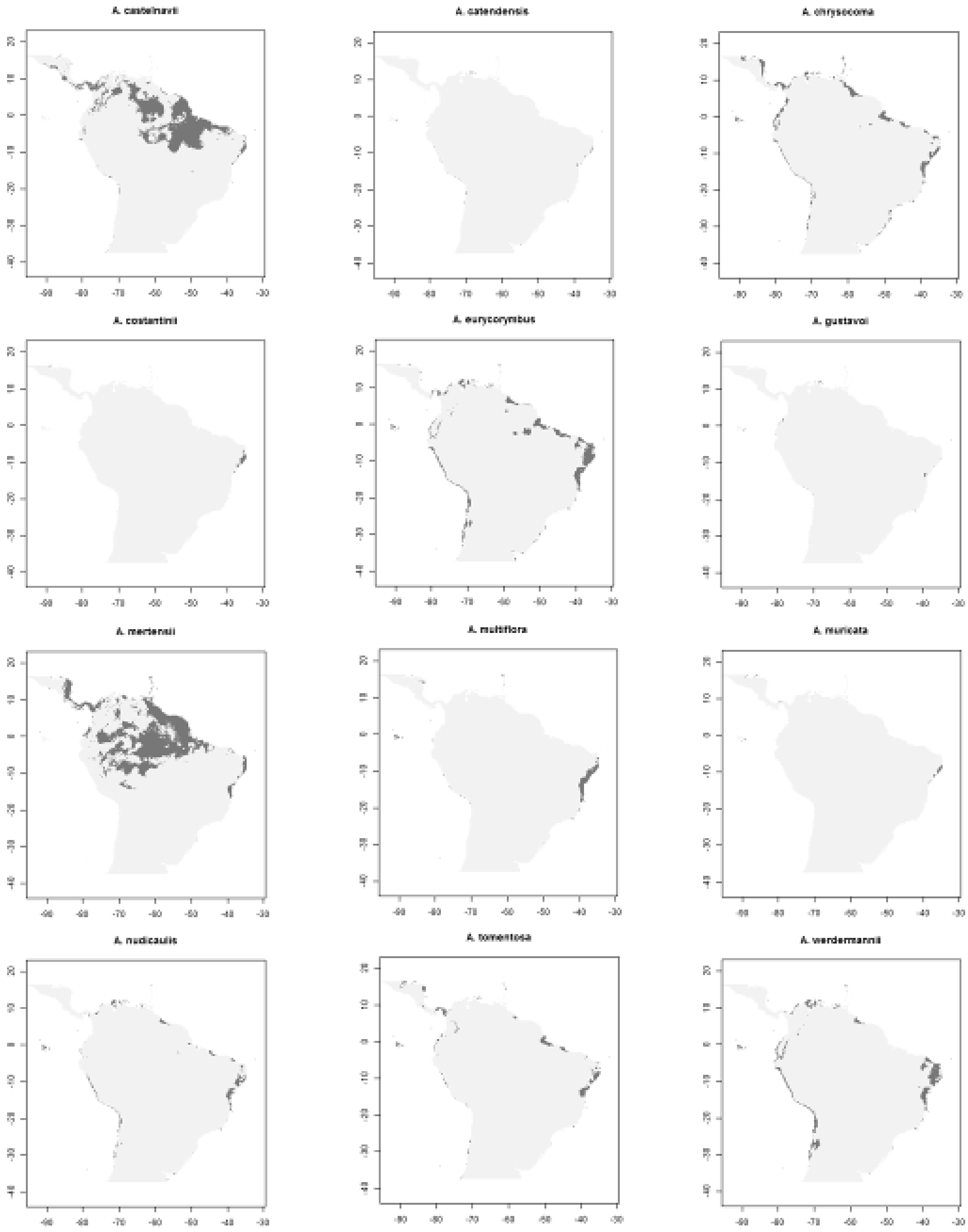

Figure 6.S3. Binary models of Maxent of other studied species of *Aechmea* (Bromeliaceae). The gray area represents presence of species based in TSS values used to recover environmental information to construct Maxent dataset.

7 Paleodistribution of epiphytic bromeliads points to past connections between the Atlantic and Amazon Forests

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Abstract

The disjunct geographic distributions of species between the Amazon and Atlantic Forests have been used as evidence of past connections through the interior of the Brazilian Northeast as a result of climate fluctuations. Herein we test this hypothesis for the first time using plant species with disjunct geographic distributions and ecological niche modelling. We generated ecological niche models for two species of *Aechmea* using two different modelling methods. These models were projected onto a Mid-Holocene and Last Interglacial climates scenarios and the results were calculated for each species separately. Our results show that the connection between the Amazon and Atlantic Forests was along the coastal region of northeastern Brazil. This result contradicts the currently most widely accepted paradigm explaining the biogeographic connections between the Amazon and Atlantic Forests through non-coastal forest formations. Our results are supported by molecular records of several other biological groups and with recently reevaluated floristic studies. However, the variations found in our analyses highlight the fact that different species can show distinct biogeographic histories, reinforcing the importance of species-specific analyses in paleodistribution modelling.

Keywords

Bromeliaceae, Bromelioideae, *Aechmea*, biogeography, evolution, ecological niche modelling, glm, MaxEnt, disjunctions.

Introduction

Disjunct distributions of species have puzzled biogeographers since the mid-twentieth century (Raven, 1972). This is particularly true for the Neotropics, where one of the most studied and discussed disjunction phenomena is found between the Amazon and Atlantic Forests (Fiaschi & Pirani, 2009). Several authors have used this disjunct distribution pattern as an example of a possible connection between these biotas, possibly favored by Pleistocene climate change (Andrade-Lima, 1953, 1966, 1982; Batalha-Filho *et al.*, 2012; Bigarella, Andade-Lima & Riehs, 1975; Ducke & Black, 1954; Rizzini, 1963; Oliveira-Filho & Ratter, 1995; Siqueira-Filho & Leme 2006).

The Atlantic and Amazon Forests are isolated from each other by a dry corridor formed by the *Caatinga* to the north, the *Cerrado* in the central portion and the *Chaco* in the south (Ab'Sáber, 2003). However, a body of evidence suggests that this isolation has been less pronounced at certain times in the geological history of the area. Some of these moments were during the Mid-Holocene and Last Interglacial, two periods known to feature climate change on a global scale, as has been recorded by several authors (Cerling *et al.*, 1997; Davis *et al.*, 2003; Dutton & Lambeck, 2012; Gagan 1998; Kukla *et al.*, 2002; Lawing & Poly, 2011; Ledru *et al.*, 2005; Lisiecki & Raimo, 2005; Mayewski *et al.*, 2004; Muhs, 2004; Pessenda *et al.*, 2005; Quigley *et al.*, 2010; Rousseu *et al.*, 2006). In South America the increase in rainfall in more arid regions coincides wholly or partially with the Mid-Holocene, as a result of the displacement of the Intertropical Convergence Zone to the south (Auler *et al.*, 2004; Behling, Arz & Wefer, 2000; Mayewski *et al.*, 2004; Oliveira, Barreto & Suguio, 1999; Pessenda *et al.*, 2005; Wang *et al.*, 2004).

Several sources of evidence show that the Brazilian Northeast experienced periods of increased moisture throughout its geologic history, more precisely between 10,000 and 5,000 years B.P and 130,000 and 110,000 years B.P. In this period, the area currently occupied by the Caatinga is thought to have been more humid (Auler *et al.*, 2004; Behling *et al.*, 2000; Oliveira *et al.*, 1999; Pessenda *et al.*, 2005; Wang *et al.*, 2004). On the other hand, the gallery forests in the Brazilian Southeast experienced moments of expansion between 6,000 and 4,000 years B.P. (Behling, 1998; Ledru, Salgado-Labouriau & Lorscheitter, 1998). These changes probably influenced the distribution of Neotropical species, particularly those from forests or others with higher moisture requirements for establishing and maintaining their populations, such as some groups of epiphytic bromeliads (Gentry & Dodson, 1987; Dynesius & Jansson, 2000; Jackson & Overpeck, 2000). During these climate events, the areas of distribution of species requiring humid environments may have expanded, reducing the isolation between the Atlantic and Amazon Forests and allowing for floristic exchange between the two biotas.

In a recent study using bird molecular data, Batalha-Filho *et al.* (2012) indicated two possible connection routes between the Atlantic Forest and the Amazon. The first for clades of Miocene origin across the Brazilian Southeast and Central-West and the second for clades of Plio-Pleistocene origin along the Brazilian Northeast, either through the interior, currently occupied by the Caatinga, or along the Atlantic coast. Similar patterns of biogeographical connection have been highlighted by Santos *et al.* (2007), using plant distribution data from the Atlantic and Amazon Forests, Costa (2003) for mammals and Oliveira-Filho & Ratter (1995), analyzing the flora of gallery forests, which in more humid periods could have served as migration corridors between the two biotas across the dry diagonal region of South America.

The expansion of geographical areas corresponding to the fundamental niche is among the effects that climate changes promote in the geographical distribution of species (Dynesius & Jansson, 2000; Jackson & Overpeck, 2000; Araújo & Rahbek, 2006). It is expected that a period of increased humidity in dry environments will enable the migration of species with geographical distribution and richness patterns deeply influenced by humid conditions, such as epiphytes (Gentry & Dodson, 1987). One of the genera that features disjunction distribution patterns of species between the Atlantic and Amazon Forests is *Aechmea* (Bromeliaceae), wherein at least three disjunct species have already been reported (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel, Louzada & Alves, 2015).

Hypotheses of connection routes between the two biotas have been tested with floristic or panbiogeographic tools (Andrade-Lima, 1953, 1966, 1982; Black & Ducke, 1954; Rizzini, 1963; Santos *et al.*, 2007) except for Batalha-Filho *et al.* (2012) and Costa (2003), who used phylogeographical approaches in studies of birds and mammals, respectively. One of the tools to address the processes generating disjunction is ecological niche modelling (ENM), which constitutes an efficient and practical method for studying species distribution (Giannini *et al.*, 2012; Nogués-Bravo, 2009; Franklin & Miller 2009). Despite the potential for applying this approach in studies of species distribution and biome dynamics under the influence of climate events in the Neotropics (Bueno *et al.* 2016, Carnaval & Moritz, 2008; Collevatti *et al.*, 2012, 2013; Peterson & Nyári, 2008; Werneck *et al.*, 2011, 2012), questions about plant disjunction between the Atlantic and Amazon Forests have not been tested under this lens.

In the present study we evaluated how Mid-Holocene and Last Interglacial conditions affected the potential distribution of two species of bromeliads that occur currently in Atlantic and Amazon Forests (in a disjunct and continuous ways). For this work we elaborated two questions: 1) fundamental niche of disjunct species in climate change events indicates former environmental connections between the Atlantic and Amazon Forests? 2) and if this connection is indicated, which is the main corridor between the two biotas predicted by projections of these species?

Materials and methods

Species analyzed

Two species of *Aechmea* (Figure 1) that occur in Atlantic and Amazon Forests (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel *et al.*, 2015) were selected. *Aechmea aquilega* (Salisb.) Griseb. occurs along the Atlantic coast from Venezuela to Brazil (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel *et al.*, 2015). *Aechmea mertensii* (G. Mey.) Schult. & Schult. f. has a wide distribution pattern, occurring in almost all of the Amazon Forest and in the Atlantic Forest (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel *et al.*, 2015).

The two selected species have morphological identity very well established and revised in several monographs of Bromeliaceae in both poles of their distribution (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel *et al.*, 2015). *Aechmea aquilega* has some morphological variation, which has been interpreted as taxonomic varieties or elevated at specific range by some authors. Here we adopted the most recent concept that recognizes two of these varieties as different species restricted to the Atlantic Forest and applied the most conservative morphological based concept of *A. aquilega* to our samples (Leme & Siqueira-Filho, 2006).

Aechmea aquilega and *A. mertensii* evolved in two independents lineages inside the Bromelioideae core, a clade formed by species that have tank habit in Bromelioideae (Sass & Specht 2010). Givinish *et al.* (2014) inferred the age of all Bromelioideae as 10 Ma and Silvestro *et al.* (2013) proposed that Bromelioideae core evolved in last 7.08Ma. Specifically, the clade *A. mertensii* has a mean age of 2.8 Ma while the Gravisia group, to which *A. aquilega* belongs (Heller *et al.* 2015), has a mean age of 3.4 Ma (Silvestro *et al.* 2013). These results clearly show that the evolutionary history of these two species took place in the last 5 Ma, when many climatic changes occurred.

The taxonomical stability of the species, the wide geographical distribution of *A. aquilega*, the disjunct distribution of *A. mertensii* and the recent evolutionary history of the species made them good models to test the connections between Amazon and Atlantic Forest supposed to exist during the climate changes in South America.

Data collection

The information for the database used in this study was gathered from the herbaria ALCB, ASE, CEPEC, EAC, HRB, HUEFS, IAN, INPA, IPA, JPB, MAC, MBML, MIRR, MPEG, NY, PEUFR, RB, UFP, UFRN, UFRR, US and VIES. The identification of each analyzed sample was confirmed based on morphological studies of the *typus* and on the literature (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel *et al.*, 2015).

A field survey was conducted between 2010 and 2014 in the Atlantic and Amazon Forests. In the Atlantic Forest collections were made in the Brazilian Federal States of Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia and Espírito Santo, extending therefore beyond the southern limit of the distribution of the studied species. In the Amazon Forest areas in the states of Amazonas, Pará and Roraima were visited. The collection aimed to confirm the presence of species and increase records in a database of local place names.

For samples without geo-referenced data, a coordinate was assigned based on a comparison of the descriptions of localities found on the labels of samples and gazetteer databases available on the Internet (http://earth-info.nga.mil/gns/html/, http://www.geonames.org/). Georeferencing tools such as Google Earth were used. When the descriptions of the location of the collections were not informative, the samples were discarded.

Selection of variables

For this study, we used the bioclimatic and elevation variables of the Worldclim database (Hijmans *et al.* 2005, available at http://worldclim.org). The environmental data for points of species occurrence were sampled and submitted to a correlation analysis. We calculated the Pearson correlation coefficient between the climatic variables and the variables with high level of correlation were eliminated ($R^2 > 70\%$). The most independent bioclimatic variables were selected: mean annual temperature, temperature seasonality, annual variation in temperature, mean temperature of the hottest quarter, precipitation seasonality, precipitation of the hottest quarter and precipitation of the coldest quarter.

To perform the projections, paleoclimatic layers of the Mid-Holocene and Last Interglacial-LIG corresponding to the same bioclimatic variables used in the creation of the models, generated from general models of climate circulation (Atmosphere-Ocean General Circulation Models or AOGCMs) (Hijmans *et al.*, 2005; detailed methodology in Peterson & Nyári, 2008). We chose these periods for analyses because they correspond to changes in climatic conditions around the world in which sea level elevation and increasing temperatures, rainfall and moisture were recorded (Cerling *et al.*, 1997; Davis *et al.*, 2003; Dutton & Lambeck, 2012; Gagan 1998; Kukla *et al.*, 2002; Lawing & Poly, 2011; Ledru *et al.*, 2005; Lisiecki & Raimo, 2005; Mayewski *et al.*, 2004; Pessenda *et al.*, 2005; Quigley *et al.*, 2010; Rousseu *et al.*, 2006). Furthermore, these periods correspond in South America to the expansion of humid forests in several regions based on palynological and geological records (Auler *et al.*, 2004; Behling, Arz & Wefer, 2000; Mayewski *et al.*, 2004; Oliveira *et al.*, 1999; Pessenda *et al.*, 2005; Wang *et al.*, 2004).

In order to avoid problems of uncertainty arising from the existing variation in different AOGCMs, the recommendation of Collevatti *et al.* (2013) and Nogués-Bravo (2009) were followed: using nine AOGCMs available at worldclim.org and properly downscaling to a spatial resolution of 5', the same used for the bioclimatic variables in this study. The AOGCMs used are BCC-CSM1-1, CCSM4, CNRM-CM5, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM, MPI-ESM-P and MRI-CGCM3 (Hijmans *et al.*, 2005). However, the layers corresponding to the Last Interglacial have just one model of circulation (Otto-Bliesner *et al.* 2006).

The study area for the preparation of models and their projection onto distinct AOGCMs of the Mid-Holocene and Last Interglacial was defined by the geographical extension of 95.75ºW, 29.42ºW, 37.42ºS and 16.5ºN. This extension corresponds to the northern and southern limits of distribution of the two species selected for the study and covers, in addition to the Atlantic and Amazon Forests, other South American biomes.

Modelling and projection

The distribution of the two species was modeled using the algorithms of Maximum Entropy (MaxEnt) and Generalized Linear Models (GLM) previously applied effectively in modelling studies (Guo, Kelly & Graham, 2005; Hijmans & Elith, 2014). The GLM algorithm is classified as a regression method, while MaxEnt is classified as a machine learning method. The two modelling methods use presence and pseudo-absence or background data (Guo *et al.*, 2005; Guisan & Edwards, 2002; Hijmans & Elith, 2014; Phillips, Anderson & Schapire, 2006). A recent review of the operation of these algorithms can be found at Hijmans & Elith (2014).

The quality of the models was evaluated by a 3-fold partition, where 66% of the data was used for training and 33% for testing. Therefore, for each species data set there were three partitions and for each partition a model. A total of 500 points were randomly collected in the study area as background data, for which the same logic of partition into training and testing data was used. We defined the background area based on the distribution limits of species. We are aware that the size of background area has effects on AUC and TSS results (Allouche, Tsoar & Kadmon 2006, Giovanelli *et al.* 2010), however the large space delimited is associated to the nature of the distribution of species and to our intent to project the model in an area comprising both the Atlantic and Amazon Forests.

To evaluate the models and construction of the confusion matrix, the threshold that maximizes the performance of the model through the True Skill Statistic (TSS) was used. The area under the operator curve (AUC) was also calculated for each model. Both based only on presence records. Models with TSS values> 0.6 and AUC> 0.7 were selected and projected onto the nine AOGCMs (More informations about models are available on Figures S1 and S2 and Table S1). These statistics tools are widely used in niche modeling studies (Hijmans 2012; Jiménez-Valverde, 2012; Jiménez-Valverde, Lobo & Hortal, 2008; 2012; Lobo, Jiménez-Valverde & Real, 2008), which allow for comparisons between the different models from the same species and different algorithms in our study. Moreover, we chose to work with the AUC and TSS at same time to complement the information, whereas the AUC and TSS are based on confusion matrix, the AUC operates without threshold while TSS is dependent of threshold. However, we use the values of these tools only to choose which model not to project on past scenarios and not to validate or choose the best models.

Finally, the projections were evaluated geographically and chi-square test was performed to evaluate the difference between the frequencies of different patterns. We combined all projections of each species to calculate a mean and standard deviations of each pixel of the projections. Then, we mapped both means and standard deviations for each species in order to construct the final consensus maps using a simple function of mean and standard deviations from raster package of R (Hijmans, 2005).

The analyses in this study were performed using the R statistical environment (R Core Team, 2014). The preparation of layers was performed using the raster package (Hijmans, 2005), the distribution models were calibrated, evaluated and projected using functions within the dismo package (Hijmans & Elith, 2014), in particular the MaxEnt function for modelling. The GLM algorithm was performed using the glm function of the stats package (R Core Team, 2014).

Results

The patterns of geographic distributions of *Aechmea aquilega* and *A. mertensii* were confirmed in 66 models for the present (Figure 1). In general, the models show the north-central and eastern portions as the main cores with the greatest potential for the occurrence of species in the Amazon region. In the Atlantic part, the model of *A. aquilega* for the present, confirms the intermediate disjunction in the northern region of dry diagonal and subsequently the continued occurrence in the Atlantic Forest. In turn, *A. mertensii* presents only a single area of greater potential in the Amazon without intermediate regions between the Atlantic and Amazon Forests (Figure 1).

A total of 55 models were projected in the nine climate scenarios of the Mid-Holocene and 11 were projected on Last Interglacial scenarios. The projections allow us to identify three patterns: 1) Northeastern coastal corridor; Northeastern interior corridor or Central-West. In some situations, it was possible to recognize the same projection combinations of the three patterns or projections that generated a null result and where no hypothesis or alternative were applicable.

The hypothesis of a connection between the Atlantic and Amazon Forests through the Brazilian Northeast was supported in 89% of 66 projections generated, and within this set (n = 59) a connection along the northeastern coast represented 75% of the models, while the connection via the interior across the Caatinga was supported in 19% (Table 1). The hypothesis of a connection via the central region of Brazil was supported in 11% of the cases (Table 1).

The paleodistribution projections of *Aechmea aquilega* and *A. mertensii* confirmed the general pattern of connection via the Northeast coast, albeit with minor differences in the configuration of this expansion, especially in the Amazon portion of the distribution (Figure 2 and 3). It was possible to detect the expansion of the habitats of these two species of bromeliads displaced to the coast as much along the northern portion as along eastern South America. In the North, the ideal habitat conditions experienced a shift toward the east and west, that is, the Amazon core approached both the Andes and the coast. In the Atlantic core, the expansion of favorable habitats possibly occurred northward along the coast to the Amazon.

The GLM models suggested the possibility of a connection between the Atlantic and Amazon Forests along the northeastern coast (Table 1). This route would have included the northeastern portion of the Atlantic Forest and would have advanced across areas today located in the dry diagonal. From this point on, the corridor would have followed along the coast to connect with the area currently occupied by the Amazon Forest. The MaxEnt algorithm offered relatively different scenario with the connection of the two forest masses throughout the entire Brazilian Northeast, expanding to the South via the Central portion.

All the AOGCMs and LIG supported, in most cases, the Northeast hypothesis (Table 1). Only HadGEM-CC showed the Central-West hypothesis prevalence among results. In this AOGCM Central-West hypothesis was supported in 60% of the models. Although the MIROC-ESM and CCSM4 models support the Northeast hypothesis, these two AOGCMs showed alternative scenarios to connection between Amazon and Atlantic Forests. The mean of CCSM4 and MIROC-ESM projections showed a connection across the entire Northeast with an extended area with conditions for expanding populations through the Central region.

Discussion

Variation in the algorithms and AOGCMs

Modelling algorithms and AOGCMs are significant sources of variation that strongly influence the interpretation and quality of results in Paleodistribution studies. These variations give limitations on the conclusions if there is no effort to measure or estimate them (Buisson *et al.*, 2010; Collevatti *et al.*, 2013; Diniz-Filho *et al.*, 2009; Dormann *et al.*, 2008; Elith *et al.*, 2006; Giovanelli *et al.*, 2010; Philips *et al.*, 2006; Wisz *et al.*, 2008).

Our study found variation in the results of the projections among the different algorithms and AOGCMs used. While HadGEM-CC showed the Central-West hypothesis prevalence, the CCSM4 and MIROC-ESM point out the connections by Northeastern interior. Interestingly, the AOGCMs CCSM4 and MIROC-ESM are the two most widely used AOGCMs in projections of the distribution of past climate scenarios in the Neotropics (Bueno *et al.*, 2016; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009; Peterson & Nyári, 2008; Poelchau & Hamrick, 2013; Sobral-Souza *et al.*, 2015;Worth *et al.*, 2013), especially in phylogenetic studies, where modelling is only a complementary tool (e.g. Lima *et al.*, 2014; Pinheiro *et al.*, 2011).

Finally, the variation found between the modelling methods used here is consistent with the reports in the literature (Buisson *et al.*, 2010; Collevatti *et al.*, 2013; Dormann *et al.*, 2008; Diniz-Filho *et al.*, 2009; Elith *et al.*, 2006; Giovanelli *et al.*, 2010; Philips *et al.*, 2006; Wisz *et al.*, 2008). The recommendation of Collevatti *et al.* (2013) and Nogués-Bravo (2009) to minimize the effect of this variation in models interpretations is applied here. Thus, conclusions about the Paleodistribution of the two species and the connections between the two Neotropical rainforests are provided with more reliability.

Connections between the Atlantic and Amazon Forests

The results support a connection route between the Atlantic and Amazon Forest across the Brazilian Northeast, confirming previous hypotheses based on species distribution data (Andrade-Lima, 1953, 1966; Bigarella *et al.*, 1975; Ducke & Black, 1954; Rizzini 1963). However, these authors suggest that the *Brejos de Altitude* are relicts of a connection between the Atlantic and Amazon Forest due to climate change, which would have been the cause of disjunctions mainly seen in elements of the flora (Andrade-Lima, 1966, 1982) and avifauna (Batalha-Filho *et al.*, 2012).

Unlike previously proposed, our results suggest that coastal areas played a more important role for this contact than the interior regions, where enclaves of humid forests can be found within the semi-arid landscape. In this sense, the importance given to the montane and submontane forests of the Northeast as the only relicts of this connection (Andrade-Lima, 1953, 1966; Bigarella *et al.*, 1975; Ducke & Black 1954; Rizzini 1963) is questioned here based on the evidence of geographical distribution modelling of the species studied. Results of the floristics and distribution patterns presented by Cavalcanti & Tabarelli (2004) already indicate that species disjunct between the Atlantic and Amazon Forests occur in the lowland forests of the Brazilian Northeast. Comparing fragments of montane forest of the semi-arid region, lowland forests of the Brazilian Northeast and Southeast regions and the Amazon Forest through a parsimony analysis of endemism, Santos *et al.* (2007) showed that the lowlands forests of the Northeast share a biogeographical history more associated with the Amazon forest than the inland forests of the Northeast.

The connections presented here are consistent with the findings of Batalha-Filho *et al.* (2012) for birds, which identified the northeastern route as the exchange pathway for lineages between the Atlantic and Amazonian biota. According to the authors, the connection could have been achieved through two patterns, one of them similar to the general pattern found in this study and the other from the interior of the Caatinga and Cerrado, which is supported by the pattern observed in part of our results. In both connection patterns prevail whose lineages evolved between the Pliocene and Pleistocene. It is worth noting here that the Pleistocene age proposed by Batalha-Filho *et al.* (2012) for the connection via the Brazilian Northeast is the same recorded for the core-Bromelioideae clade including *Aechmea* of ca. 5 Mya (Givnish *et al.*, 2007, 2011, 2014; Silvestro *et al.* 2013) and for median 2.8 Ma age of *A. mertensii* as reported by Silvestro *et al.* (2013).

This reinforces the suggestion that climate events allowed the expansion of populations of these species and the route found in our results may have in fact been a contact region between the Atlantic and Amazon Forests. Givnish *et al.* (2011) pointed out that among the events that gave origin to and promoted the diversification of the core-Bromelioideae group in the Atlantic Forest were the orogeny of the highlands of the central Andean region and the intensification of orogeny in the Serra do Mar. These factors were also associated with the climate change in South America, which was mainly influenced by the Andes (Antonelli & Sanmartín, 2011; Ehlers & Poulsen, 2009). Such events would have intensified rainfall and increased humidity, thus reducing the isolation between the Atlantic and Amazon Forests, which according to Givnish *et al.* (2011) would have been the cause for the exchange of various groups of Bromeliaceae between the two floras.

Increased humidity is one of the conditions necessary for increasing the richness of bromeliad communities and one of the causes of regional differences in the composition and richness of the group in the Neotropics (Gentry & Dodson, 1987). Additionally, the increase in humid conditions in more arid environments in the Brazilian Northeast is supported by various pieces of geological evidence dating from the last 200,000 years (Auler *et al.*, 2004; Behling *et al.*, 2000; Bezerra *et al.*, 2003; Hila *et al.*, 2002; Oliveira *et al.*, 1999; Suguio *et al.*, 2011; Wang *et al.*, 2004). These distinct evidence also suggest that cyclical events of increased humidity recur in 10,000-year intervals. Given that since the Pliocene climate changes have regularly taken place on a global scale (Ravelo *et al.*, 2004; Zachos *et al.*, 2001), it is reasonable to assume that since their origin 5 Mya, species of core-Bromelioideae had several opportunities to disperse between the Atlantic and Amazon Forests, across the dry diagonal of South America along occasional humid corridors.

New niche opportunities appear to have been fundamental to the mobility of the populations of the species studied and floristic exchange between the two biotas associated with the dispersal of *A. aquilega* and *A. mertensii*. For example, *A. mertensii* depends on ants to transport its diaspores and for the survival of individuals (Carrias *et al.*, 2012; Céréghino *et al.*, 2011) which does not seem to be an impediment since the species is one of the most widely distributed one in Bromelioideae core group and its disjunct distribution has been widely confirmed in the literature as well as by the results obtained here (Smith & Downs, 1979; Leme & Siqueira-Filho, 2006; Maciel *et al.*, 2015).

This proposal supports the importance of our results for understanding the evolution of Bromeliaceae in South America. Specifically, the results demonstrate that under climate events that intensified humidity, Bromeliaceae species found increasingly favorable conditions for their expansion. This is one of the expected effects in situations of climate change (Araújo & Rahbek, 2006; Dynesius & Jansson, 2000; Jackson & Overpeck, 2000).

The possible processes by which climate change could have influenced the biotic exchanges between the Atlantic and Amazon Forests and contribute to the understanding of the evolution of the core-Bromelioideae clade in its process of radiation in South America are presented here. Our results is indirectly supported by evidences from several sources, such as floristics (Cavalcanti & Tabarelli, 2004; Santos *et al.*, 2007), phylogeny (Givnish *et al.*, 2007, 2011, 2014), geology (Auler *et al.*, 2004; Behling *et al.*, 2000; Pessenda *et al.*, 2005; Wang *et al.*, 2004), palaeopalinology (Behling *et al.*, 1998; Ledru, Salgado-Laboriau & Lorscheitter, 1998; Oliveira *et al.*, 1999) and molecular biology of distinct groups (Batalha-Filho *et al.*, 2012; Costa, 2003).

Despite our conclusions have support in independent evidences, we recognize the limitations of this work due the lack of other integrative tools (eg., phylogeography, phylogeny) to give more information about demographic dynamics of species in time and space. However, it is possible to infer that clarifying the evolution of the biomes in South America requires an understanding of the specific responses that each taxon gives to the same evolutionary pressure. Lastly, testing these hypotheses for other taxonomic groups emerges as a valuable and urgent target for the better understanding of paleodistribution processes in South America. In this way, we can design a better picture of consequences of climatic changes on Neotropical biota to implement effective conservation programs.

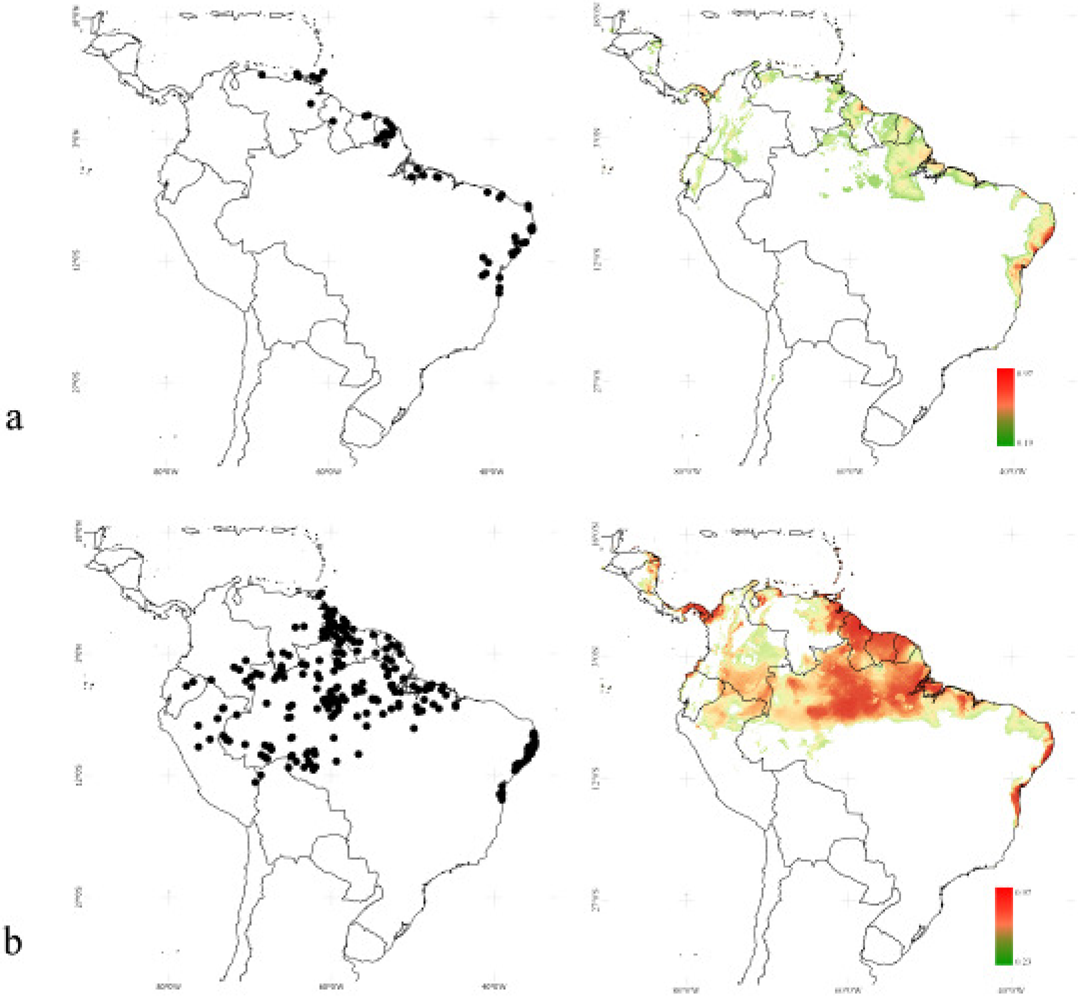

Figure 7.1. Geographical distribution and mean maps of the ecological niche modelling of *Aechmea aquilega* (a) and *A. mertensii* (b). Black dots represent occurrence points based on herbarium data taxonomically validated and field surveys conducted between 2012 and 2014. These data were used in the datasets of the two species to perform the modelling and subsequent projection. The maps of ecological niche modelling were made on the current climate scenario and represent means of each three partitions of *A. aquilega* and *A. mertensii* models, respectively (see Table 1 for n values and Table S1 for further information). The colour bar represents the mean values of each cell on maps.

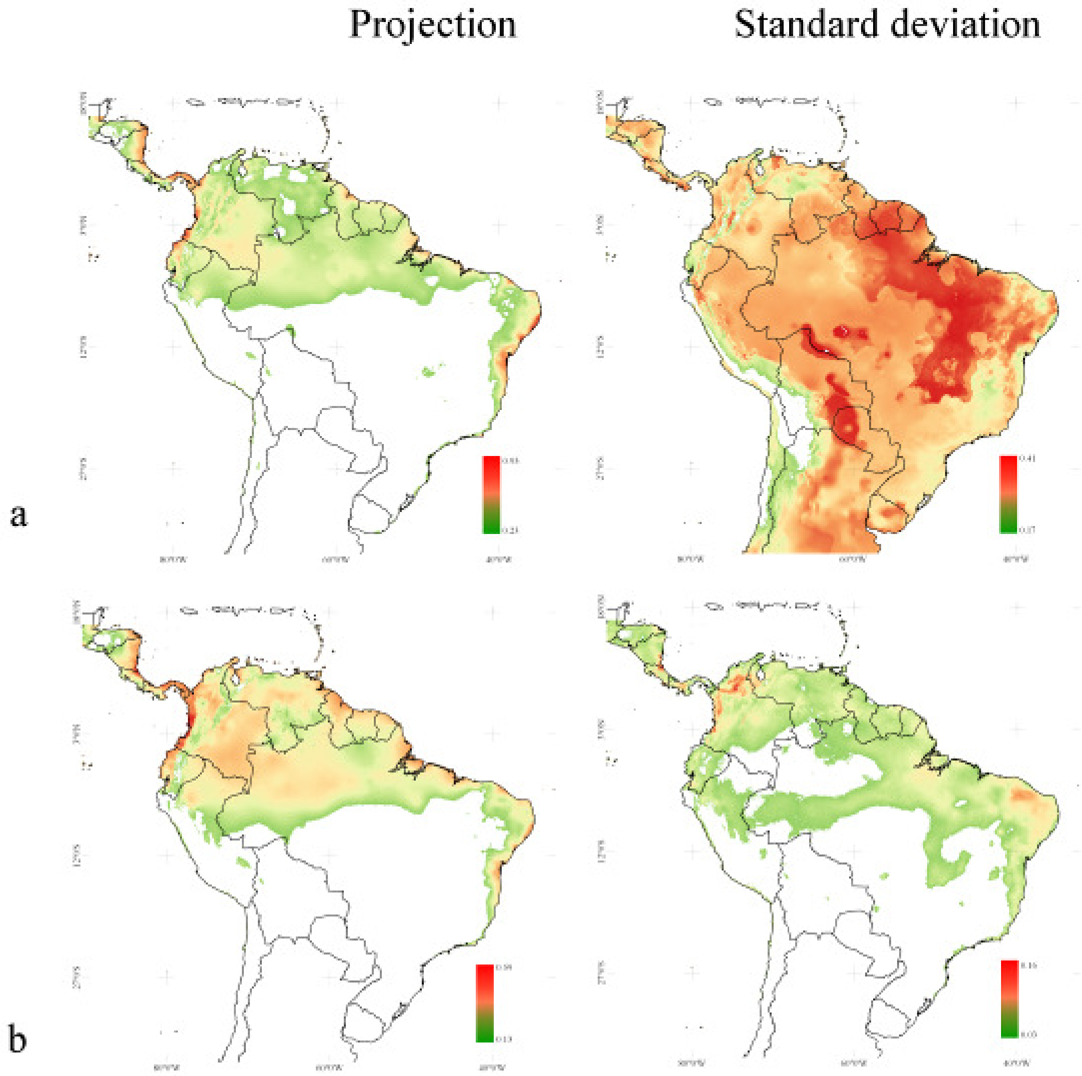

Figure 7.2. Means of the distribution of potential habitats of *Aechmea aquilega* (a) and *A. mertensii* (b) projected on climate scenario of Mid-Holocene and its respectives standard deviations. The maps represent means values of each pixels from from 54 and 26 projections of *A. aquilega* and *A. mertensii* models and projected in nine Mid-Holocene AOGCMs (see Table 1 for n values and Table S1 for further information). The colour bar represents the mean values and standard deviation of each cell on maps.

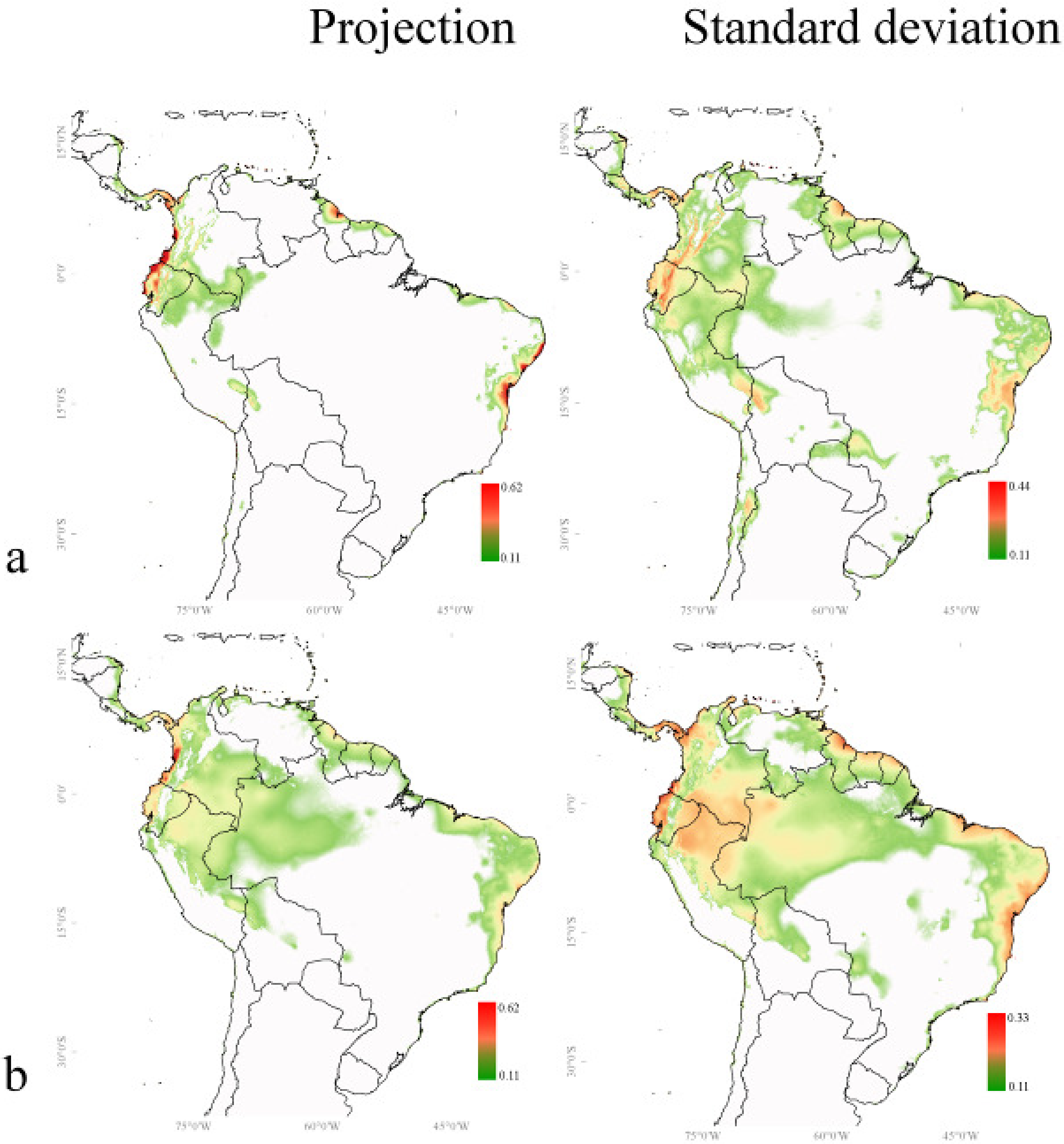

Figure 7.3. Means of the distribution of potential habitats of *Aechmea aquilega* (a) and *A. mertensii* (b) projected on climate scenario of Mid-Holocene and its respectives standard deviations. The maps represent means values of each pixels from 54 and 26 projections of *A. aquilega* and *A. mertensii* models and projected in Last Interglacial climatic scenarios (see Table 1 for n values and Table S1 for further information). The colour bar represents the mean values and standard deviation of each cell on maps.

Table 7.1. Number of projections (n) and relative frequencies of the patterns recorded for the different species, algorithms and circulation models (AOGCMs) and possible combinations. The chi-square (χ^2) for each species, algorithm and circulation models was calculated using four degrees of freedom. NC, Northeast along the coast; NI, Northeast through the interior; and CW, Central-West.

	NC	NI	NC+NI	CO	CO+NI	n	χ^2	p-value
Species								
A. aquilega	69.8	4.6	13.9	7	4.6	57	158	2.2×10^{-15}
A. mertensii	60.9	0	21.74	4.3	13	29	118	2.2×10^{-15}
Algorithms								
glm	78.8	0	9	12.1	0	33	222	2.2×10^{-15}
maxent	50	6.2	25	0	18.7	32	768	1.3×10^{-14}
Climatic scenarios								
BCC-CSM	100	0	0	0	0	6	400	2.2×10^{-15}
CCSM	0	25	50	0	25	8	87	2.2×10^{-15}
CNRM	75	0	0	25	0	4	212	2.2×10^{-15}
HadGEM-CC	33.3	60	0	6.7	0	15	138	2.2×10^{-15}
HadGEM-ES	100	0	0	0	0	4	400	2.2×10^{-15}
IPSL-CM5A-LR	66.7	0	0	33.3	0	6	178	2.2×10^{-15}
MIROC-ESM	0	0	71.4	0	28.6	7	196	2.2×10^{-15}
MPI-ESM-P	100	0	0	0	0	9	400	2.2×10^{-15}
MRI-CGCM	75	0	25	0	0	4	212	2.2×10^{-15}
LIG	72.7	0	9	0	18.2	11	185	2.2×10^{-15}

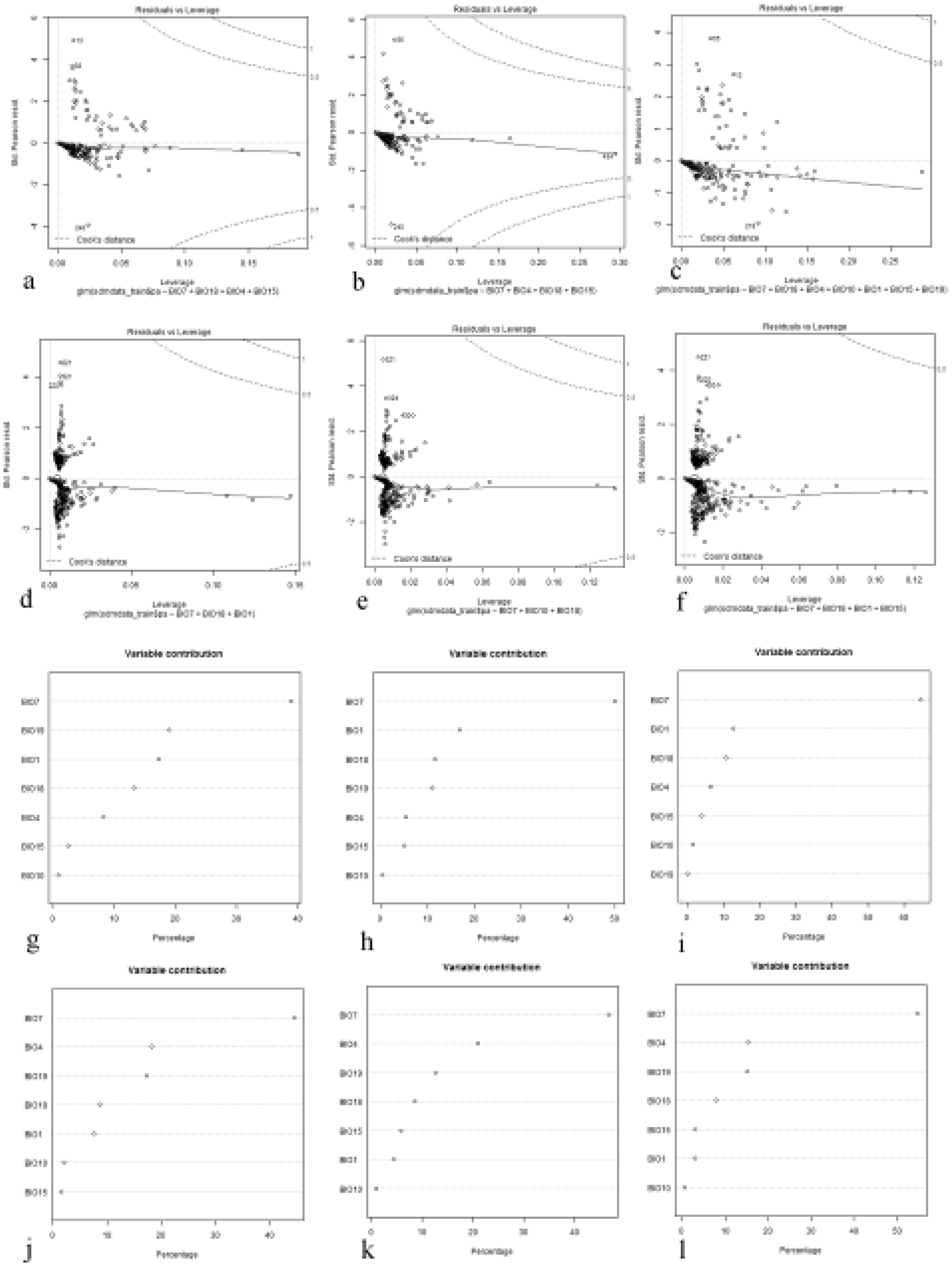

Figure 7.S1. Variables contributions and responses of GLM and MAXENT models. Variable contributions and response of GLM models of *A. aquilega* in first (a), second (b) and third (c) partitions; variable contributions and response of GLM models of *A. mertensii* in first (d), second (e) and third (f) partitions. Variable contributions of MAXENT models of *A. aquilega* in first (g), second (h) and third (i) partitions; variable contributions of MAXENT models of *A. mertensii* in first (j), second (k) and third (l) partitions.

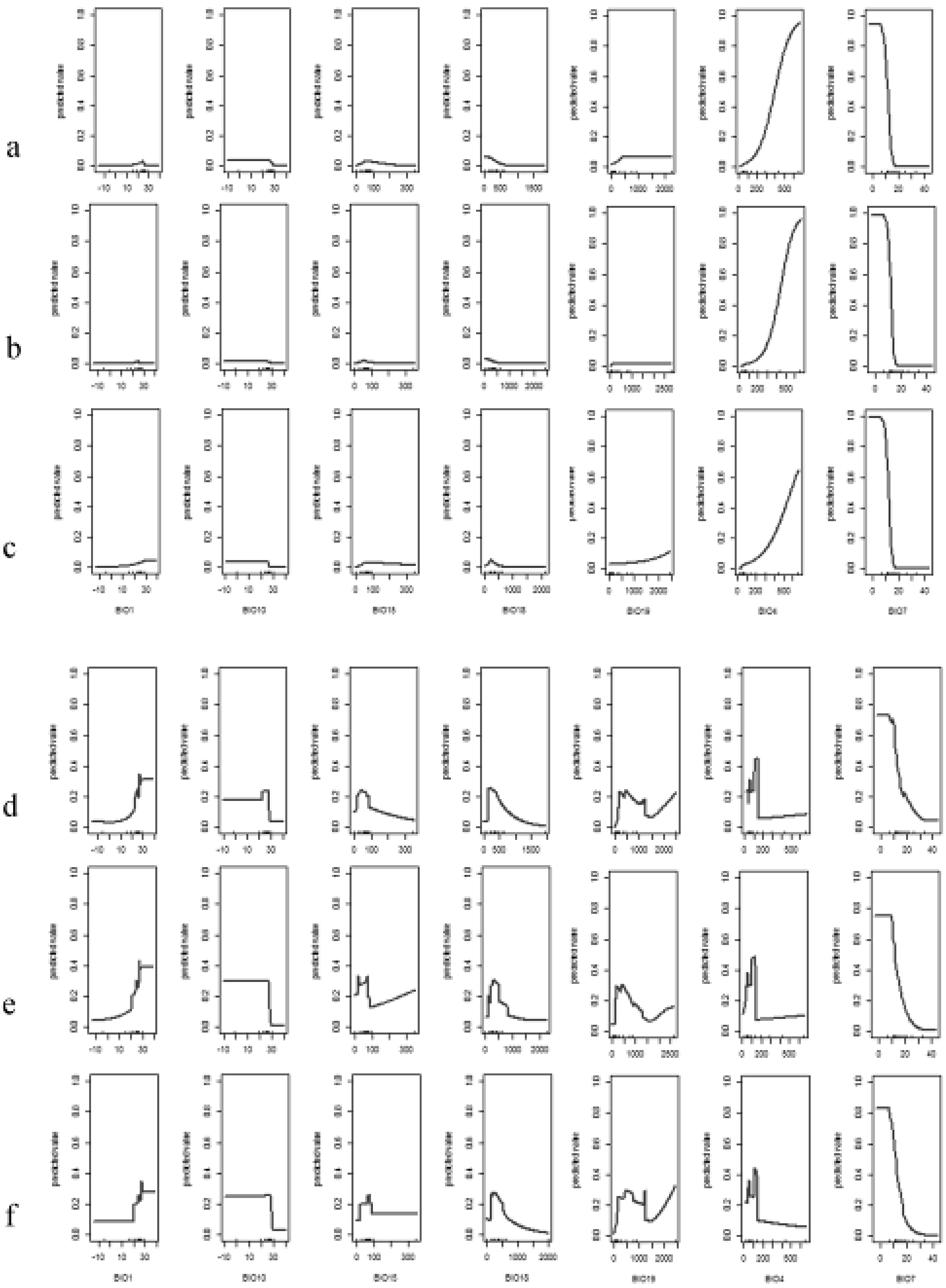

Figure 7.S2. Variable response of MAXENT models of each partition. Variable response of MAXENT models of *A. aquilega* in first (a), second (b) and third (c) partitions; variable response of MAXENT models of *A. mertensii* in first (d), second (e) and third (f) partitions.

Table 7.S3. Complementary statistics information of each model selected and projected in nine AOGCMs.

Species	**Kappa**	**Species sensitivity**	**Omission**	**Prevalence**	**Equal Sens. Species**	**Sensitivity**	**AUC**	**TSS**	**Algorithm**	**Partition**
A. aquilega	0.1887	0.0803	0.0460	0.1001	0.0838	0.0809	0.9194	0.7522	glm	1
A. aquilega	0.3383	0.0822	0.0822	0.0995	0.1575	0.1114	0.8845	0.7152	glm	1
A. aquilega	0.1018	0.1018	0.0430	0.1018	0.1117	0.1096	0.9250	0.8019	glm	1
A. aquilega	0.2725	0.0410	0.0410	0.1049	0.0942	0.0483	0.8744	0.6933	glm	1
A. aquilega	0.1533	0.0851	0.0159	0.1028	0.1337	0.0876	0.9053	0.7534	glm	1
A. aquilega	0.3149	0.1009	0.1009	0.1045	0.1550	0.1100	0.9303	0.7791	glm	1
A. aquilega	0.2009	0.1292	0.0449	0.1059	0.1582	0.0633	0.9137	0.7118	glm	1
A. aquilega	0.3193	0.1793	0.0449	0.1051	0.2171	0.1074	0.9105	0.7240	glm	1
A. aquilega	0.4124	0.0525	0.0525	0.1065	0.1065	0.0860	0.9102	0.7125	glm	1
A. aquilega	0.3810	0.0784	0.0784	0.1046	0.1504	0.0854	0.9204	0.7529	glm	2
A. aquilega	0.3805	0.0820	0.0352	0.1061	0.1061	0.0563	0.8639	0.6160	glm	2
A. aquilega	0.3180	0.1051	0.0522	0.1060	0.1233	0.0614	0.9000	0.6870	glm	2
A. aquilega	0.3470	0.0912	0.0680	0.1080	0.1324	0.0914	0.9171	0.7386	glm	2
A. aquilega	0.3937	0.0977	0.0977	0.1040	0.1442	0.1113	0.9168	0.7824	glm	2
A. aquilega	0.2014	0.0505	0.0177	0.1060	0.0790	0.0513	0.8751	0.6436	glm	2
A. aquilega	0.4345	0.0657	0.0657	0.1046	0.1430	0.0966	0.9014	0.6994	glm	2
A. aquilega	0.4852	0.0397	0.0397	0.1034	0.1004	0.0545	0.8355	0.6570	glm	2
A. aquilega	0.2555	0.0317	0.0178	0.1040	0.1042	0.0337	0.8891	0.6684	glm	2
A. aquilega	0.5256	0.0979	0.0225	0.1014	0.2103	0.1014	0.8986	0.7066	glm	3
A. aquilega	0.2638	0.1219	0.0397	0.1097	0.1651	0.1246	0.8932	0.7064	glm	3
A. aquilega	0.2362	0.0878	0.0878	0.1028	0.1705	0.0975	0.9109	0.7108	glm	3
A. aquilega	0.2693	0.1497	0.0344	0.1070	0.2062	0.1511	0.9272	0.7498	glm	3
A. aquilega	0.2145	0.0461	0.0461	0.1034	0.1218	0.0663	0.9021	0.6909	glm	3
A. aquilega	0.2783	0.0801	0.0532	0.1057	0.1647	0.0917	0.8976	0.6730	glm	3
A. aquilega	0.3760	0.0819	0.0819	0.1083	0.1431	0.1083	0.9357	0.7975	glm	3
A. aquilega	0.3717	0.1238	0.1238	0.1042	0.1723	0.1460	0.9316	0.7866	glm	3
A. aquilega	0.2665	0.1489	0.1489	0.1030	0.1660	0.1560	0.9439	0.8313	glm	3
A. aquilega	0.2129	0.2129	0.0664	0.1064	0.2129	0.2141	0.9571	0.8695	maxent	1
A. aquilega	0.4932	0.2424	0.2424	0.1026	0.3300	0.3319	0.9789	0.8802	maxent	1
A. aquilega	0.3049	0.3049	0.0696	0.0992	0.3023	0.3535	0.9663	0.8995	maxent	1

Species	Kappa	Species sensitivity	Omission	Prevalence	Equal Sens. Species	Sensitivity	AUC	TSS	Algorithm	Partition
A. aquilega	0.1622	0.1622	0.0327	0.1044	0.0982	0.0549	0.9297	0.7403	maxent	1
A. aquilega	0.6123	0.2300	0.0149	0.0973	0.2498	0.2360	0.9395	0.8037	maxent	1
A. aquilega	0.4546	0.1227	0.1227	0.0997	0.1351	0.1351	0.9716	0.8862	maxent	1
A. aquilega	0.2936	0.1640	0.0392	0.1015	0.1731	0.1731	0.9505	0.8456	maxent	1
A. aquilega	0.5247	0.1638	0.0338	0.1060	0.1648	0.1648	0.9562	0.8396	maxent	1
A. aquilega	0.2413	0.1943	0.1943	0.0966	0.1956	0.1956	0.9685	0.9162	maxent	1
A. aquilega	0.4512	0.0534	0.0255	0.1071	0.0887	0.0556	0.9084	0.7090	maxent	2
A. aquilega	0.2930	0.1077	0.0180	0.1077	0.1172	0.1162	0.9217	0.8054	maxent	2
A. aquilega	0.3967	0.2357	0.1016	0.1052	0.2664	0.2396	0.9446	0.8235	maxent	2
A. aquilega	0.2963	0.1190	0.1191	0.1062	0.1805	0.1439	0.9633	0.8313	maxent	2
A. aquilega	0.4683	0.1080	0.1080	0.1080	0.1484	0.1138	0.9602	0.8373	maxent	2
A. aquilega	0.3586	0.1890	0.0514	0.1050	0.1894	0.0648	0.9437	0.7735	maxent	2
A. aquilega	0.3043	0.2217	0.0716	0.1119	0.1853	0.1018	0.9620	0.8157	maxent	2
A. aquilega	0.1893	0.1893	0.0205	0.1062	0.1893	0.0577	0.8949	0.6994	maxent	2
A. aquilega	0.3747	0.0413	0.0414	0.1110	0.0895	0.0551	0.9110	0.7229	maxent	2
A. aquilega	0.3376	0.2337	0.0056	0.1085	0.1908	0.1283	0.9430	0.8169	maxent	3
A. aquilega	0.5562	0.1513	0.0206	0.1030	0.1513	0.0269	0.9136	0.6804	maxent	3
A. aquilega	0.1891	0.0513	0.0513	0.0920	0.0920	0.0740	0.9512	0.8503	maxent	3
A. aquilega	0.2260	0.2260	0.0248	0.0999	0.1492	0.0999	0.9546	0.8289	maxent	3
A. aquilega	0.1930	0.0331	0.0331	0.0967	0.1343	0.0376	0.9039	0.6826	maxent	3
A. aquilega	0.2069	0.1352	0.0450	0.1061	0.1473	0.1473	0.9477	0.8336	maxent	3
A. aquilega	0.3544	0.2397	0.0876	0.0990	0.2500	0.2500	0.9559	0.8516	maxent	3
A. aquilega	0.4091	0.1602	0.0134	0.0982	0.1627	0.0157	0.9281	0.7570	maxent	3
A. aquilega	0.4938	0.1624	0.1624	0.0975	0.2431	0.2166	0.9663	0.8683	maxent	3
A. mertensii	0.5817	0.4807	0.0395	0.3957	0.5262	0.3089	0.8792	0.6079	glm	1
A. mertensii	0.5599	0.5599	0.0453	0.3852	0.5846	0.4341	0.8765	0.6296	glm	2
A. mertensii	0.5007	0.5007	0.0512	0.3916	0.5113	0.3109	0.8965	0.6664	glm	3
A. mertensii	0.5197	0.5197	0.0417	0.3990	0.5040	0.2047	0.8596	0.6005	glm	3
A. mertensii	0.4890	0.4435	0.0331	0.4072	0.4831	0.2575	0.8821	0.6238	glm	3
A. mertensii	0.3826	0.3467	0.0165	0.3922	0.3495	0.1818	0.8870	0.6095	maxent	1
A. mertensii	0.2927	0.2927	0.0280	0.3928	0.2621	0.1544	0.8937	0.6353	maxent	1
A. mertensii	0.4138	0.3714	0.0762	0.3902	0.2896	0.1908	0.9218	0.6754	maxent	1

Species	**Kappa**	**Species sensitivity**	**Omission**	**Prevalence**	**Equal Sens. Species**	**Sensitivity**	**AUC**	**TSS**	**Algorithm**	**Partition**
A. mertensii	0.1793	0.1793	0.0466	0.3900	0.2561	0.1901	0.9130	0.6797	maxent	1
A. mertensii	0.2086	0.2086	0.0386	0.3940	0.3201	0.2236	0.9161	0.6958	maxent	1
A. mertensii	0.3105	0.2212	0.0179	0.3917	0.2405	0.1567	0.9117	0.6589	maxent	1
A. mertensii	0.4541	0.1894	0.1590	0.3966	0.3553	0.2668	0.8999	0.6374	maxent	1
A. mertensii	0.4162	0.3329	0.0157	0.3909	0.2940	0.1535	0.8856	0.6107	maxent	1
A. mertensii	0.2319	0.2319	0.0338	0.3926	0.3014	0.1763	0.8920	0.6294	maxent	2
A. mertensii	0.3724	0.2245	0.0157	0.3940	0.3336	0.2337	0.8765	0.6099	maxent	2
A. mertensii	0.3605	0.3605	0.0832	0.3978	0.3613	0.2543	0.9051	0.6739	maxent	2
A. mertensii	0.2618	0.0896	0.0365	0.3947	0.2930	0.1548	0.8943	0.6228	maxent	2
A. mertensii	0.4218	0.3286	0.0211	0.3894	0.3305	0.2419	0.9221	0.6772	maxent	2
A. mertensii	0.4047	0.2745	0.0582	0.3949	0.2771	0.1981	0.9178	0.6586	maxent	2
A. mertensii	0.2577	0.1345	0.0188	0.3952	0.2714	0.1511	0.8929	0.6198	maxent	3
A. mertensii	0.2742	0.2742	0.0184	0.3848	0.3201	0.2351	0.9114	0.6809	maxent	3
A. mertensii	0.2197	0.2197	0.0193	0.3855	0.2532	0.1380	0.8857	0.6236	maxent	3
A. mertensii	0.2590	0.1889	0.0183	0.3918	0.3081	0.2212	0.9032	0.6505	maxent	3
A. mertensii	0.2071	0.2071	0.0185	0.3870	0.2993	0.2177	0.8785	0.6258	maxent	3
A. mertensii	0.2161	0.1279	0.0167	0.3854	0.2509	0.1396	0.8875	0.6019	maxent	3
A. mertensii	0.3275	0.3275	0.0689	0.3914	0.3480	0.2664	0.9032	0.6589	maxent	3

8 Polyphyly and morphological convergence in *Aechmea* subg. *Chevaliera*

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Abstract

Aechmea subg. *Chevaliera* is one of eight subgnera recognized to *Aechmea*. *Aechmea* subg. *Chevaliera* is unique based on its huge plants with massive, compact and strobiliforms inflorescences. However, a limited taxon sampling is hampering an understanding about the monophyly of the subgnera. In this work we test whether *Aechmea* subg. *Chevaliera* and its species complexes are monophyletic. Our results should highlight (1) *Chevaliera* relationships, (2) disjunct distribution evolutionary significance in this subgenus, and (3) the evolution of morphological space peculiar to *A.* subg. *Chevaliera*. We used two nuclear (ETS and phyC) and one plastidial (matK) regions to construct a dataset and carry out a bayesian and maximum likelihood analysis for a dataset of 22 species of *A.* subg. *Chevaliera* with all lineages of Bromelioideae recovered in recent studies. Morphological reconstruction and a comparison of morphological space of body volume in Bromelioideae were also conducted. *Aechmea* subg. *Chevaliera* is recovered in our results as a polyphyletic group with strong statistical support. Morphological traits used traditionally in taxonomy and delimitation of subg. *Chevaliera* have been arisen multiple times in evolutionary history of Bromelioideae. Our phylogenetics results do not support the most accepted circumscription of *A. subg. Chevaliera* thus do not confirm the disjunct distribution between Atlantic and Amazon Forest. Finally, morphological convergence between sympatric groups in Bromelioideae is one of the most striking finding in this study.

Keywords

Bromelioideae, phylogeny, biogeography, evolution, neotropics

Introduction

Bromeliaceae is a main example of adaptive radiation in Neotropics, where its 58 genera and 3.352 species occur except for *Piticairnia feliciana*, the only one found in Africa (Butcher & Gouda, cont. updated, Givnish *et al.* 2007, 2011, 2014). Recent advances in phylogeny recognized eight monophyletic subfamilies in Bromeliaceae. Bromelioideae is one of them with 936 species and 33 genera and has Puyioideae as a sister group (Barfuss *et al.* 2005, Crayn *et al.* 2004 Escobedo-Sartí 2013, Givnish et al 2007, 2011, 2014, Horres *et al.* 2000, 2007, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008, Silvestro *et al.* 2014, Terry *et al.* 1997). Divergence time studies estimated a probable origin of Bromelioideae at 10Ma in Andean region and further colonization process in eastern Brazil which made the Atlantic Forest the richest area in species and endemism for the subfamily (Givnish *et al.* 2007, 2011, 2014, Silvestro *et al.* 2014).

Many authors have been issued difficulties in disentangling phylogenetic relationships in Bromelioideae (Aguirre-Santoro *et al.* 2015, 2016, Evans *et al.* 2015, Faria *et al.* 2004, Heller *et al.* 2015, Horres *et al.*, 2000, 2007, Louzada *et al.* 2014, Sass & Specht 2010, Schulte *et al.*, 2005, 2009; Schulte & Zizka, 2008). Despite that, growth form defines two main lineages in subfamily: in the early diverging lineages, species are non-tank forming, while tank forming are found in a second lineage called Bromelioideae-core (Sass & Specht 2010, Schulte *et al.* 2009, Silvestro *et al.* 2014).

Aechmea is the most diverse genus of Bromelioideae-core with ca. 288 species, but it is nonmonophyletic (Aguirre-Santoro *et al.* 2015, 2016, Butcher & Gouda cont. updated, Evans *et al.* 2015, Faria *et al.* 2004, Heller *et al.* 2015, Horres *et al.*, 2000, 2007, Louzada *et al.* 2014, Sass & Specht 2010, Schulte *et al.*, 2005, 2009; Schulte and Zizka, 2008, Silvestro *et al.* 2014). Nevertheless, the classification and the concept proposed by Smith & Downs (1979) to *Aechmea* is still used and tested in taxonomic and phylogenetic studies showing a geographical conservatism pattern (Aguirre-Santoro 2015, 2016, Evans *et al.* 2015, Goetze *et al.* 2016, Heller *et al.* 2015, Sass & Specht 2010).

Aechmea subg. *Chevaliera* is one of the eight subgenera described and typified by Smith & Downs (1979). *Chevaliera*, as a genus, was proposed by Gaudichaud (1844) but validly published by Beer (1857). In 1879, Baker established *Chevaliera* as a subgenus of *Aechmea*, which was followed by other authors (Baker 1889, Mez 1892), even by Smith & Downs (1979). Smith & Kress (1989, 1990) restablished *Chevaliera* as a genus but with no explanation. However, recent taxonomic studies did not follow this categorization of *Chevaliera* as genus but using *Chevaliera* as subgenus (Canela *et al.* 2003, Silva 2003, Sousa 2004).

The concept most accepted of *Aechmea* subg. *Chevaliera* is based on a morphological unity and ca. 30 species that share simple, strobiliform, or rarely digitated, polystichous, and often perene inflorescences; floral bracts coriaceous or ligneous; free or conate sepals; and petals appendages reduced or absent (Leme 2010, Leme & Kollman 2009, Leme & Kollman 2011, Leme *et al.* 2010, 2014, Maciel *et al.* 2014, Smith & Downs 1979, Sousa & Wanderley 2014). Additionally, the subgenus *Chevaliera* is recognized as the only group in Bromelioideae that combines massive and strobiliform inflorescences with large rosettes forming dense clumps (Maciel *et al.* 2015, Silva 2003, Smith & Downs 1979, Sousa 2004). These species occur in Central America, Andes, Amazon and Atlantic Forest in a disjunct distribution between north and east of South America. The Atlantic Forest along Brazilian east coast is the diversity center (Canella *et al.* 2003, Leme 2010, Leme & Kollman 2009, Leme & Kollman 2011, Leme *et al.* 2010, 2014, Maciel *et al.* 2014, 2015, Silva 2003, Smith & Downs 1979, Sousa 2004, Sousa & Wanderley 2014).

Silva (2003) provided a consistent and broad comment on *A.* subg. *Chevaliera* concept of Smith & Downs (1979). According with him, Amazon-Andean species are different from the Atlantic species and these differences are good enough to split the subgenus in two groups. This point of view is similar to Mez (1896), who recognized Andean species as subgenus of *Aechmea* (*A. fernandae*, *A. germinyana*, *A. magdalenae*, *A. rubiginosa* and *A. veitchii* under *A.* subg. *Purpurospadix*) and kept the Atlantic species as *Chevaliera*. The results found by Silva (2003) become more relevant from perspective of geographical conservatism in phylogeny of Bromelioideae (Sass & Specht 2010).

Many taxonomic complexes in the subgenus associated to a strong geographical conservatism give more support to the hypothesis that *A.* subg. *Chevaliera* is not a natural group. At least three species complexes are recognized in *A.* subg. *Chevaliera*: *A. multiflora* complex (*A. multiflora*, *A. depressa*, *A. nigribracteata* and *A. saxicola*), *A. conifera* complex (*A. conifera, A. heterosepala, A. recurvipetala* and *A. serragrandensis*), and a morphological group based in *A. sphaerocephala* (Canella *et al.* 2003, Leme 2010, Leme & Kollman 2009, 2011, Leme & Siqueira-Filho 2001, Leme & Silva 2002, Maciel *et al.* 2014).

A better understanding of the subgenus *Chevaliera*, monophyly and its taxonomic complexes is hampered by a limited taxon sampling in molecular studies of Bromelioideae (Aguirre-Santoro *et al.* 2015, 2016, Evans *et al.* 2015, Faria *et al.* 2004, Horres *et al.* 2000, 2007, Sass & Specht 2010, Schulte *et al.* 2005, 2009, Schulte & Zizka, 2008, Silvestro *et al.* 2014, Sass & Specht 2010). These studies with irregular samplings show conflicting patterns. For example, Sass & Specht (2010) included in their analysis four species, none from the Atlantic Forest, and recovered a polyphyletic *Chevaliera* in two lineages placed in Bromelioideae core and in early diverging Bromelioideae. Silvestro *et al.* (2014), based on two species and none of them with an Andean-Amazon distribution, found subgneus *Chevaliera* as paraphyletic in Bromelioideae-core.

Thus, the main goal here is figure out whether *Aechmea* subg. *Chevaliera* and its species complexes are monophyletic. Moreover, we want to provide a better understanding on morphological characters evolution that are traditionally used on taxonomy of the group. Our results should highlight (1) *Chevaliera* relationships, (2) disjunct distribution evolutionary significance in this subgenus, and (3) the evolution of morphological space peculiar to *Aechmea* subg. *Chevaliera*.

Material and methods

Sampling

The current subgenus *Chevaliera* concept circumscribes ca. 30 species. We sampled 22 species of the subgenus (75% of the taxa). This sampling also includes all geographical and morphological range of the subgenus. Additionally, we included species of main lineages found in Silvestro *et al.* (2014). Our dataset is composed by 69 species (one sample each) of early diverging and core Bromelioideae lineages. All lineages morphologically related to subg. *Chevaliera* with simple inflorescences were included too (eg. *Aechmea* subg. *Macrochordion*, *Aechmea* subg. *Pothuava,* and *Quesnelia*). Among the samples, 37 were selected from Genebank collection based on Silvestro *et al.* (2014), six were provided from the living collection from

Jardim Botânico do Rio de Janeiro (Brazil) and 26 were collected from natural population by the authors. The supplementary material shows the sample list (Table 3).

Extraction and sequencing

We used only fresh material to extract DNA for new sequences. Fresh leaves fragments were stored in a solution of NACL/CTAB (hexacetyltrimethylammonium bromid). We applied a standard protocol developed by Doyle & Doyle (1987) and modified by Horres *et al.* (2000), which use CTAB (cetyltrimethylammonium bromid) to total DNA extraction.

The plastidial region matK amplification followed Schulte *et al.* (2009) and the nuclear regions ETS and phyC amplification was based in primers and protocols described by Louzada *et al.* (2014), Silvestro *et al.* (2014) and Sass & Specht (2010).

Alignment and congruence

We edited and aligned sequences of all three DNA regions on software Geneious v7.1.7 (Kearse *et al.* 2012) using the function ClustalW (Thompson *et al.* 1994). We proceeded manual adjusting in each alignment when needed. We selected species with sequences for all regions to compound individual datasets for each region in order to perform congruence analyses. Then, trees of each dataset were inferred using Maximum Likelihood analysis (ML; Stamatakis 2014) throughout Cipres Science Gateway (Miller *et al.* 2011). Finally, the congruence was verified with Shimodaira-Hasegawa test (SH-test, Shimodaira & Hasegawa 1999) implemented in RaxML (Stamatakis *et al.* 2008) and the comparison was made following the example of Wanntorp *et al.* (2014). Results are described in Table 1. The visual inspection and the SH-test results show no strong incongruence in data used. Thus, we concatenated the final alignments on software Geneious v7.1.7 (Kearse *et al.* 2012).

Phylogenetic Analysis

The dataset was partitioned in order to analysing each DNA region independently. For each partition we selected a substitution model using AIC scores (Akaike 1973) implemented on software JModeltest (Posada 2008) (Table 2). We run a bayesian analyses (BI) on Mr. Bayes 3.2.3 (Ronquist *et al.* 2012) through Cipres Science Gateway (Miller *et al.* 2011). Four independent MCMC channels ran for 100.000.000 generation and at each 10000 generations was selected one tree. After analyses we discarded 25% of 10.001 trees in the final dataset and used the remaining to access the maximum credibility tree with the posterior probability results at each node. The convergence among each MCMC channel was accessed with software Tracer (Rambaut & Drummond 2009).

We carried out a Maximum Likelihood (ML) on software RaxML HPC2 on XSEDE (Stamatakis 2014) through Cipres Science Gateway (Miller *et al.* 2011), based on a rapid search for 1000 repetitions to estimate bootstrap values (BS).

Ancestral character reconstruction and morphological space analyses

A binary bayesian MCMC ancestral character reconstruction analysis was ran out on software RASP (Yu *et al.* 2015). To this analyses we used the previous dataset of 10.001 trees generated from phylogenetic bayesian analyses and selected 1000 trees randomly to calculate the mean frequency of ancestral variation. For each character we selected a number of states according to verified on morphological survey. Two independent channels of 10.000.000 generations sampled at each 1000 generations were run. The final result is a combination of each channel.

The characters and its states selected were: 1) floral bract margins (A=entire, B=dentate); 2) width of central axis of inflorescence (A=narrow, B=enlarged). The inflorescence morphology are widely used on *A.* subg. *Chevaliera* taxonomy (Canella *et al.* 2003, Leme 2010, Leme & Kollman 2009, Leme & Kollman 2011, Leme *et al.* 2014, Maciel *et al.* 2014, Silva 2003, Smith & Downs 1979, Sousa 2004, Sousa & Wanderley 2014). We codified the character states based on literature, living specimens analysis and herbaria survey from collections ALCB, ASE, CEPEC, EAC, HRB, HUEFS, IAN, INPA, IPA, JPB, MBML, MIRR, MPEG, NY, PEUFR, RB, UFP, UFRN, UFRR, US e VIES (acronyms according Thiers continuously updated and available in http://sweetgum.nybg.org/ih/).

The vegetative body of bromeliads is essentially compound by leaves, with steam reduced or absent (Benzing 2000). Thus, the best proxies to compare differences in body volume or size in Bromeliaceae are the leaves length and width measures. In order to test if morphological space of subgenus *Chevaliera* is unique among Bromelioideae, we did a database with minimum-maximum lenght of leaves (sheat + blade leaves), and a minimum-maximum width of leaf blades of 780 Bromelioideae species. These data were collected from the herbaria and literature surveys. Lastly, we compare the measures in three levels: 1) all

Bromelioideae; 2) only Bromelioideae from Alantic Forest; and 3) only Bromelioideae from ombrophilous habitats in the Atlantic Forest, which is the main habitat of subgenus *Chevaliera*. The species names were based on Butcher & Gouda (cont. upd.), distribution and habitat followed BFG (2015).

Results

Sequence data and congruence

The nuclear region ETS showed a significant variability and high number of informative characters, while matK is lesser informative among the three datasets. The statistical results and information about SH-test are summarized on Table 1.

The trees of each region show incongruence only on resolution quality. For some clades in Bromelioideae-core, ML analysis did not show support. However, the two clades with species of subgenus *Chevaliera* had support in both analyses and were always recovered in single datasets analysis. The ML and bayesian trees did not show incogruence and we adopted the topology of maximum credibility tree from bayesian analisis as phylogenetic hypothesis of this work.

Phylogenetic relationships

Aechmea subg. *Chevaliera* is recovered in our results as a polyphyletic group with strong statistical support (species in bold in Figure 1). The results also show two main groups with different sets of species formerly classified as subgenus *Chevaliera* (Figure 1). Other species appear in different parts of Bromelioideae phylogeny (Figure 1). Our results also recovered the early diverging and core Bromelioideae lineages, but just with moderated support.

Two species formerly classified as *Chevaliera* emerge among early diverging lineages of Bromelioideae. *Aechmea fernandae* and *A. magdalenae* show different relationships in this group. *Aechmea fernandae* emerges with species of *Bromelia* in a highly supported clade (BS 93, PP 1, Figure 1). While *A. magdalenae* seems more related to a lineage composed by *Ananas* species and other relatives, but this clade does not show support (Figure 1).

The remainder species classified formerly in *Chevaliera* are in Bromelioideae core. *Aechmea rodriguesiana* emerges in a clade with Amazonian species of *Araeococcus* and species of *Gravisia* complex (PP 0.98); *Aechmea ornata* belongs to a clade formed by species of *A*. subg. *Macrochordion* and *Pothuava* with strong statistical suport (BS 100, PP 1) (Figure 1). The majority of *Chevaliera* species is gathered in two groups, which are named here as *A. multiflora* group and *A. sphaerocephala* group (Figure 1).

The group *A. multiflora* is formed by seven species (*A. gustavoi*, *A. multiflora, A. nigribracteata*, *A. depressa*, *A. hostilis, A. prasinata* and *A. saxicola*). It shows strong statistical support and good resolution in terminal taxa (BS 88, PP 1, see Figure 1) allowing recognize two main events of speciation. The sister lineage of *A. multiflora* group is not solved yet, even though a relationship with species of *Ronnbergia* clade is pointed out but lacks statistical support.

The *A. sphaerocephala* group has moderated to high support (BS 78, PP 1, see Figure 1) and it is formed by eleven species in our analyses (*A. digitata*, *A. serragrandensis*, *A. heterosepala*, *A. muricata*, *A. sphaerocephala*, *A. castanea*, *A. cariocae*, *A. paratiensis*, *A. leucolepis*, *A. perforata* e *A. aguadocensis*). The *A. sphaerocephala* group emerges in a polytomy with clades *Macrochordion+Pothuava* (*A. maasii*, *A. lamarchei*, *A. bromeliifolia*, *A. nudicaulis*, *A. pineliana* and *A. ornata*) and species of other lineages. This makes the sisterhood relationship of *A. sphaerocephala* group not solved. The internal resolution of *A. sphaerocephala* group leads us to recognize two main clades.

Ancestral character reconstruction and morphological space analyses

Morphological traits used traditionally in taxonomy and delimitation of *Chevaliera* have been arisen multiple times in evolutionary history of Bromelioideae (Figure 2). The simple and strobiliform inflorescence originated several times along the Bromelioideae history with recurrent reversion events (Figure 2). In *A. multiflora* and *A. sphaerocephala* groups, this kind of inflorescence had only one origin in each clade and point out a history of convergence between them. The floral bract margin dentate also had multiple origins in Bromelioideae, but suggests one origin and evolution restricted to *A. multiflora* group in Bromelioideae core (Figure 2).

In *A. multiflora* and *A. sphaerocephala* groups was noted also a convergence in morphological space of body size (Figure 3). Clearly, the results show both groups as species richest among Bromelioideae from the Atlantic Forest regarding morphological space of huge body size. When body size is compared to all Bromelioideae, both groups are inserted in a general variation. They become more isolated in this morphological space when only species of Atlantic Forest are selected. And finally, there are few species of *Bromelia*, *Aechmea* alliance and *Hohenbergia* with the similar morphological space than *A. multiflora* and *A. sphaerocephala* in Atlantic Forest.

Discussion

Phylogenetics relationships of *Aechmea* subg. *Chevaliera*

Insufficient resolution in plastidial phylogenies of Bromeliaceae is quite often and creates many difficulties in phylogenetics studies (Aguirre-Santoro *et al.* 2015, Barfuss *et al.* 2005, Evans *et al.* 2015, Faria *et al.* 2004, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008, Horres *et al.* 2007). In another hand, multi-loci option had been more effective in improving resolution in several specific studies in Bromelioideae and other subfamilies of Bromeliaceae (Aguirre-Santoro *et al.* 2016, Chew *et al.* 2010, Louzada *et al.* 2014, Sass & Specht 2010, Schulte *et al.* 2009, Silvestro *et al.* 2014). Sass & Specht (2010) and Chew *et al.* (2010) made progress in phylogenetic resolution with emphasis in *Aechmea* and *Tillandsia* by applicating ETS. Recently, Silvestro *et al.* (2014) and Louzada *et al.* (2014) improved resolution in Bromelioideae phylogenies by using phyC.

Increase the dataset with nuclear regions (ETS and phyC) was useful on our analyses to establishing relationships and to demonstrating *A.* subg. *Chevaliera* clades position in subfamily Bromelioideae. Nevertheless, no conclusive answer about sister lineages of the main groups was found. However, this is the first study that integrates a broad taxonomic and geographic sampling of subgenus *Chevaliera* in overall Bromelioideae phylogeny, which could be the reason of small incongruence found between our results and those presented by Silvestro *et al.* (2014).

Silva (2003) issued a possible nonmonophyletic nature of *A.* subg. *Chevaliera* in a morphological study in which he demonstrated strong morphological differences between groups of Atlantic and Andean-Amazon species, such *A. fernandae*, *A. magdalenae* and *A. rodriguesiana*. The main differences highlighted by Silva (2003) are regarded to habit, sheath and blade leaf, floral bracts, flowers, ovaries and ovules. Sousa (2004) followed a traditional classification of *A.* subg. *Chevaliera* and expanded the circumscription to include species formerly classified as *A. subg. Pothuava* (Smith & Downs 1979, Wendt 1997). Our results confirm the proposals of Silva (2003) and reinforces that some species transferred from *A.* subg. *Pothuava* to *A.* subg. *Chevaliera*, as *A. ornata*, do not belong to any of the two recognized groups here. These species have smaller flowers and bracts than species of *A. multiflora* and *A. sphaerocephala* groups, and their flowers are not dorsiventrally compressed (Smith & Downs 1979).

Aechmea magdalenae and *A. fernandae* are nonforming tank plants (Silva 1993), in a different way from Atlantic species and even so *A. rodriguesiana.* Therefore, the position of these species in Bromelioideae early diverging lineages confirms previous morphological and phylogenetic studies (Sass & Specht 2010, Silva 1993).

Smith (1966) described *A. rodriguesiana* under *Gravisia* and Smith & Downs (1979) subordinated most of *Gravisia* species to *A.* subg. *Aechmea* except for *A. rodriguesiana* which was transferred to *A.* subg. *Chevaliera*. Sousa (2004), Sousa & Wanderley (2007) and Sousa *et al.* (2009) followed that arrangement and related *A. rodriguesiana* to *A. digitata* based on similar branching inflorescence pattern. However, our results confirm the original *A. rodriguesiana* systematic position closer to species of *Gravisia* complex than to formerly subgenus *Chevaliera* species (*A. multiflora* and *A. sphaerocephala* groups). The morphological similarity between *A. rodriguesiana* and *A. digitata* is clearly superficial. While on first species the inflorescence always has six up to 20 branches (Sousa & Wanderley 2007), in *A. digitata* the inflorescences have two branches, but the second one grows, occasionally, from a lateral bud on peduncle (Sousa *et al.* 2009).

The two groups recovered in our analysis are in accordance with previously recorded morphological patterns. *Aechmea multiflora* group emerges as one of the first lineages in Bromelioideae core with species of *Ronnbergia* alliance (Aguirre-Santoro *et al.* 2015, 2016) as a sister group, but lacks suppport. Canela *et al.* (2003) circumscribed the *A. multiflora* complex as formed by *A. multiflora*, *A. depressa*, *A. hostilis* and *A. saxicola*. This concept is confirmed here and expanded to include *A. gustavoi* and two more species as previously suggested (Maciel *et al.* 2014, Leme & Siqueira-Filho 2001, Sousa & Wanderley 2014).

Lack of a single and exclusive synampomorphy in *A. multiflora* group repeats a general rule in Bromelioideae (Aguirre-Santoro *et al.* 2015, Evans *et al.* 2015, Faria *et al.* 2004, Horres *et al.* 2007, Sass & Specht 2010, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008). Although, is possible to identify a set of homoplastic characters that confers morphological identity to group as: Atlantic Forest plants with tank habit, leaves with more than 1 m length; simple, compact, strobiliforms, multiflowered, and inserted inflorescences; main axis of inflorescence dilated (more than 5 cm width); floral bracts lignified with margins totally or partially dentate; and flowers dorsiventrally compressed with rigid sepals.

Aechmea sphaerocephala group has the type-species of the subgenus (*A. sphaerocephala*, Smith & Downs 1979) and should be formally named *A.* subg. *Chevaliera*. This group has a strong statistical support but inconclusive to its sister relationships because of a politomy with *A.* subg. *Macrochordion* and *Pothuava* (Faria *et al.* 2010, Smith & Downs 1979, Wendt 1997). *Aechmea sphaerocephala* and *A. multiflora* groups share many similar characters, but they are different regarding floral bract margins and petal shapes.

Aechmea sphaerocephala group gather two different clades that confirm stablished taxonomic complexes based on morphology. Leme & Kollman (2011) presented a key and a morphological circumscription to *A. conifera* complex, which included *A. conifera*, *A. heterosepala*, *A. recurvipetala* and *A. serragrandensis* (Leme 2010, Leme & Kollman 2011, Leme & Siqueira-Filho 2001). In our analyses, we have three of these species in a monophyletic lineage within *Aechmea sphaerocephala* group. Despite we have not the typical species, this complex is expanded here to include *A. digitata*.

On description of *A. aguadocensis*, Leme & Kollman (2009) proposed a morphological group formed by *A. sphaerocephala*, *A. aguadocensis*, *A. cariocae*, *A. castanea* and *A. muricata*. Neither formally nor informally named (Leme & Silva 2002, Leme & Kollman 2009), this group is confirmed here by our analysis though the lack of resolution in this clade does not allow confirm if it is monophyletic or paraphyletic. This group shares floral bracts acuminate or caudate and lilac or blue flowers (Leme & Silva 2002, Leme & Kollman 2009, Sousa 2004).

Several authors had been suggested nonconventional characters as a solution to genera delimitation in Bromeliaceae, specifically in Bromelioideae because homoplastic features are often used as diagnostic characters (Aguirre-Santoro *et al.* 2016, Brown & Gilmartin 1984, Evans *et al.* 2015, Faria *et al.* 2004, Heller *et al.* 2015, Horres *et al.* 2000, Sass & Specht 2010, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008). However, we confirm that morphological circumscription of taxa in Bromelioideae should be fixed by using a specific combination of characters instead only one.

Biogeographical implications

The phylogeny of *A. subg. Chevaliera* confirms former observations that disjunct distributions in Bromeliaceae have to be reviewed thoroughly (Aguirre-Santoro *et al.* 2015, Sass & Specht 2010). Our phylogenetics results do not support the circumscription of *A. subg. Chevaliera* presented by Smith & Downs (1979) and Sousa (2004) thus do not confirm the disjunct distribution between Atlantic and Amazon Forest. Clearly, Amazonian species traditionally placed under *A.* subg. *Chevaliera* arose several times on early diverging and core Bromelioideae. Notwithstanding, the two main groups recovered in our analyses are endemic to Atlantic Forest, where they are found in ombrophilous forests, *restingas* and semideciduous forests (BFG 2015, Leme 2010, Leme & Kollman 2011, Leme & Silva 2002, Leme & Kollman 2009, Leme & Siqueira-Filho 2001, Maciel *et al.* 2014, Sousa 2004, Sousa & Wanderley 2014).

Similar examples in refuse disjunct patterns of geographical distribution are growing as phylogenetic studies in Bromelioideae accumulate advancing. Aguirre-Santoro *et al.* (2015) showed *Ronnbergia* is not monophyletic, and the disjunct geographical distribution of this genus among Atlantic Forest, Central America and Caribbean is also a non natural pattern when considered the genus as it is. The same was verified for many taxa in Bromelioideae by Sass & Specht (2010), and the most relevant example was evidenced by the polyphyletic genus *Hohenbergia*. However, a clear trend contradicting those finding should be highlighted. While taxon morphologically defined by traditional taxonomy in Bromelioideae (Smith & Downs 1979) reveals being restricted to some particular geographical regions (Sass & Specht 2010), new delimitations of taxa in the subfamily suggests disjunct distributions are possible. For example, recent rearrangement in *Ronnbergia* alliance includes Andean, Atlantic and Caribbean groups disjunct distributed unlike traditional *Ronnbergia* genus concept (Aguirre-Santoro *et al.* 2016).

Phylogenetics relationships in subgenus *Chevaliera* are partially in accordance with geographical conservatism hypothesis in Bromelioideae (Schulte *et al.* 2005, 2009, Sass & Specht 2010). It means that endemic species to the Atlantic Forest with huge bodies and strobiliform infllorescences are not monophyletic rather than geographical conservatism hypothesis foresees. It also suits that morphological characters traditionally used on taxonomy of subgenus *Chevaliera* (Leme 2010, Leme & Kollman 2011, Leme & Silva 2002, Leme & Kollman 2009, Leme & Siqueira-Filho 2001, Maciel *et al.* 2014, Smith & Downs 1979, Sousa 2004, Sousa & Wanderley 2014) were overvalued leading to misinterpretation on relationship of species with strobiliform and compact inflorescence in *Aechmea*.

Evidences of morphological convergence in Atlantic Forest

In light of our results, there is a clear morphological convergence in *A. multiflora* and *A. sphaerocephala* groups, endemic to Atlantic Forest. Both groups share the same tank habit, huge vegetative bodies and compact strobiliform inflorescences. However, they differ from each other by floral bracts margins, and shape and flower colors. The morphological convergence pattern also differentiates *A. multiflora* and *A. sphaerocephala* groups from other group with strobiliform inflorescences recovered in our analysis, which occur in the Atlantic Forest. The acquisition of strobiliform inflorescences by subgenera *Pothuava* and *Macrochordion* is followed by reductions in body volume, reduction in number of flowers as pointed out by Faria *et al.* (2010) and Wendt (1997). Other differences in floral bracts and sepal also separate the two groups from species of *Pothuava* and *Macrochordion* (Faria *et al.* 2010, Sousa 2004, Wendt 1997).

Sass & Specht (2010) proposed morphological similarities could indicate similar ecological niche characteristics. They regard to specific taxonomic level but the results here show two morphological convergent groups evolving independently in the same geographical area, which may represent a new phenomenon in Bromeliaceae to be better investigated. Morphological convergence inside adaptive radiation is a common event (Losos 2011) and had been cited to Bromeliaceae, even as an explanation to high homoplasy incidence found in several taxa (Faria *et al.* 2004, Givnish *et al.* 2007, 2011, 2014, Schulte *et al.* 2009, Schulte & Zizka 2008). However, until now there is any study concerning morphological convergence in sympatric groups of Bromeliaceae.

Conclusions

Our results are relevant to redefine the taxonomic arrangement of *A. subg. Chevaliera*. A new circumscription of *A.* subg. *Chevaliera* is mandatory or even a resurrection of *Chevaliera* as a genus should be considered based on the phylogenetic delimitation of *A. sphaerocephala* group. *Aechmea multiflora* group could be described as a new genus as one of the first lineages in Bromelioideae-core, placed together with taxa morphologicaly very distinct, and its clear morphological identity among Bromelioideae. However, the sister lineages relationships in both groups have to be solved before any taxonomic decision. A wider group with clear morphological coherence might be delimitated if *Machrochordion* and *Pothuava* subgnera are confirmed as sister lineages of *A. sphaerocephala* group.

The *A. subg. Chevaliera* nonmonophyletism is another indication that some morphological characteres were overvalued in systematic history of Bromelioideae. A better and carefully look to unconventional characters to redefine the groups in the subfamily is reaffirmed by our results. Nevertheless, we are advocating using specific characters combination in substitution to the traditional idea of only one character to defining genus in Bromelioideae.

Finally, morphological convergence between sympatric groups in Bromelioideae is one of the most striking finding in this study. Understanding dynamics that allows both groups occupy similar morphological and geographical spaces could highlight which evolutionary forces potentiate speciation processes in a biodiversity hotspot. Furthermore, a comparison of the ecological spaces of two groups would be a great opportunity to test some aspects of niche conservatism hypothesis.

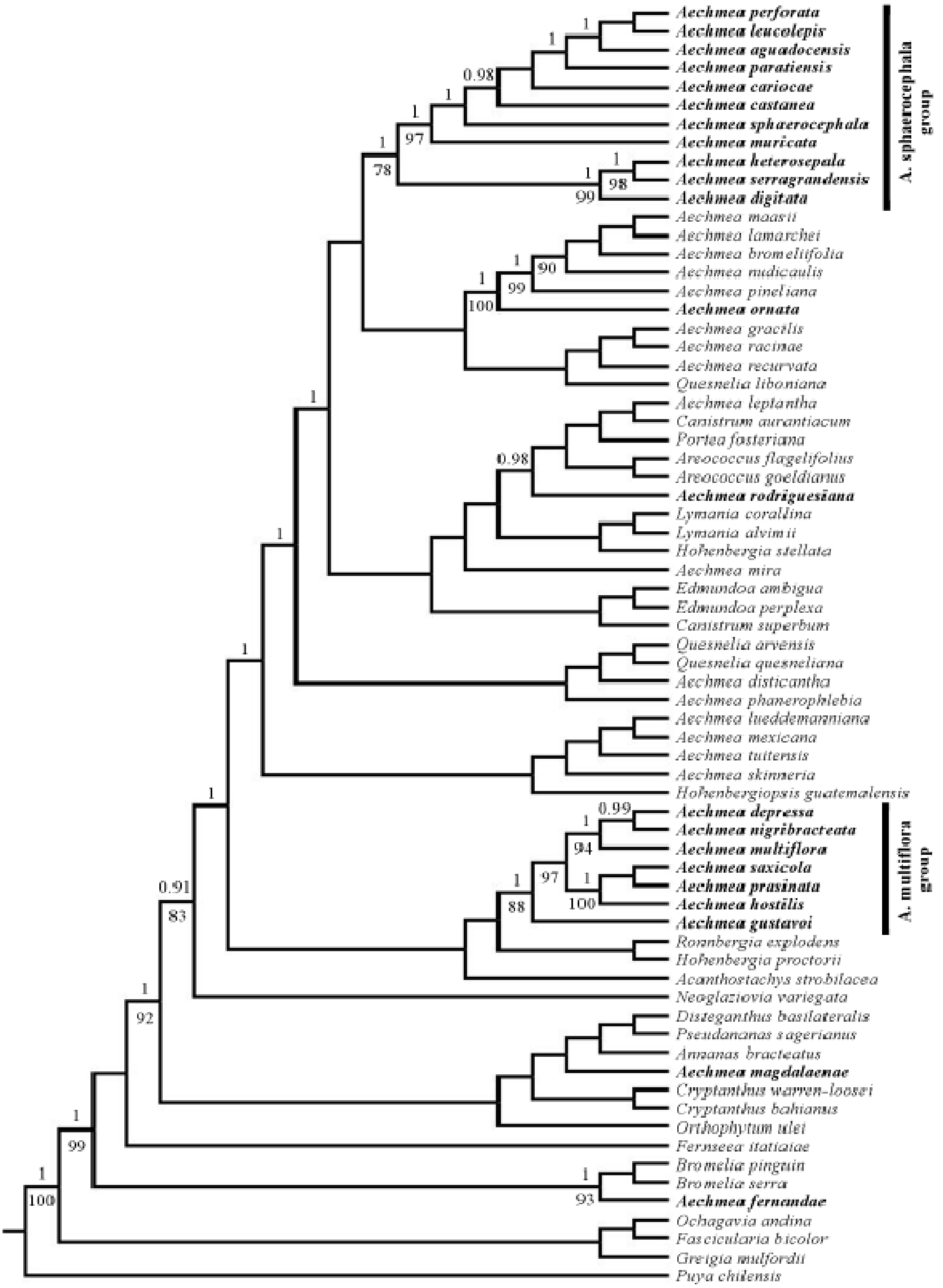

Figure 8.1. Topology of maximum credibility tree from bayesian analysis. Number of posterior probability (PP) and bootstrap (BS) is only for clade that got moderated to high support (PP> 90% above branches, BS>75% below branches). Names in bold are *A.* subg. *Chevaliera* species.

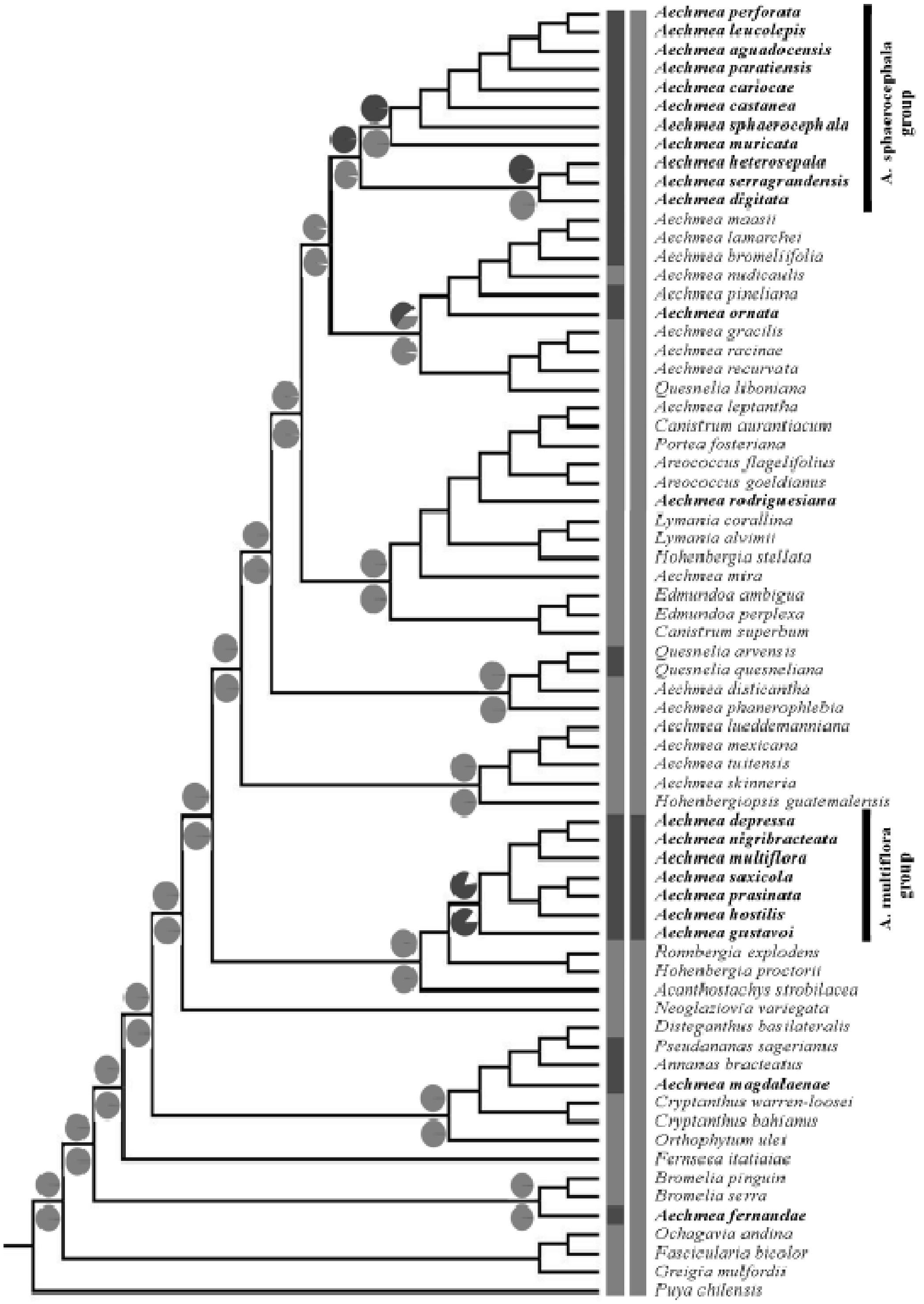

Figure 8.2. Ancestral reconstruction and distribution of characters traditionally used on taxonomy of *A.* subg. *Chevaliera*. Evolution and distribution of simple and strobiliform inflorescences showing convergence in *A. multilflora* and *A. sphaerocephala* groups (graphs above branches and first column; expanded and branched inflorescences=light, simple and strobiliform inflorescences=dark). Floral bract margins evolution in Bromelioideae showing dentate margin exclusive to *A. multiflora* group (graphs under branches and second column; entire=light, dentate=dark).

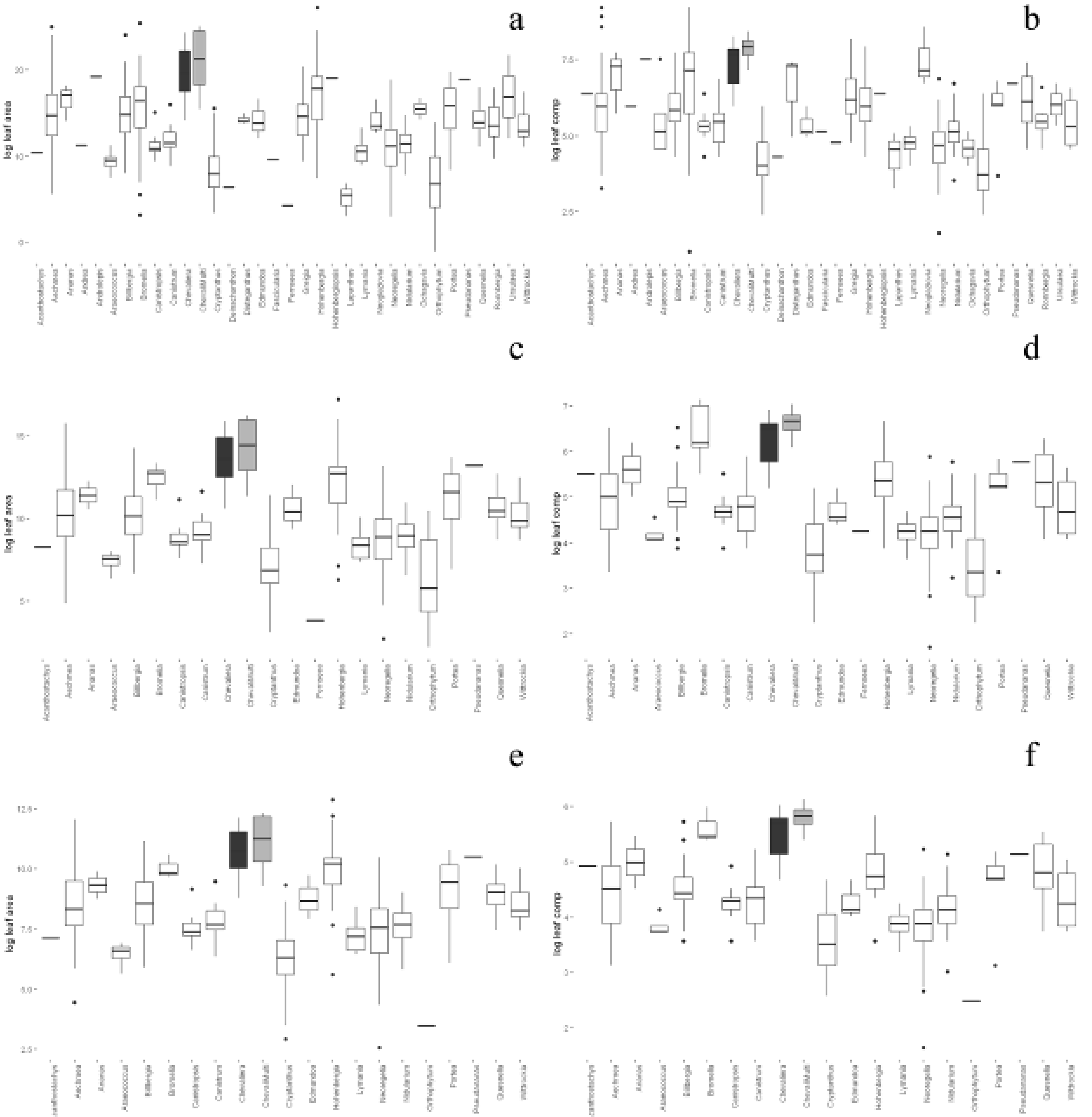

Figure 8.3. Morphological space of body size in Bromelioideae, according to leaf measures of 780 species. *Aechmea sphaerocephala* group in dark box plot and *A. multiflora* group in light box plot. a-b: comparison of foliar area (a) and leaf lenght (b) among all Bromelioideae; c-d: comparison of foliar area (c) and leaf lenght (d) among Bromelioideae from Atlantic Forest according to BFG (2015); e-f: comparison of foliar area (e) and leaf lenght (f) among Bromelioideae from ombrophilous Atlantic Forest according to BFG (2015).

Table 8.1. Result of Shimoidaira-Hasegawa congrunce test. Comparison follow Wanntorp *et al.* 2014. Highlighted are base values of datasets. SW = response of null hypothesis; D(LH) = logLikelihood deviation; SD = standard deviation.

		ETS, alignment	**matK, alignment**	**phyC, alignment**
ETS tree, InL		-2609.8842	-3016.886229	-2833.523102
SW			yes	Yes
D(LH)		0	-407.00209	-223.638901
SD		0.000624	58.298606	33.621627
matK tree, InL	-3365.281524	-3190.971285	-3324.643653	
SW	yes		Yes	
D(LH)	-174.312135	-0.001896	-133.674264	
SD	35.496486	0.001047	33.340677	
phyC tree, InL	-3306.69502	-3409.690067	-3115.936278	
SW	yes	yes		
D(LH)	-190.758742	-293.753789	0	
SD	35.893925	56.06581	0.002297	

Table 8.2. Basics statistics of alignment and jModel test result. Model subst = substitution model; Align. Lenght = alignmento lenght; Cons. Loc. = number of conserved locus; Var. Loc. = number of variable locus; Infor. Loc. = number of parsimony informative locus; Infor(%) = relative number of parsimony informative locus; Unique loc = sites of unique variable.

Dataset	**Model subst**	**Align Lenght**	**Cons. Loc**	**Var. Loc**	**Infor. Loc**	**Infor(%)**	**Unique loc**
Concatenado		3392	2850	542	294	8.67	248
ETS	GTR+I	480	70	410	242	50.42	168
phyC	GTR+I+G	1119	990	209	115	10.28	94
matK	GTR+I+G	1713	1574	139	68	3.97	71

Table 8.3. List of sequences used. Codes indicate sequences from GENBANK, new sequences made in this work = !, and absent sequences = x.

Species	**ETS**	**matK**	**phyC**
A. bromeliifolia	FJ942985	JX649234	JX649386
A. aguadocensis	!	!	X
A. cariocae	!	!	!
A. castanea	!	!	!
A. cstrobilacea	FJ943050	JX649231	JX649382
A. depressa	!	!	!
A. digitata	!	!	!
A. distichantha	FJ943000	KJ579988	JX649388
A. skinneri	FJ943054	AY950005	JX649414
A. fernandae	!	!	!
A. gracilis	FJ943010	AY950038	JX649394
A. gustavoi	X	!	!
A. heterosepala	!	!	!
A. hostilis	!	!	!
A. lamarchei	FJ943015	AY950044	JX649397
A. leptantha	FJ943095	AY950052	JX649474
A. leucolepis	!	!	!
A. lueddemanniana	FJ943016	AY950029	JX649398
A. maasii	!	X	X
A. magdalenae	!	!	!
A. mexicana	FJ943022	AY950028	JX649400
A. mira	!	!	!
A. multiflora	!	!	!
A. muricata	!	!	!
An. bracteatus	FJ943051	JX649241	JX649410
A. nigribracteata	!	!	!
A. nudicaulis	!	!	!
A. ornata	!	!	!
A. paratiensis	X	!	!
A. perforata	!	!	!
A. phanerophlebia	!	X	!
A. pineliana	!	!	!
A. prasinata	!	!	!
A. racinae	FJ943033	AY950030	JX649404

Species	**ETS**	**matK**	**phyC**
A. recurvata	FJ943035	KJ580011	JX649405
Ar. flagellifolius	FJ943055	AY950003	JX649415
Ar. goeldianus	FJ943056	AY950002	JX649416
A. rodriguesiana	!	!	!
A. saxicola	!	!	!
A. serragrandensis	!	!	!
A. tuitensis	FJ943104	AY950027	JX649488
B. pinguin	X	JX649247	JX649422
B. serra	X	AY950019	JX649423
C. aurantiacum	FJ943067	JF295094	JX649426
Cr. ybahianus	X	AY950011	JX649431
Cr. ywarren-loosei	X	JX649255	JX649436
A. sphaerocephala	X	AY950045	JX649430
C. superbum	FJ943105	AY950025	JX649489
D. basilateralis	X	JX649256	JX649438
E. ambigua	FJ943069	JX649257	JX649439
E. perplexa	FJ943071	JX649258	JX649441
F. asbicolor	X	AY950023	JX649442
F. eritatiaiae	X	AY949999	JX649443
G. mulfordii	X	AY950016	JX649445
H. proctorii	FJ943079	JX649261	JX649452
H. sguatemalensis	FJ943076	AY950020	JX649455
H. stellata	FJ943082	AY950026	JX649453
L. alvimii	FJ943083	AY950000	JX649456
L. corallina	FJ943085	JX649263	JX649457
N. variegata	X	AY950051	JX649458
O. candina	X	JX649264	JX649462
O. rtulei	X	JX649270	JX649471
P. fosteriana	FJ943092	KJ580106	FJ968235
Ps. sagerianus	!	!	JX649476
Pu. chilensis	X	EU780851	FJ968260
Q. arvensis	FJ943098	EU780850	X
Q. liboniana	FJ943100	AY950048	JX649481
Q. quesneliana	X	JX649274	JX649482
R. explodens	FJ943102	JX649275	JX649483

9 A new genus of Bromeliaceae endemic to Brazilian Atlantic Forest

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Abstract

Previous phylogenetic work revealed that *Aechmea* subg. *Chevaliera* is not a monophyletic group. In our phylogenetic analysis, a number of species of the subgenus form a clade with strong statistical support and in sister position to morphologically distinct members of other genera.We present morphological and phylogenetic evidences to segregate seven species in a new genus named *Gravatarum*. Description of the new genus, its seven species as well as a key for identification, distribution maps and illustrations are provided.

Keywords

Phylogeny, Taxonomy, Bromelioideae, *Aechmea*, *Gravatarum*.

Introduction

Aechmea comprises 288 species and it is the most diverse genus of the bromeliad subfamily Bromelioideae (Butcher & Gouda cont. updated). The genus has been shown to be polyphyletic, but the classification proposed by Smith & Downs (1979) is still the most recent comprehensive revision and therefore an important reference for recent taxonomic and phylogenetic studies (Aguirre-Santoro et al. 2015, 2016, Evans et al. 2015, Faria et al. 2004, Goetze et al. 2016, Heller et al. 2015, Horres et al., 2000, 2007, Louzada et al. 2014, Sass & Specht 2010, Schulte et al., 2005, 2009; Schulte and Zizka, 2008, Silvestro et al. 2014). Smith & Downs (1979) split the genus in eight subgenera based on morphology of inflorescences and floral characters, however, these subgenera have been shown to be poly- or paraphyletic too.

Aechmea subg. *Chevaliera* (Gaudich. *ex* Beer) Baker is the only one among eight subgenera (Smith& Downs 1979) which is characterized by a combination of massive and strobiliform inflorescences with large rosettes forming dense clumps (Maciel et al. 2015, Silva 2003, Smith & Downs 1979, Sousa 2004, Sousa *et al.* 2009). It is polyphyletic and – as the whole *Aechmea* alliance – needs a nomenclatural updating, despite the apparently clear morphological similarities (Silvestro et al. 2013, Aguirre-Santoro et al. 2016, Maciel et al. in prep., see Chapter 6). A comprehensive phylogenetic analysis and thorough followed by evaluation of morphological characters of *A.* subg. *Chevaliera* revealed two main monophyletic clades (Maciel et al. in prep.) and several species grouped with other groups of the *Aechmea* alliance. One of the groups gathers species around the typical *A.* subg. *Chevaliera* and a second one is related to *Aechmea multiflora* complex, which is the focus of this study.

A concept of the *A. multiflora* complex can be deduced from the key presented by Smith & Downs (1979), where species of this complex were split among *Chevaliera* species by floral bracts and sepals and geographical distribution. Together with *A. multiflora*, Smith & Downs (1979) grouped *A. multiflora*, *A. depressa*, *A. saxicola* and *A. hostilis*. Canela et al. (2003) used the concept of a *A. multiflora* complex to investigate the species delimitation based on more samples and morphological data than Smith & Downs (1979). Canela et al. (2003) reduced the number of species and proposed *A. hostilis as* synonym of *A. saxicola.* However, shortly after, Sousa (2004) reestablished *A. hostilis* based on leaves and inflorescences characters.

Since Canela et al. (2003) and Sousa (2004), new species have been described and associated to *A. multiflora* complex (Maciel et al. 2014, Sousa &Wanderley 2014). Thus, a more updated delimitation of this taxonomic complex includes *A. multiflora*, *A. depressa*, *A. hostilis*, *A. nigribracteata*, *A. prasinata,* and *A. saxicola*. The monophyly of this group was confirmed recently in a phylogenetic study of subgenus *Chevaliera* (Maciel et al. in prep.).

The main aim of this work is to present morphological and phylogenetic evidences of *A. multiflora* complex as a monophyletic group to support a proposal as a new genus. This nomenclatural decision will also contribute to clarifying the notoriously problematic taxonomy of the *Aechmea* alliance by providing a molecular and morphological characterization for it.

Material and Methods

Morphological studies

Data about distribution and morphology of species is based on herbaria survey at ALCB, ASE, B, BM, BHCB, BR, C, CEPEC, COL, CVRD, ESA, F, FR, G, GH, GUA, HB, HBR, HUEFS, HUESC, IAN, INPA, IPA, K, LG, MBML, MAC, MG, MIR, MO MUFAL, NY, P, PMA, R, RB, RFA, RUSU, S, SP, SPF, TEPB, U, UEC, UFP, UFRR, US, VEN, VIES, W and WU. In order to complement the information and evaluate morphological characters in natural populations and living plants, we performed expeditions to different regions in Brazil. Collected samples are kept at SP and UFP herbaria. All species descriptions are based on herbarium and fresh samples material collected during the fieldtrips. The morphological terminology follows Radford et al. (1974), Smith & Downs (1979), Stearn (1992), Troll (1964) and Weberling (1989).

Sampling, DNA extraction, sequencing, alignment, phylogenetic analysis

Procedures of sampling to molecular studies, DNA extraction, sequencing, alignment and phylogenetic analysis were the same used by Maciel et al. (in prep.). We adopted the topology of maximum credibility tree from Bayesian analysis for this study after confirming, that no incongruences exist between topologies of Bayesian and Maximum Likelihood trees. Values of posterior probability and bootstrap are shown in Figure 1 for the main clades in Bromelioideae and for the new genus.

Ancestral character state reconstruction and morphological space analyses

A binary Bayesian MCMC ancestral character reconstruction analysis was run under the software RASP (Yu et al. 2015). For this analysis, the previous dataset of 10,001 trees generated from the Bayesian analyses and selected 1,000 trees randomly to calculate the mean frequency of ancestral variation. For each character, we selected states according to a morphological survey. Two independent channels of 10,000,000 generations sampled at each 1,000 generations were run. The final result is a combination of each channel.

The selected characters and their states were: 1) floral bract margins (A=entire, B=dentate) and 2) petal color (A=white, B=green, C=yellow, D=orange, E=blue, and F=red to lilac). We coded the character states based on literature, living specimens and herbaria survey.

Results and discussion

The phylogeny of Bromelioideae with a wide sampling of *A.* subg. *Chevaliera* clearly recovers a polyphyletic subgenus with a morphologically and phylogenetically well supported monophyletic group of seven species (*A. gustavoi*, *A. multiflora*, *A. nigribracteata*, *A. depressa*, *A. hostilis*, *A. prasinata* and *A. saxicola*; see figure 1). Most of these species were formerly recognized as *A. multiflora* complex, except *A. gustavoi* (Leme & Siqueira-Filho 2001, Canela et al. 2003, Maciel et al. 2014, Sousa & Wanderley 2014).

Aechmea gustavoi was described by Leme & Siqueira-Filho (2001) and then could not be clearly related by the author to any other taxon in *Aechmea*. The species was not included among the studied ones by Canela et al. (2003). The first mention of any morphological relationship of *A. gustavoi* with species of the *A. multiflora* complex appears in Sousa (2004), who compared floral bracts of *A. gustavoi* and *A. hostilis*. Maciel et al. (2014) included the newly described *A. nigribracteata* in the *A. multiflora* complex, but did not relate the new species to *A. gustavoi*. Finally, Sousa & Wanderley (2014) related *A. prasinata* to *A. hostilis* and *A. gustavoi*.

However, Aguirre-Santoro et al. (2016) included in their analysis three species of the *A. multiflora* complex (*A. multiflora, A. saxicola,* and *A. gustavoi*) and found a monophyletic group with *A. gustavoi* being sister to two other species – a topology that is congruent with that of our study. Based on a complete sampling of the group, our results confirm the sister group relationship of *A. gustavoi* and the remaining species previously assigned to the *A. multiflora* complex (fig. 1). This result highlights the importance of some valuable morphological features. Inserted strobiliform inflorescences with dilated central axis and floral bracts with dentate margins (fig. 1) are key characters uniting *A. gustavoi* (Sousa et al. 2009) and the remaining species of the new genus.

The clade formed by the species of the *A. multiflora* complex receives statistical support and good resolution in terminal taxa (BS 88, PP 1, see figure 1). However, the sister lineage of the complex is not fully resolved yet. Finally, the clade composed of the *A. multiflora* complex is placed together with representatives of the morphologically quite heterogenous genera *Acanthostachys*, *Neoglaziovia* and *Ronnbergia*.

Acanthostachys is a dispecific genus that occurs in the southern part of the Atlantic forest (Smith & Downs 1979). It is a typical epiphyte with long and narrow leaves. The inflorescence is simple and short (3-7 cm long). *Neoglaziovia* is a genus formed by three species from the Brazilian semi-arid region locally called “caatinga” (Leme1990, Smith & Downs 1979). In this genus, the inflorescence is simple, but lax, few-flowered, and peduncle and ovaries are fully exposed (Leme 1990, Smith & Downs 1979). Both genera have no morphological characters resembling the species of the *A. multiflora* complex.

A third species placed together with the *A. multiflora* complex is *Ronnbergia explodens*, which belongs to *Ronnbergia* alliance. As defined by Aguirre-Santoro et al. (2016), this alliance encompasses a large and morphologically diversified group of species lacking a clear morphological definition. Nevertheless, the characteristics found here allow differentiate the *A. multiflora* complex by the restricted distribution in the Atlantic Forest, besides habit and inflorescence characters (large plants forming dense and huge clumps, inflorescence strobiliform, compact and multiflowered).

In the *A.* subg. *Chevaliera* identification key published by Smith & Downs (1979), it is possible to recognize some morphological unity to species placed in the *A. multifora* complex. It is based on floral bracts serrulate, sepals not exceeding 20 mm long and geographical distribution restricted to eastern Brazil. This concept was followed by Canela et al. (2003) and Sousa (2004) adding more extensive morphological information than Smith & Downs (1979).

Our results confirm, based on morphological and phylogentics support, this group of species including *A. gustavoi* and the other ones previously reported as part of *A. multiflora* complex as members of a new genus here proposed.

Taxonomy

Gravatarum J.R. Maciel & G. Sousa, gen nov.

Type:—*Gravatarum multiflora* (L.B. Sm.) J.R. Maciel & G. Sousa = *Aechmea multiflora* L.B Sm. (1937: 117)

It is segregated from *Aechmea* subg. *Chevaliera* and combines plants of huge size and tank-forming with a simple strobiliform, multi-flowered inflorescence, dentate or serrulate floral bracts and white or greenpetals.

Plants epiphytic, terrestrial or saxicolous, shortly rhizomatous. Leaves spiraled, erect; leaf-sheaths elliptical to triangular, castaneous, contrasting in colour to the leaf-blades, margins entire, imbricate, tank-forming; leaf-blades green, both sides with argenteous indument, apex pungent. Peduncle terminal, erect, robust, foliaceous, green to castaneous, lepidote. Peduncle bracts imbricate, covering the peduncle, lanceolate, linear, or triangulate, castaneous or vinaceous, lepidote, coriaceous, apex pungent, margins serrate. Inflorescence terminal, polytelic, spadici or capituliform, central axis enlarged, elongated or compressed, conical to truncate, lepidote, multi-flowered. Floral bracts persistent, acrescent, spathulate, lanceolate, oblong or ovate, red, green or castaneous, lepidote, apex mucronate, erect, retroflex to squarrose, margins serrate. Flower trimerous, perfect, sessil. Sepals asymmetric with lateral wings hyalinous, green, lepidote, rigid, carinate, mucronate, adnate in basal portion forming a hypanthium. Petals free or conate above the hypanthium, then forming a tube, spathulate, oblong or ovate, white or green, erect to patent after anthesis, apex acute; petal appendages on adaxial side of petals, 2-calosities, margins erose, lacerate or fimbriate. Stamens 6, included, in two series, filamente adnate to hypanthium base, the external stamens sold on base, the internal stamens epipetalous; anthers basifixed or sub-basifixed, linear to narrowlybilobed. Stigma included, 3-lobed, spirally-conduplicate. Epigynous tube conspicuous, crateriform.

Ovary inferior, obconical, complanate on basal portion; axilar placentation. Fruit baccate, obconical, castaneous, fleshy. Seed fusiform, castaneous.

Comments:—*Gravatarum* holds seven species endemic to the Brazilian Atlantic Forest with distribution extending from 7º to 25º southern latitude (Figs. 3-5). The growth form (huge plants) and inflorescence type (strobiliform) of *Gravatarum* are superficially similar to other species still placed in *A.* subg. *Chevaliera*. However, species of *Gravatarum* have floral bracts partially or wholly dentate or denticulate, and petals green or white while other species from the same habitat, habit and inflorescence have floral bracts entire and petals blue or vinaceous. Some Andean, Amazonian and Caribbean species of *Aechmea* subg. *Chevaliera* (*A. fernandae* and *A. magdalenae*) also have floral bracts dentate or denticulate, but they differ from *Gravatarum* in not forming a tank, having yellow petals and occurring outside the geographical area of *Gravatarum*.

Etymology:—The name *Gravatarum* refers to the vernacular name used to identify bromeliads plants by local people in Brazil, particularly species of subgenus *Chevaliera,* from which the *Gravatarum* species were segregated. The word is from Tupi, a language largely used by native people before colonization, and means bromeliads.

Key to the species of *Gravatarum*

1\. Inflorescence capituliform, axis compressed… 2

\- Inflorescence in spadix, axis elongated ... 5

2\. Leaf blades lanceolate, petals white … *G. gustavoi*

\- Leaf blades oblong or linear-oblong, petals green … 3

3\. Petals free above the epygynous tube … *G. depressa*

\- Petals connate above the epygynous tube … 4

4\. Floral bracts green, flower 4–4.5 cm long … *G. prasinata*

\- Floral bracts red, flower 3.6-4 cm long … *G. hostilis*

5. Floral bracts blackish, margins wholly dentate, anthers narrowly bilobed at the base .... *G. nigribracteata*

- Floral bracts green to red, margins entire in basal portion, serrate in apical portion, anthers entire at the base 6

6. Floral bracts 3-4.5, petals free above epigynous tube .. *G. multiflora*

- Floral bracts 4.2-5, petals connate above epygynous tube .. *G. saxicola*

1. *Gravatarum depressa* (L.B. Sm.) J.R. Maciel & G. Sousa, comb. nov. (Fig. 2a, 2g, 3a-b, 4)

Basionym:—*Aechmea depressa* L.B. Sm. (1941: 54).

Type:—BRASIL. Bahia, Água Preta (Uruçuca), 03 June 1939 (fr.), *M.B Foster & R. Foster* 71 (holotype GH!, isotype R, photo US! SP!).

Chevaliera depressa L.B. Sm. & Kress (1989: 78)

Terrestrials or epiphytes, 70-100 cm tall. Leaves 180-250 cm long; leaf sheath 27-36,5 x 15-18.5 cm, elliptical; leaf blade 150-200 x 9-19 cm, green, flattened, oblong, apical spine ca. 1 cm long, prickles in margins 2-3 mm long. Peduncle 50-73 cm long, green to white-lepidote. Peduncle bracts 12-29 x 6-7 cm, linear-lanceolate to triangulate on inflorescence base, reddish on basal portion, greenish on apical portion, white-lepidote, apical spines ca. 7 mm, margins serrate; involucral bracts red. Inflorescence capituliform 8.5-10 cm long, axis compressed, enlarged; mucilage present. Floral bracts 4-5 x 1.5-1.7 cm, oblong, red, white-lepidote, apex cuspidate, straight to squarrose after antesis, margins entire in basal portion, serrate on apical portion, above the sepals long. Flower 4-5.5 cm long. Sepals 2-2.3 cm long, green, dorsally white-lepidote, two carenate and one without carene, apex mucronate. Petals free above epigynous tube 2-2.5 x 0.5-0.6 cm, oblong-lanceolate, green, margins white, apex acute, erect; petal appendage free in basal portion, cupuliform, erose margins. Stamens of external series with free filaments over epigynous tube, 1-1.2 mm long, of internal series epipetalous, free at 5-6 mm long; anthers 0.8 cm, basifixed, linear. Ovary 2-2.3 cm long; epigynous tube ca. 0.7 cm; style stout; stigma margins digitated. Fruits 5.6 cm long, brownish. Seeds 3-4 mm, brownish.

Selected specimens:—BRAZIL. Bahia: Ilhéus, Mata da Esperança, 14º46'55"S 39º04'09"W, 16 February 1995 (fr.), *J. Jardim et al. 612* (CEPEC); Porto Seguro, Estação Ecológica do Pau Brasil, 16º23'27"W 39º10'48"W, 04 April 2003 (fr.), *T. Wendt et al. 479* (RFA); Santa Cruz da Vitória, Fazenda Uruguaiana, 15°01'50.4"S 39°47'47"W, 07 May 2001 (fl. fr.), *G. Sousa et al. 491* (SP, TEPB).

Distribution, habitat and conservation:—*Gravatarum depressa* is endemic to the state of Bahia and can be found in dense ombrophilous forest from 100 to 400 m.s.m in epiphytic or terrestrial habitats (Fig. 3). Flowering and fruiting from January to November. This species is evaluated as Endangered in Brazilian Red List due habitat loss degradation. However, the two known populations of *G. depressa* are protected in natural reserves.

Comments:—This species is morphologically similar to *G. multiflora* by their red floral bracts, and petals free above epygynous tube. However, it differs by the inflorescence type (capituliform with axis compressed in *G. depressa vs.* inflorescence in spadix with axis elongated in *G. multiflora*) and form and length of petals (see Figure 2 b and f). Sousa (2004) also pointed out differences between both species based on polen exine (rugulate-perforate in *G. depressa vs.* perforate in *G. multiflora*).

2. *Gravatarum gustavoi* (J.A. Siqueira & Leme) J.R. Maciel & G. Sousa, comb. nov. (Fig. 2b, 3c, 4)

Basionym:—*Aechmea gustavoi* J.A. Siqueira & Leme (2001: 147-148).

Type:—BRASIL. Pernambuco, Jaqueira, Usina Frei Caneca, Mata do Jasmim, 8º4'15"S 35º50'13"W, 08 September 2000 (fl. fr.), *J.A. Siqueira-Filho 1091* (holotype UFP!, isotype HB!).

Epiphytes, ca. 40 cm tall. Leaves 100-200 cm long; leaf sheath 14-18 x 7.5-9.5, triangular; leaf blade 80-200 x 3.4-5 cm, green with dark stains, flattened, lanceolate, apical spine ca. 1 cm long; prickles in margins 3-5 mm long. Peduncle ca. 13 cm long, under foliar sheats, castaneous. Peduncle bracts 25-40 x 2-3 cm, linear, castaneous on basal portion, red on apex, apical spine ca 1 cm, margins serrate; involucral bracts red. Inflorescence capituliform 7-10 cm long, axis compressed, enlarged; mucilage absent. Floral bracts 5.5-7 x 0.4-4.5 cm, lanceolate, castaneous, lepidote-tomentose, apex cuspidate, strainght after antesis, magins serrate until median region, above sepal long. Flower 6-7 cm long. Sepals 3.5-4 cm long, white, dorsally lepidote, two carenate, one without carene, apex acuminate. Petals conate above epygynous tube, tube 1.8-2 cm long, lacinae 2-2.2 x 0.4-0.6 cm, ovate, white, apex acute, erect; petal appendages free in basal portion, callous, lateral margins free. Stamens of two series adnate to corola, free ca 7 mm long; anthers ca. 1 cm long, at the same long of lacines, basifixed, linear. Ovary 2-2.5 cm long, epigynous tube ca. 1 cm long; style stout; stygma 2.8-3 cm long, margins digitate.

Selected specimens:—BRAZIL. Bahia: Una, Reserva Biológica de Una, 15º09'S 39º05'W, 1 May 2000 (fr.), *J. Jardim et. al. 3021* (CEPEC, NY). Pernambuco: Jaqueira, Serra do Urubu, 29 April 2014 (fr.), *J.R. Maciel et al. 1929* (UFP).

Distribution, habitat and conservation:—*Gravatarum gustavoi* has a disjunct distribution between Pernambuco and Bahia states (Fig. 3). It is an epiphyte in submontane ombrophilous forest (500 to 600 m.s.m.). Flowering and fruiting from April to September. This species is evaluated as Critically endangered because its narrow distribution, loss of habitat, detected reduction of wild populations and presence of invasive alien species in its natural habitat. However, this species is under cultivation at Botanic Gardens and private collections. Known populations of *G. gustavoi* are protected in natural reserves in its area of distribution.

Comments:—*Gravatarum gustavoi* is a unique species because its long and narrow leaf blade, inflorescence capituliform with long and narrow involucrate bracts, adaxially red during and white petals. However, it has lanceolate floral bracts like *G. nigribracteata* and *G. hostilis*.

3. ***Gravatarum hostilis*** (L.B. Sm.) J.R. Maciel & G. Sousa, comb. nov. (Fig. 3d, 5)

Basionym:—*Aechmea hostilis* E. Pereira (1972: 277).

Type:—BRASIL. Espírito Santo, Domingos Martins, Alto Rio Jucu, 21 March 1972 (fl. fr.), *A. Seidel* 625 (holotype HB!).

Chevaliera hostilis (E. Pereira) L.B. Sm. & W.J. Kress (1989: 78)

Terrestrials or epiphytes, ca. 70 cm tall. Leaves 90-183 cm long; leaf sheath 18-31 x 7.5-13 cm, elliptical; leaf blade 70-183 x 3-5 cm, green, flattened, oblong, apical spine ca. 1.5 cm long, prickles in margins ca. 2 mm long. Peduncle 13-20 cm long, castaneous. Peduncle bracts 18-21 x 3-4 cm long, linear, vinaceous on basal portion, green on apical portion, apical spine ca. 1 cm long, margins serrate; involucral bracts red. Inflorescence capituliform 7-10 cm long, axis compressed, enlarged; mucilage present. Floral bracts 4-7 x 1.5-2 cm, lanceolate, red, white-lepidote, apex cuspidate, straight, margins serrate, over sepal long. Flower 3.6-4 cm long. Sepals 2.5-2.7 cm long, green, dorsally lepidotes, two carenate and one without carene, apex mucronate. Petals conate above epygynous tube, tube 1.5-2 cm long, laciniae 1-1.2 x 0.4-0.6 cm long, ovate, pallid-green, apex apiculate, erect; petal appendages free, callous, sallience at lacinias base. Stamens of two series adnate to corolla tube, free, ca. 5 mm long, anthers ca. 1 cm long, equal to lascinias, basifixed, linear. Ovary 1.3-1.5 cm long, epigynous tube ca. 1 cm long; style stout; stygma 2.5-2.8 cm long, margins digitate. Fruits 4-4.5 cm long, yellow to castaneous.

Selected specimens:—BRAZIL. Espírito Santo: Santa Teresa, Estação Biológica de Santa Lúcia, 19°57'54'' S, 40°31'53'' W, 09 September 2014 (fr.), *J.R. Maciel & B.S. Amorim 1972* (UFP); Terreno do Bosa, 30 May 2000 (fl. fr.), *G. Sousa et al. 323* (SP, TEPB).

Distribution, habitat and conservation:—*Gravatarum hostilis* is narrow endemic and known from restricted areas of dense ombrophilous forest in Espírito Santo state (Fig. 4), occurring as terricolous or epiphyte from 500 to 900 m.s.m. Flowering and fruiting from February to September. Because *G. hostilis* was considered under synonimy of *A. saxicola*, it was not evaluated in red lists. *Gravatarum hostilis* has a narrow distribution and its natural area of occupancy is now severely fragmented and under anthropics pressure causing habitat loss. Therefore, *G. hostilis* must be evaluated as Endangered. Nevertheless, *G. hostilis* has its main population protected in natural reserves, there is a clear danger to its conservation. Thus, ex-situ emergencial measures are necessary to protect the genetic pool of this species.

Comments:—Canela *et al.* (2003) synonimized *G. hostilis* under *A. saxicola*. However, Sousa (2004) demonstrated that both could be differentiated by length of involucrate bracts (short in *G. saxicola* and ultrapassing inflorescence length in *G. hostilis*); length of peduncle (short in *G. saxicola* and long in *G. hostilis*). In addition, floral bracts and flowers of *G. hostilis* is shorter than *G. saxicola* (see Fig 3 d and j).

4. *Gravatarum multiflora* (L.B. Sm.) J.R. Maciel & G. Sousa, comb. nov. (Fig. 2c-d, 3e-f, 6)

Basionym:—*Aechmea multiflora* L.B Sm. (1937: 117).

Type:—BRASIL. Bahia, Forests of Rio Grongory basin, 30 October to 01 November 1915 (fl. fr.), *Curran 297* (holotype US!, Foto SP!, F!, NY!, GH!).

Aechmea frassyi Leme & J.A. Siqueira (2001: 146-147). Type:—BRASIL. Alagoas, Entre Feliz Deserto e Piaçabuçu, February 2001, *E. Leme 5086*, flowering under cultivation (holotype HB!).

Terrestrial or epiphytes, ca. 1.5 m tall. Leaves 100-280 cm long; leaf sheath 35-40 x 16-19 cm, elliptical; leaf blades 60-280 x 11-14 cm, green to yellow-green, flattened, oblong, apical spines ca. 1 cm long, prickles in margins ca. 1 mm long. Peduncle 60-120 cm long, green, white-lepidote. Peduncle bracts 13-15 x 5-7 cm, triangular, green in basal portion, red on apical portion, white-lepidote, apical spines ca. 1.3 cm, margins serrate; involucral bracts red. Inflorescence spadix 11-16.5 cm long, axis elongated, enlarged; mucilage absent. Floral bracts 3-4.5 x 1.2-2.5 cm, spatulate, red, white-lepidote, apex cuspidate, pattent or retroflexed, margins entire in basal portion, serrate on apical portion, over the sepals long. Flower 3-3.5 cm long. Sepals 1.5-1.7 cm long, dark-green, imbricated, dorsally white-lepidote, two carenate and one without carene, apex mucronate. Petals free over above epigynous tube 1.5-2 x 0.5-0.7, ovate, pallid-green, margins white, apex acute, erect; petal appendage free in basal portion, cupuliform, erose margins. Stamens of external series with free filaments over epigynous tube, 1-1.2 cm long, of internal series epipetalous, free, 3-4 mm long; anthers 7-8 mm, basifixed, linear. Ovary1-1.3 cm long; epigynous tube 5-8mm; style stout; stigma margins digitated; Fruits 3-5 cm long, castaneous. Seeds 3-4 mm, castaneous.

Selected specimens:—BRAZIL. Alagoas: Feliz Deserto, 04 November 1979 (fr.), *D. Andrade-Lima 79-8772* (IPA). Bahia: Boa Nova, Parque Nacional de Boa Nova, 14°19'56'' S, 40°12'52'' W, 16 December 2013 (fr.), *J.R. Maciel et al. 1861* (UFP); Maraú, 14º07’43”S 39º00’09”W, 02 February 2000 (fr.), *M. Alves et al. 1901* (CEPEC, HUEFS, NY, SP); Salvador, Parque das Dunas, 12°55'04'' S, 38°19'02'' W, December 2013 (fl. fr.), *J.R. Maciel & B.S. Amorim 1837* (UFP). Sergipe: Pirambu, Reserva Biológica de Santa Isabel, 10º47’19”S 36º58’35”W, 16 June 2000 (fl. fr.), *G. Sousa et al. 358* (CEPEC, SP).

Distribution, habitat and conservation:—*Gravatarum multiflora* has the widest distribution in Atlantic Forest among the species of *Gravatarum* (Fig. 5). It can be found as terrestrial or epiphyte in restingas (open coastal forest in sandysoils), ombrophilous forest and seasonally forest from 50 to 400 m.s.m. Flowering and fruiting along the year. *Gravatarum multiflora* is dominant in bromeliad community in some places, like Marau in southern of Bahia state (Maciel et al. 2015). Because its large distribution and good conservation of natural populations this species is evaluated as Least Concern on conservation. In addition, populations of *G. multiflora* are protected in natural reserves in Brazil.

Comments:—Inflorescences of this species has a variation in color depending on flower maturation. Young inflorescence is often green and becomes orange to red during flowering period. This species is clear morphologically related to *G. depressa* as discussed before. Moreover, distributions of *G. multiflora* and *G. depressa* are overlapped, which lead to many errors on identification. Nevertheless, *G. multiflora* can be easily identified by elongate inflorescences and floral bracts with apex retroflexed.

5. *Gravatarum nigribracteata* (J.R. Maciel, Louzada & M. Alves) J.R. Maciel & G. Sousa, comb. nov. (Fig. 2e, 2h, 3g-h, 5)

Basionym:—*Aechmea nigribracteata* J.R. Maciel, Louzada & M. Alves (2014: 233).

Type:—BRAZIL. Bahia: Una, Entrada no Km 49 da BA-001, 15°13’19”S, 39°01’45”W, 31 May 2014 (fl. fr.), *J.R. Maciel, L. Daneu, D. Cavalcanti & B.S. Amorim 1950* (holotype UFP!, isotype FR!).

Terrestrials or epiphytes, 70–80 cm tall. Leaves 150–230 cm long; leaf sheaths 25–35 × 20–30 cm, oblong; leaf blade 125–200 × 10–15 cm, green, flattened, linear-oblong, apical spines ca. 1.2 cm long, prickles in margins 4–7 mm long. Peduncle 35–60 cm long, greenish to white-lepidote. Peduncle bracts 44–50 × 5–6.5 cm, oblong-lanceolate, green to castaneous, black at the base, white-lepidote, apical spines ca. 1 cm, margins serrulate; involucral bracts black. Inflorescences spadix 24–30 cm long, axis elongated, enlarged; mucilage present. Floral bracts 6.3–7 × 1.1–1.3 cm, lanceolate, blackish, lepidote, apex acute, straight after antesis, margins wholly dentate, over the sepals. Flowers 6–7 cm long. Sepals 2.8–3.5 long, castaneous at the base and green toward the apex, lepidote on both surfaces, two carinate and one without carene, apex mucronate. Petals free above epigynous tube 3.3–3.5 × 0.3–0.5 cm, spathulate, green, apex acute, erect; petal appendages free in basal portion, crenate-laciniate margins. Stamens of two series free, 18–20 mm long; anthers 10–12 mm long, basifixed, narrowly bilobed at the base. Ovary 1.9–2.1 cm long; epigynous tube 0.8–1 cm long; style stout; stigma margins lacerate. Fruits 6–8 cm long, green.

Selected specimens:—BRAZIL. Bahia: Una, Arredores da REBIO Una, 15°13’19”S, 39°01’45”W, 8 December 2013 (fr.), *J.R. Maciel et al. 1839* (UFP; RB); ib., Fazenda Nossa Senhora das Graças, 26 July 2000 (fr.), *J. Jardim et al. 3062* (CEPEC; NY; RB).

Distribution, habitat and conservation:—*Gravatarum nigribracteata* is narrow endemic and only known from a restricted area of Atlantic coastal forest (Una region) in southern Bahia state, northeastern Brazil (Fig. 4). Maciel et al. (2014) classified *G. nigribracteata* as Critically Endangered because its narrow distribution. Moreover, natural habitats of *G. nigribracteata* are under pressure because high levels of fragmentation and explotation, despite this species is protected by Conservation Reserves. There is no notice about cultivation of this species in public or private collection, thus emergencial *ex-situ* strategies are urgent to *G. nigribracteata.*

Comments:—It grows as an epiphyte on the lower and stronger branches of trees or can be found as a terrestrial plant in sandy soils in coastal shrubby vegetation. Flowering and fruiting between May and July. *Gravatarum nigribracteata* is related to *G. multiflora* and *G. saxicola* by their elongated inflorescence. However, the blackish, lanceolate and dentate floral bracts associated to lobed anthers make this species unique in genus *Gravatarum*.

6. ***Gravatarum prasinata*** (G. Sousa & Wanderley) J.R. Maciel & G. Sousa, comb. nov. (Fig. 3i, 5)

Basionym:—*Aechmea prasinata* G. Sousa & Wanderley (2014: 1).

Type:—BRASIL. Espírito Santo, Município de Cariacica, Reserva Biológica de Duas Bocas, Trilha de acesso ao lajeiro, 20°16′21″ S 40°28′40″ W, 02 Jun 2000 (fl. fr.), *G. Sousa, M. Alves & M. Gomes 331* (holotype SP, isotype TEPB).

Epiphytes or rarely terrestrials, ca. 50 cm tall. Leaves 150–150 cm long; leaf sheath 22–26 × 15-16 cm, elliptical; leaf blade 125-150 × 5–7 cm, green, flattened, oblong, apical spine ca. 1 cm long, prickles in margins ca. 4 mm long. Peduncle 10–15 cm long, green. Peduncle bracts 10–25 × 3.5–5 cm, linear-triangular, green, lepidote, apical spine ca. 1 cm long, margins serrate; involucral bracts red. Inflorescence capituliform ca. 13 cm long, surrounded by involucral bracts which exceed the inflorescence; axis compressed, enlarged; mucilage absent. Floral bracts 5–5.3 × 1.3–2.5 cm, oval to oblong, green, apex cuspidate, straight, margins serrate from the middle to the apex, about the sepal long. Flower 4–4.5 cm long. Sepals 2.5–2.7 cm long, green, white-lepidote, two carenate and one without caren, apex acuminate. Petals connate above the epygynous tube, tube 1.5–1.6 cm long, laciniae 1.3–1.4 × 0.5–0.6 cm, oval, green, apex apiculate; erect; petal appendage two bilateral calluses, prominent at the base of the laciniae. Stamens with the filaments of the two series partially adnate to the corolla tube, free, ca. 4 mm; anthers 0.9–1 cm long, basifixed, linear. Ovary 1.0–1.5 cm long; epigynous tube ca. 7 mm long; style stout; stigma margins digitated,

Selected specimens:—BRAZIL. Espírito Santo: Cariacica, Reserva Florestal de Duas Bocas, 20°17′57″ S40°32′77″ W, 8 August 1999 (fl. fr.), *G. Martinelli et al. 15623* (RB).

Distribution, habitat and conservation:—*Gravatarum prasinata* is restricted to Espírito Santo state (Fig. 4), in submontane Atlantic forest (650–700 m.s.m.). It is an epiphyte or rarely terrestrial in ombrophilous vegetation around forest streams. Flowering and fruiting from February to August. Known populations of *G. prasinata* are protected by natural reserves. In addition, the species is cultivated in public collections. However, its narrow distribution and loss of habitat make this species as Endangered.

Comments:—*Gravatarum prasinata* is related to *G. hostilis* by capituliform inflorescence, floral bracts straight and petals connate above the epygynous tube. However, in *G. prasinata* bracts are always green, and flowers are longer than in *G. hostilis*.

7. ***Gravatarum saxicola*** (L.B. Sm.) J.R. Maciel & G. Sousa, comb. nov. (Fig. 3j-k, 6)

Basionym:—*Aechmea saxicola* L.B. Sm. (1950: 118).

Type:—BRASIL. Espírito Santo, Cachoeiro do Itapemirim, "colecionada estéril 07 July 1939 e florindo em Orlando, Florida 07 july 1947" (fl. fr.), *Foster & Foster 164* (holotype US!, isotype GH!, foto F!, NY!, SP!, US!).

Saxicolous or epiphytes, ca. 1.5 m tall. Leaves 120-220 cm long; leaf sheath 20-38 x 11-18 cm, elliptical; leaf blade 100-220 x 5-12 cm, green or yellow-green, flattened, oblong, apical spine ca. 1 cm long, prickles in margins 2-4 mm long. Peduncle 50-65 cm long, green to white-lepidote. Peduncle bracts 7-46 x 4-5 cm linear-lanceolate, green to purple-green, white-lepidotes, apical spine 0.8-1 cm, margins serrate; involucral bracts red. Inflorescence spadix 7-20 cm long, axis elongated, enlarged. Floral bracts 4.2-5 x 1.2-2.5 cm, lanceolate, red, white-lepidote, apex cuspidate, straight, margins entire in basal portion, serrate in apical portion, above the sepals long. Flower 3.5-4.5 cm long. Sepals 1.5-1.8 cm long, green, white-lepidote, two carenate and one without carene, apex mucronate. Petals conate above epygynous tube, tube 1.2-1.8 cm long, laciniae 0.8-1 x 0.4-0.6 cm long, ovate, green, apex acute; petal appendages callous, sallience at lacinias base. Stamens in two series adnate to corolla tube, free at ca. 6 mm long; anthers ca. 8 mm long, basifixed, linear. Ovary 0.8-1 cm long; epigynous tube ca. 6 mm long; style stout; stygma ca. 2 cm long, margins digitate. Fruits 3.5-4.5 cm long, castaneous.

Selected specimens:—BRAZIL. Espírito Santo: Aracruz, Comboios, 19 July 1992 (fl. fr.), *O. Pereira & J. Gomes 3610* (VIES); Linhares, Reserva da Vale do Rio Doce, 19°07'52'' S, 39°53'10'' W, 04 September 2014 (fl. fr.), *J.R. Maciel et al. 2014* (UFP). Rio de Janeiro: Rio das Ostras, February 2000 (fl. fr.), *Pablo* (SP 363887).

Distribution, habitat and conservation:—*Gravatarum saxicola* occurs in Espírito Santo and Rio de Janeiro states between 50 to 600 m.s.m in ombrophilous forest as epipyhte and saxicolous (Fig. 5). Flowering and fruiting from August to February. *Gravatarum saxicola* has a wide distribution and several recorded populations, many of them are protected under natural reserves. In addition, *G. saxicola* is under cultivation in public collections. Despite that, it occurs in small population (Wendt *et al.* 2008) and its habitats is lossing because anthropic pressure. Thus, *Gravatarum saxicola* is classified as Vulnerable.

Comments:—*Gravatarum saxicola* is related to *G. multiflora* based on its inflorescences with elongated axis, which leads to many incorrect identification in herbaria. However, this is a superficial morphological similarity because *G. saxicola* has longer floral bracts and petals connate above epygynous tube. Sousa (2004) also report that *G. saxicola* has polen exine rugulated while *G. multiflora* has polen exine perforated.

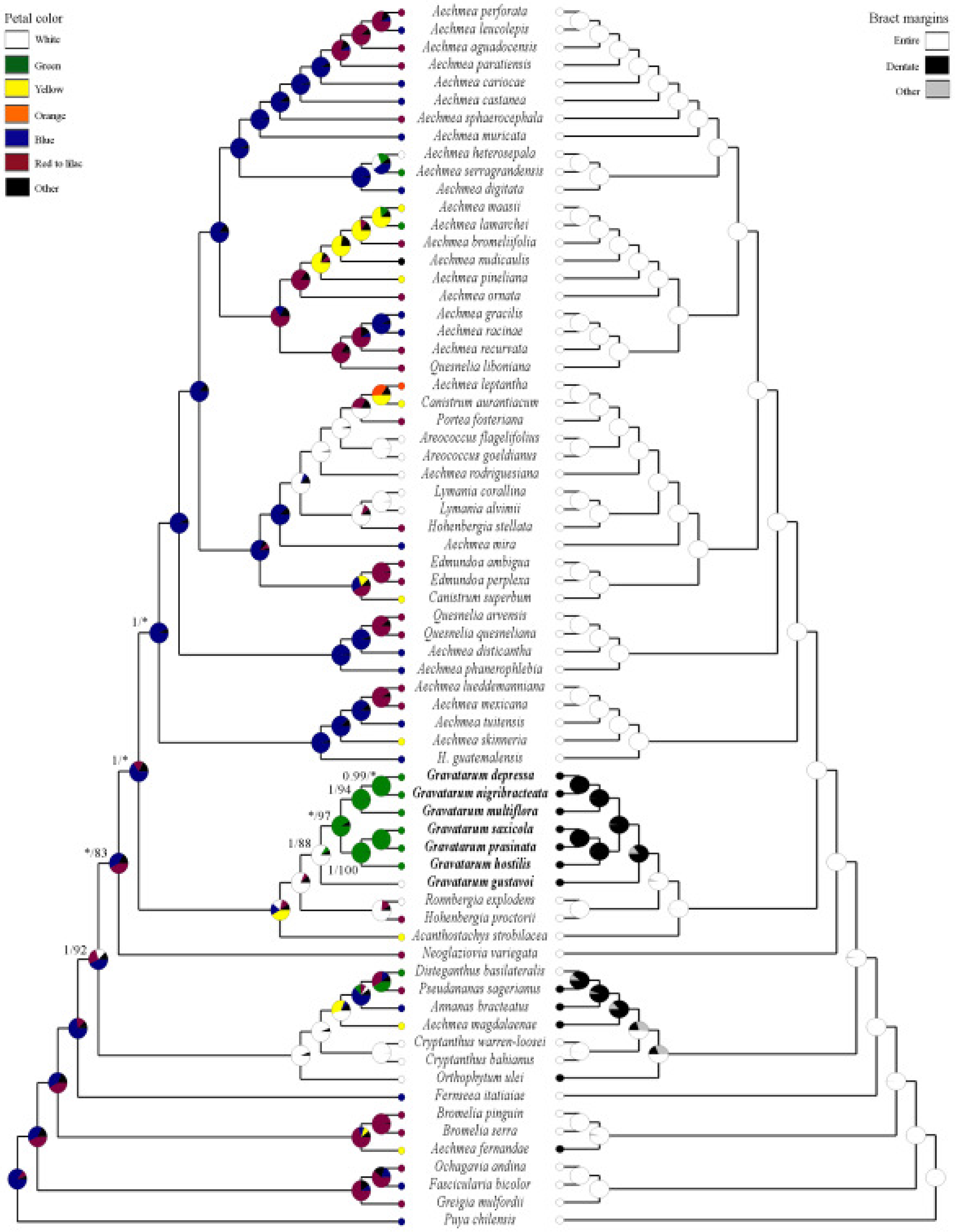

Figure 9.1. Topology of maximum credibility tree from bayesian analysis and ancestral reconstruction and distribution of petal colors and floral bract margins in Bromelioideae and especially to *Gravatarum*. Values of posterior probability (PP) and bootstrap (BS) is only for main clades of Bromelioideae and *Gravatarum* (PP/BS, * = PP< 95%, BS,<75%).

Figure 9.2. Species of *Gravatarum*. a. *G. depressa* J.R. Maciel & G. Sousa, inflorescence. b. *G. gustavoi* J.R. Maciel & G. Sousa, inflorescence. c-d. *G. multiflora* J.R. Maciel & G. Sousa. c. young green inflorescence. d. typical inflorescence. e. *G. nigribracteata* J.R. Maciel & G. Sousa, inflorescence. f. *G. hostilis* J.R. Maciel & G. Sousa, inflorescence. g-*G. depressa* J.R. Maciel & G. Sousa, details of flower and floral bracts in. h-*G. nigribracteata* details of flower and floral bracts in. Fotos: J.R. Maciel.

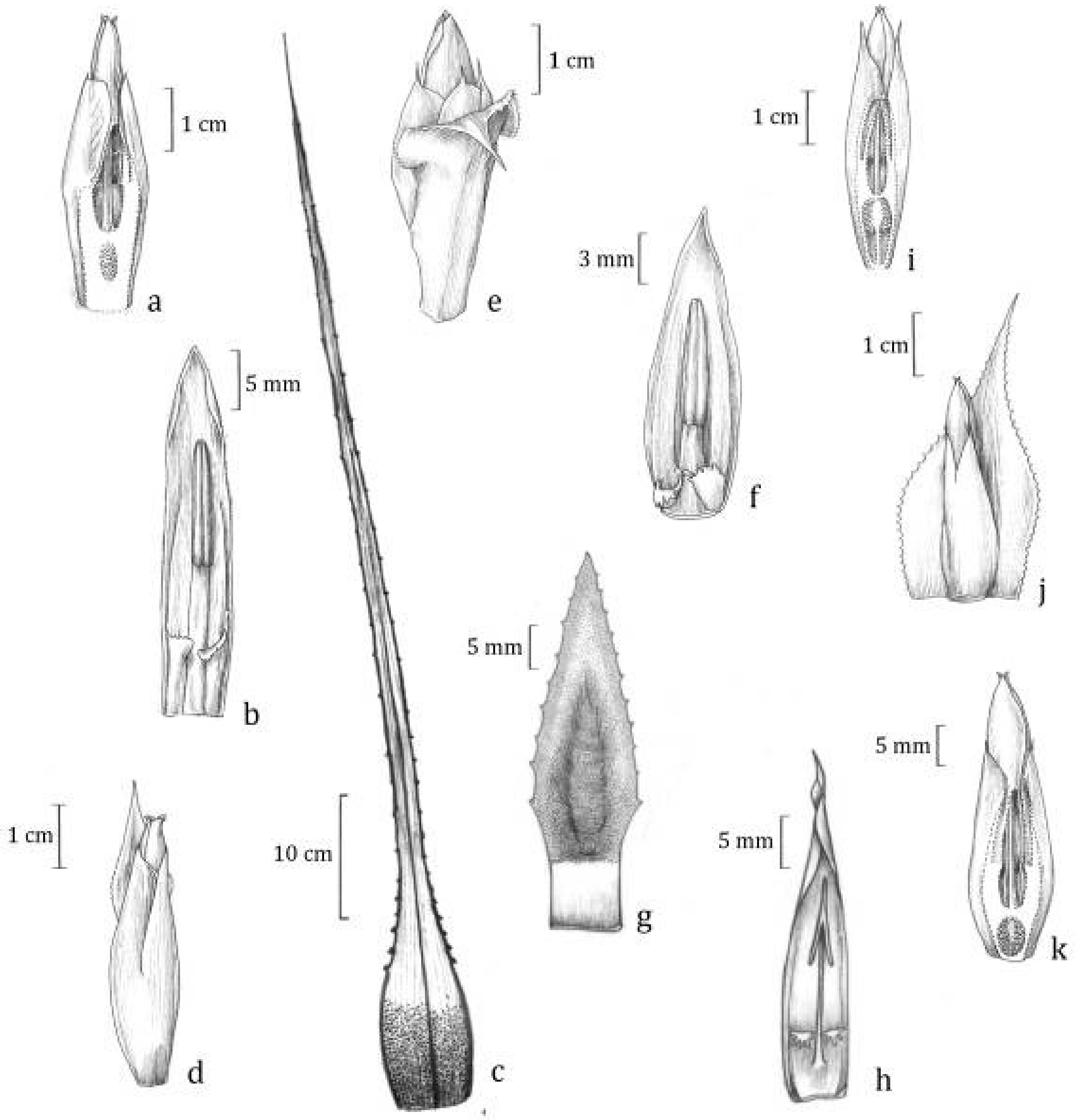

Figure 9.3. Some diagnostics characters of *Gravatarum* species. a-b. *G. depressa.* a. flower; b. petal, stamen and petal appendages (*G. Sousa et al. 491*). c. *G. gustavoi*. leaf blade and leaf sheats (*J.R. Maciel et al. 1929*). d. *G. hostilis*. flower and floral bract (*G. Sousa et al. 323*). e-f. *G. multiflora*. e. floral bract with retroflexed apex and flower; f. petal, stamen and petal appendages (*G. Sousa et al. 358*). g-h. *G. nigribracteata*. g. floral bract; h. petal, stamen and petal appendages (*J.R. Maciel et al. 1950*). i. *G. prasinata* flower in longitudinal section(*G. Sousa et al. 331*). J-k. *G. saxicola*. j. flower and floral bract; k. flower in longitudinal section (*Pablo SP-363887*).

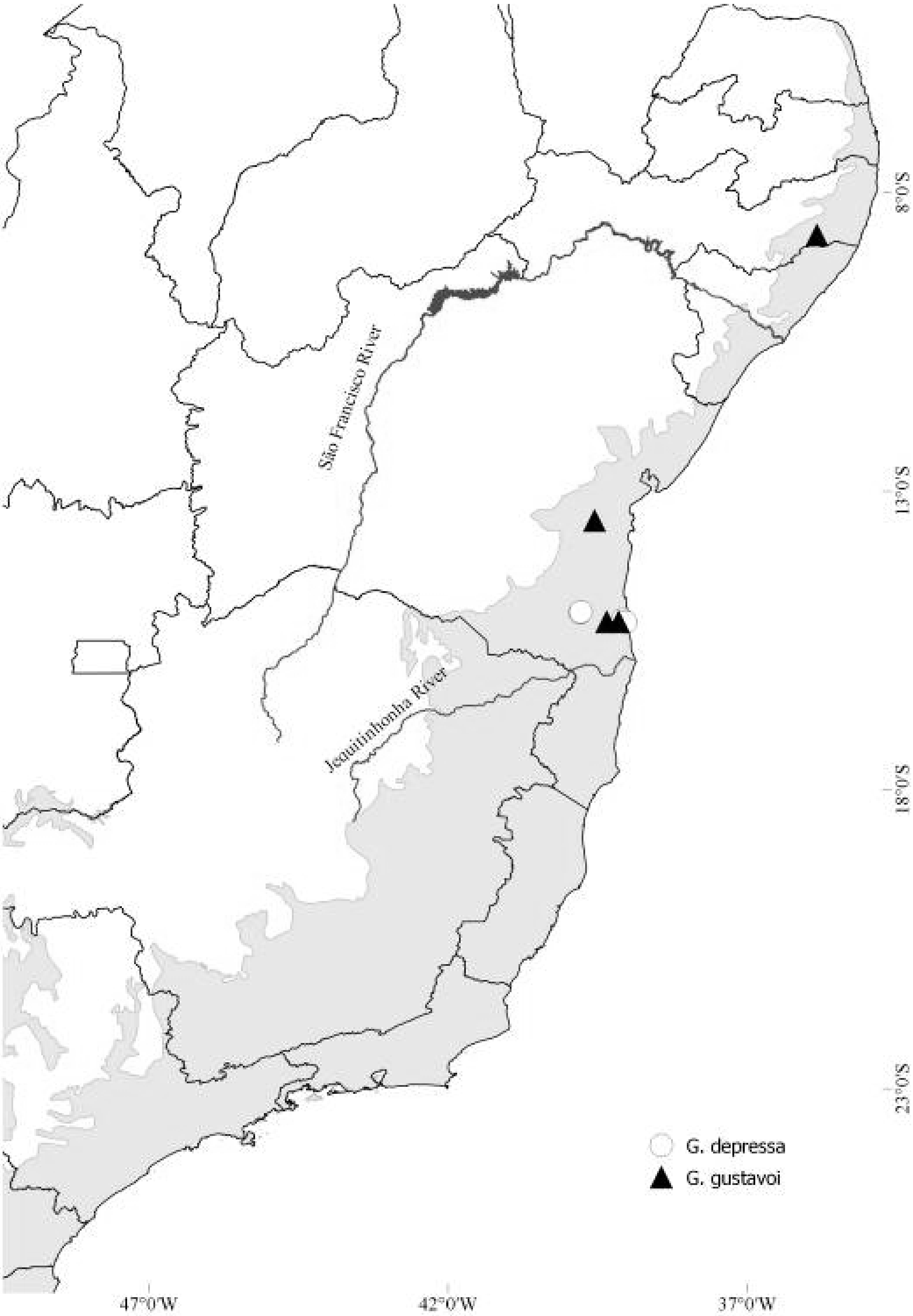

Figure 9.4. Geographic distribution of species of *Gravatarum*. Shaded area represents Atlantic Forest.

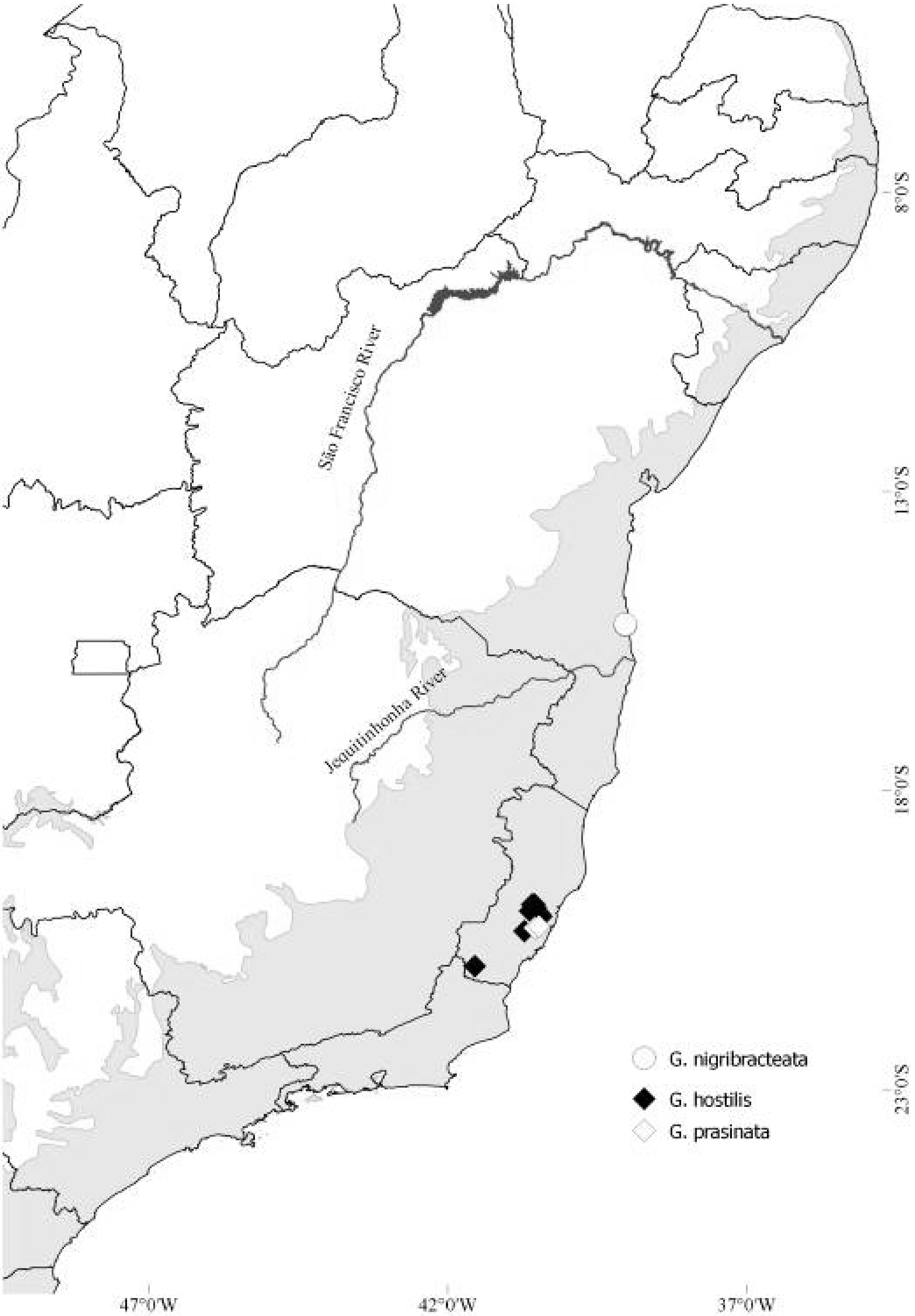

Figure 9.5. Geographic distribution of species of *Gravatarum*. Shaded area represents Atlantic Forest.

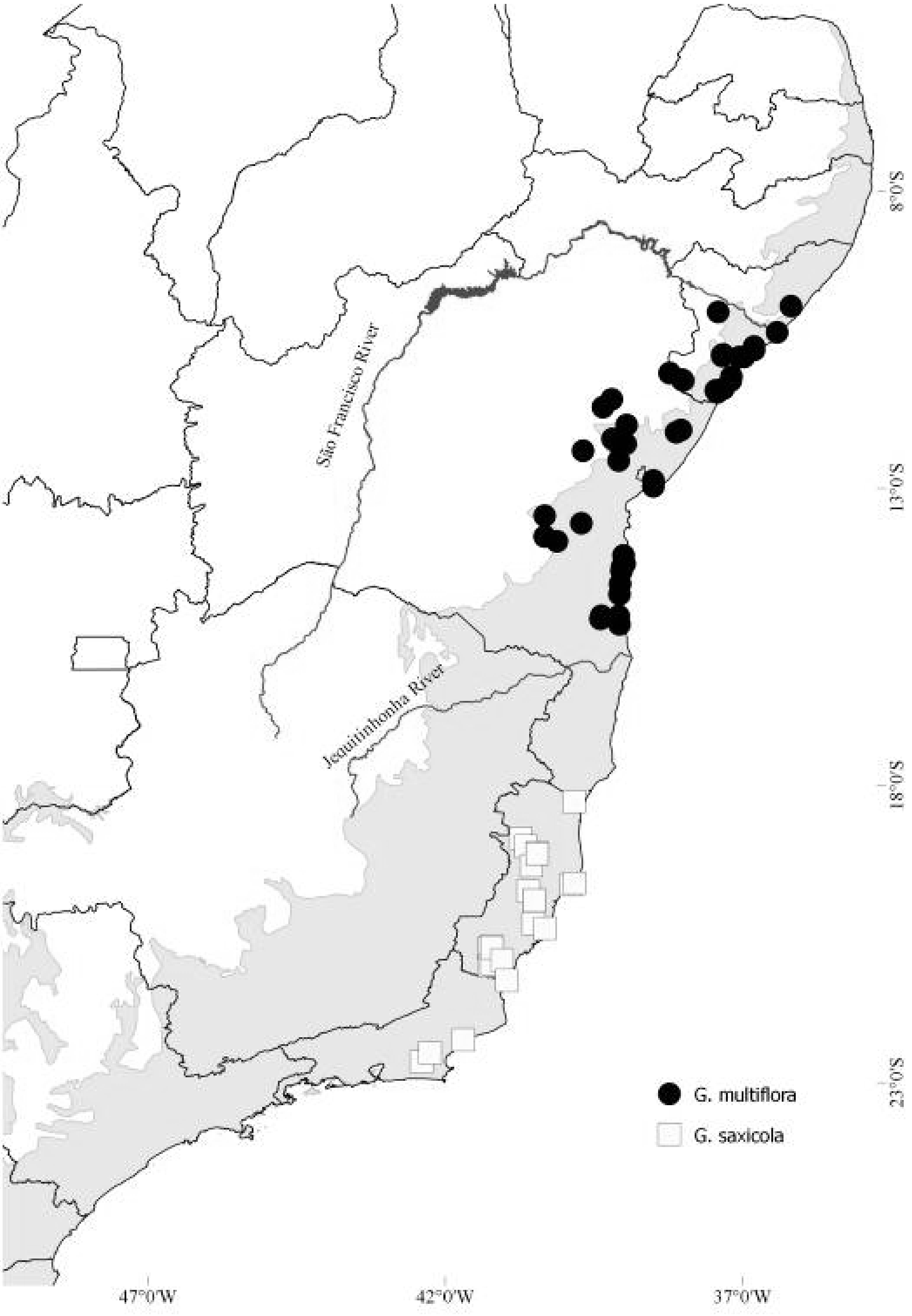

Figure 9.6. Geographic distribution of species of *Gravatarum*. Shaded area represents Atlantic Forest.

List of examined material

Alves, M. 1901 (4); **Amorim, A.M.** 1480 (4), 3581 (1), 3582 (1); **Amorim, B.S.** 297 (4); **Andrade-Lima, D.** 79-8763 (4), 79-8772 (4), 80-8813 (4); **Araújo, D. & Peixoto, A.** 6515 (7); **Assis, A.M.** 1428 (7); **Canela, B.** 01 (4), 02 (4); **Cardoso, D.** 1432 (4); **Carvalho, A.M.** 6320 (4); **Carvalho, D.N.** 85 (4); **Chamas, C.C.** 251 (3); **Conceição, S.F.** 25 (4); **Córdula, E.** 156 (4); **Coser, T.S.** 590 (7); **Costa, S.M.** 286 (4); **Cruz, A**. 76 (4); **Curran, H.M.** 297 (4); **Demuner, V.** 1883 (7), 2207 (7), 2384 (7), 2605 (7), 2774 (7), 3052 (7), 3196 (7), 3742 (7); **Dias, E.** ALCB-61419 (4), ALCB-67913 (4); **Farias, G.L.** 493 (1); **Farney, C.** 3410 (7); Favo**reto, F.C.** 114 (7), 147 (7), 162 (7); **Folli, D.A.** 3174 (7), 3879 (7), 4468 (1); **Fonseca, M.** ASE495 (4); **Fontana, A.P**. 1349 (7), 3222 (7); **Foster, M.** (7), 164 (7), 188 (7), 2451 (4), 2478 (4); **Foster, M. & Foster, R.** 71 (1), 118 (7), 224 (7); **Freire, G.S.** 21 (4); **Giaretta, A.O.** 25 (1); **Gomes, J.M.** 2392 (7), 2875 (7), 3011 (7); **Gomes, P**. 634 (4); **Grupo Pedra do Cavalo** 496 A (4); **Harley, E.** 17622 (4); **Hatschbach, G.** 58113 (7); **Jardim, J.G.** 3021 (2), 3062 (5), 3110 (4), 612 (1), 612 (4); **Kollmann, L.** 3736 (7), 3841 (7), 4018 (7), 4115 (7), 4915 (3), 8851 (7); **Landim, M.F.** 704 (4), 970 (4); **Leitman, P.** 183 (4), 262 (2), 262 (2), 395 (4); **Leme, E.M.** 5086 (4); **Lopes, L.C.** 16 (7); **Maciel, J.R.** 1837 (4), 1839 (5), 1861 (4), 1929 (2), 1934 (4), 1949 (1), 1950 (5), 1951 (4), 1965 (7), 1972 (3); **Manhães, V.C.** 27 (7); **Martinelli, G**. 15344 (4), 15377 (2), 15379 (4), 15623 (6), 15868 (4), **Melo, D.S.** 47 (4), 55 (4); **Melo, E.** 5417 (4); 6310 (4); **Oliveira, A.L.** ALCB-29469 (4); **Oliveira, R.P.** 764 (4); **Pereira, O.J.** 1618 (7), 2009 (7), 3610 (7), VIES-4618 (7); **Popovkin, A.V.** 327 (4); **Prata, A.P.** 2180 (4); **Queiroz, L.P.** 12981 (4), 3018 (4), 957 (4), **Read, R.W.** 3452 (4); **Read, R.W. & Daniel, G.S.** 3565 (5); **Ribeiro, M.** 510 (1); **Rogério, R.S**. (3); **Roque, N.** 2605 (4), 2715 (4); **Santana, S.J.** 01 (4); **Santos, J.R.** 11 (3); **Santos, R.** 59 (1); **Scardino, L.** 496 (4); **Seidel, A.** 625 (3); **Silva, P.E.** 109 (4); **Siqueira Filho, J.A.** 1436 (4), 1091 (2), 1436 (4); **Sousa, G.M.** 300 (4), 308 (1), 318 (3), 319 (7), 321 (3), 322 (3), 323 (3), 324 (3), 331 (6), 334 (4), 354 (4), 355 (4), 357 (4), 358 (4), 491 (1); **Thomas, W.W.** 12598 (4); **van den Berg, C.** 865 (4); **Varassin, I.G.** 12 (3); **Vervloet, R.R.** 2334 (3), 405 (3); **Viana, G.** 185 (4); **Wendt, T.** 286 (7), 327 (7), 449 (4), 479 (1).

10 Convergent evolution within an adaptive irradiation: elucidating diversification processes in Atlantic Forest

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Abstract

Aechmea subg*. Chevaliera* is polyphyletic and the majority of species which were classified in this subgenus emerge, basically, in two groups: *Gravatarum* and *A. sphaerocephala* group. Both groups share the same geographical and morphological space as an example of convergent evolution in Atlantic Forest. Thus, our aims are 1) to verify whether climatic niche and habitats of the *Gravatarum* and *A. sphaerocephala* group are similar; 2) to test whether they colonized in the same way Atlantic Forest; and 3) to evaluate whether they had the same evolutionary dynamics of environmental space occupation. We used the phylogeny of previous chapter to apply an analysis of divergence time of lineages, the reconstruction of ancestral area and habitat and the evolution of both groups in environmental space. We also compared the environmental niches of the two groups. The data available point differences in spatial and environmental evolutionary dynamics of both groups allow them to occupy similar habitats, environmental and geographical spaces in Atlantic Forest.

Keywords

Bromeliaceae, Bromelioideae, *Aechmea*, biogeography, evolution, neotropics

Introduction

Aechmea subg. *Chevaliera* is polyphyletic and the majority of species which were classified in this subgenus emerge, basically, in two clades with strong statistical support. The first clade is called *Gravatarum*, a genus with seven species; and the second clade is *A. sphaerocephala* group (Maciel *et al.* in prep.). They converge morphologically in growth form and both have huge rosettes forming tank plants. Evidences (Maciel *et al.* in prep.) pointed out the main events of diversification within this morphological space occurred in *Gravatarum* and *A. sphaerocephala* groups among Bromelioideae species from Atlantic Forest. In addition to extra large size, both share compact, large and multiflowered inflorescences; lignified floral bracts; and rigid sepals. However, the two groups are differentiated by floral bract margins dentate and flowers white or green in *Gravatarum* and floral bract margins entire and flowers lilac or blue in *A. sphaerocephala* group. Thus, study of comparative evolution between them is a great opportunity to understand process and dynamics that allow evolutionary lineages diversify in the same morphological and geographical space.

Convergent evolution is a common process and is defined as the evolution of similar features in different evolutionary lineages (George *et al.* 2014, Harmon *et al.* 2005, Losos 2011, Moen *et al.* 2013, Ord & Summers 2015). Terminology used to convergent evolution is controversial and several authors propose terminological constraints giving rise to terms like repeated evolution, phylogenetics repetition, combined convergence and homoplasy in order to avoid confusion with parallel evolution or parallelism (Losos 2011).

Losos (2011) proposed morphological convergence sometimes is not driven by natural selection and it does not represent adaptation to selective pressure of environments. Thus, convergent evolution may be the result of a random process of the exaptation over adaptation or a correlated response of another character which is under selective pressure. However, convergent evolution is always preceded of environmental similarities (Harmon *et al.* 2005, Losos 2011, Ord & Summers 2015, Patterson & Givnish 2011).

Several authors recorded convergent evolution within process of adaptive irradiation (Losos *et al.* 1994, Moen *et al.* 2013, Muschick *et al.* 2012, Pinto *et al.* 2008). Bromeliaceae is almost exclusive to the Neotropics with a striking adaptive irradiation process (Givnish *et al.* 2007, 2011, 2014). Common cases of homoplasy in Bromeliaceae reinforce morphological convergence along the evolutionary history of the family (Barfuss *et al.* 2005, Crayn *et al.* 2004, Givnish *et al.* 2007, 2011, 2014, Horres *et al.* 2000, 2007, Sass & Specht 2010, Schulte *et al.* 2005, 2009, Schulte & Zizka 2008, Silvestro *et al.* 2014, Terry *et al.* 1997). However, these cases were never studied to understand which dynamics, patterns and process allowed the morphological convergence.

In Bromelioideae, which is one of the eight subfamilies of Bromeliaceae, morphological convergence associated with low resolution of molecular data are the main causes of unclear systematics and evolutionary relationships in subfamily (Aguirre-Santoro *et al.* 2015, 2016, Evans *et al.* 2015, Faria *et al.* 2004, Heller *et al.* 2015, Horres *et al.* 2000, 2007, Louzada *et al.* 2014, Sass & Specht 2010, Schulte *et al.* 2005, 2009; Schulte & Zizka 2008). Sass & Specht (2010) proposed niche conservatism as hypothesis to explain high levels of homoplasy and geographical conservatism in Bromelioideae phylogeny, on the most representative sampling made in phylogenetics studies of subfamily until now. The same hypothesis had been issued by Schulte *et al.* (2005, 2009).

Thus, our aims are 1) to verify whether climatic niche and habitats of *Gravatarum* and *A. sphaerocephala* group are similar; 2) to test whether they colonized in the same way Atlantic Forest; and 3) to evaluate whether they had the same evolutionary dynamics of environmental space occupation. In this way, we can answer if the morphological convergence between the two groups is preceded of environmental similarities and place a testing hypothesis to future studies about natural selection.

Material and Methods

Divergence time analyses and diversification dynamics

In this analyse we used alignments, models substitution and bayesian topology from previous work (Maciel *et al.* in prep.). Then, we ran a combined and partitioned analysis of bayesian inference and time divergence assuming birth-death model of speciation in a relaxed molecular clock. To this analysis, we used the software BEAST 1.8.2 through Cipres Science Gateway phylogenetics services website (Drummond & Rambaut 2007, Miller *et al.* 2011). Fossil still unknown to Bromeliaceae, thus we input a secondary age for Bromelioideae based on previous studies of time divergence (Givnish *et al.* 2011, Silvestro *et al.* 2014). We applied a normal distribution for divergence between *Puya* and the rest of Bromelioideae with median age of 11.9 Ma and in the same way a median age of 7.09 Ma to Bromelioideae core. The genus *Puya* is the sister lineage of all Bromelioideae (Givnish *et al.* 2014, Silvestro *et al.* 2014). Then, the analysis was carried out in four independents Markov Chain (MCMC) with 100.000.000 generations and sampling after each 10.000 generations. The analysis was fixed on previous maximum credibility of Bayesian topology. Convergence among the Markov Chains was analyzed using the software Tracer (Rambaut & Drummond 2009) and the Chains were combined to access a maximum credibility tree using 10.000 generation randomly selected.

To analyse whether speciation dynamics in *A. sphaerocephala* group and *Gravatarum* were different, we performed a Bayesian Analysis of Macroevolutionary Mixtures-BAMM (Rabosky 2014, Rabosky et al. 2013 and www. bamm-project.org for more details about the analysis). We set the prior using BaMM priors function on R package BaMMtools to aplly the correct prior on the consensus tree. We followed the default to choose a Poisson rate prior 1.0 as a conservative approach. The analysis was run on four chains of 30.000,000 generation sampling after each 30.000 of generations. Convergence and effective sample size were tested in BaMMtools and after discarded 25% of the MCMC generations as burn-in we performed an analysis of BaMM to trace clade-specific diversification and to plot diversification rates through times.

Ancestral area and habitat reconstructions

We carried out DEC Lagrange (Dispersion-Extinction-Cladogenesis) and S-DIVA (Statistical-Dispersal Vicariance) analysis on software RASP (Yu *et al.* 2015) to reconstruct ancestral habitat and ancestral geographical distribution. To these analyses we used 10.000 trees generated from the combination of each four Markov Chains of the bayesian and divergence time estimations. We selected 1000 trees randomly among these 10.000 to calculate the mean frequency of ancestral variation. For each character we fixed a maximal number of characters states according to the numbers of observed. For each analysis we ran two independents chains with 10.000.000 generations and trees sampling at each 1000 generations. We did not apply constraints to analyses.

We collect distribution and habitat data of species of *A. sphaerocephala* group and *Gravatarum* in herbaria collection from ALCB, ASE, CEPEC, EAC, HRB, HUEFS, IAN, INPA, IPA, JPB, MBML, MIRR, MPEG, NY, PEUFR, RB, UFP, UFRN, UFRR, US and VIES (acronyms according Thiers continuously updated and available in http://sweetgum.nybg.org/ih/), field work on Atlantic Forest and other Brazilian vegetation along 2013-2015, and bibliographical survey.

Categorization of occurrence areas was based on patterns of distribution of species. We plotted all data distribution and found three endemism centers: a northeastern portion of Atlantic Forest, which partially overlaps Pernambuco Center of Endemism (Magalhães *et al.* 2014, Siqueira-Filho & Tabarelli 2006); a central distribution in Atlantic Forest with meridional limits in Jequitinhonha river; and finally a southeastern distribution with setentrional limits in Jequitinhonha river. Thus, we established the classification as A = northeastern of São Francisco river, B = central corridor of Atlantic Forest, C = south of Jequitinhonha river. Some species occupy two or more of these areas. These patterns of distribution are coherent with geographical distribution and paleomodelling studies in Atlantic Forest (Carnaval & Moritz 2008, Carnaval *et al.* 2014, Grazziotin *et al.* 2006, Turchetto-Zolet *et al.* 2013) and with previous geographic studies in Bromeliaceae (Martinelli *et al.* 2008).

We followed partially the dataset provided by BFG (2015) about distribution of species in Brazilian phytophysiognomies and combine it with our data to establish the habitat classification. Thus, the habitat codification is: A = ombrophilous forest, B = restinga, C = semi-decidual forest, D = Caatinga.

Environmental niche similarities

We selected eight more independent bioclimatic and altitudinal variables after a Pearson correlation analysis: altitude, mean annual temperature, temperature seasonality, annual variation in temperature, mean temperature of the hottest trimester, precipitation seasonality, precipitation of the hottest trimester and precipitation of the coldest trimester. We downloaded these variables from WorldClim database (available in http://worldclim.org and described in Hijmans *et al.* 2005).

We used these environmental variables to perform niche similarity, equivalency and overlap analyses using a principal component analysis calibrated on all climatic space of combined occurrence areas of both groups in order to evaluate whether the environmental niche occupied by *Gravatarum* and *A. sphaerocephala* group are similar in Atlantic Forest (PCA-env, described in Broennimman *et al.* 2012, Warren *et al.* 2008). PCA-env is implemented in ecospat package of R statistical environment. Niche overlap is based on D metrics of Schoener (Broennimman *et al.* 2012) and equivalency and similarity tests are based on statistical framework of Warren *et al.* (2008).

Environmental space evolution

To reconstruct the evolutionary history of each clade in their environmental spaces, we first calculated the mean value of each eight altitudinal and bioclimatic variables for each species. Then, we performed a specific analysis to each group based on topology of maximum likelihood tree. In this way we projected the phylogeny of each group in the environmental space defined for each environmental variable assuming a Brownian model of evolution according Revell (2013). This analysis was carried out on Phytools package implemented on R statistical environment (Revell 2012).

Results

Divergence time analyses and diversification dynamics

The time divergence analysis reveals both groups probably share a Pliocene origin (Table 1, Figures 1 e 2). *Gravatarum* diverged from the probable sister lineage at 4.5 Ma and the crown group has a mean age of 2.03Ma (CI = 3.22-1.02). While, *A. sphaerocephala* group had the initial divergence at 3.5Ma and the crown group has age of 2.41Ma (CI = 3.23-1.37). Speciation processes of them occurred in the same timeframe, since the lasts 2Ma during the Pleistocene (Figures 1 e 2). The graphs of diversification rates through time show no alteration in diversification rates in *A. sphaerocephala* group and *Gravatarum* (Figure 3). The dynamics of diversification in both groups were the same since.

Ancestral area reconstructions

General results of ancestral geographic area reconstruction are summarized in Table 1 e Figure 2. S-DIVA analysis showed the origin of *Gravatarum* to the central corridor of Atlantic

Forest. An ancestral distribution of remainder species in this group in the central corridor and south of Jequitinhonha River was broken in two areas in an event of vicariance (Figure 2). In this scenario, the Jequitinhonha River could be considered as a geographical barrier. However, none of these scenarios show any statistical support (Table 1). For the *A. sphaerocephala* group the S-DIVA analysis showed a combination of all three areas as ancestral distribution. Two vicariants events were identified for internal nodes (Table 1, Figure 2). The first separated an event of speciation in north of São Francisco river from the other areas (p=0.00) and the second separated two species in a former distribution comprising the north of Sao Francisco river and the central corridor (p=1). In both scenarios Sao Francisco River played a major role as geographical barrier.

DEC results show the same geographical dynamics scenarios to *Gravatarum* as found in S-DIVA analysis, with high probability. However, the DEC model is quite different than S-DIVA model for *A. sphaerocephala* group. In DEC results the ancestral area of *A. sphaerocephala* group was the north of São Francisco River. The vicariants scenarios were the same as these showed in S-DIVA analysis. Finally, the combined analysis confirms the scenarios of DEC. However, the origin of *A. sphaerocephala* group has low statistical support with probabilities less than 50%.

The data available point both groups with different geographical origins and dynamics during Atlantic Forest occupation. While *Gravatarum* colonized the Atlantic Forest in an unidirectional way (north-south) from central corridor to the south of Jequitinhonha River, the *A. spherocephala* group spread its distribution in north-south and south-north directions from a wide distribution in Atlantic Forest. The historical spatial segregation between both groups has other deepening level. *Gravatarum* had two centers of speciation: the first located at north and another one at south from Jequitinhonha River, more specifically close to Doce River. In its turn, *A. sphaerocephala* group had speciation processes at northeastern of São Francisco River, north and south of Jequitinhonha, more specifically close to north of Serra do Mar.

Ancestral habitat reconstruction

Results of habitat ancestral reconstruction showed the same origins in ombrophilous forest for both groups (Table 1, Figure 2). However, the observation of habitat distribution of species in each group show that *A. sphaerocephala* group colonized more habitats than

Gravatarum, which had its evolutionary history almost completely restricted to ombrophilous forest.

In *A. sphaerocephala* group, *A. digitata* had event of colonization in more open habitats, like semidecidous forest and Caatinga. In another clade of the same group, two other species colonized open habitats in restinga and semidecious forest (*A. muricata* and *A. sphaerocephala*). Finally, another two colonizations in open habitats were performed by *A. perforata* and *A. leucolepis*.

Environmental niche similarities

Results of niche similarities analysis demonstrated similar niches occupied by the two groups (n1->2 p= 0,009, n1<-2 p= 0,009). However, the values of niches overlap test and equivalency validation show niches partially overlapped and not equivalents (D=0.624, p=1). Thus, it was demonstrated that both groups evolved in similar but not overlapped environmental spaces in Atlantic Forest (Figure 4).

Environmental space evolution

Evolution on environmental space in the two groups followed a trend of ecological divergence among the species. In *Gravatarum*, however, the geographical proximity also indicated niche conservatism (Figures 5 and 6). The two clades formed in this genus (*A. multiflora+A. depressa+A.nigribracteata* and *A. saxicola+A. hostilis+ A. prasinata*) diverged in occupation of geographical spaces. Also, the divergence among the species of the same clade is smaller than among species of different clades (Figures 5 and 6). These results point out geographical and niche conservatism at level of each clade on *Gravatarum* diversification.

Environmental space occupation by *A. sphaerocephala* group did not indicate geographical conservatism. Species more closely related showed a significant divergence on variables altitude, mean annual temperature, annual variation in temperature and precipitation seasonality (Figures 5 and 6). In this way, *A. sphaerocephala* group speciation followed a clear ecological divergence as sympatric species.

Despite both groups share similar environmental spaces, they show differences on dynamics of environmental niche evolution. While in *Gravatarum* the dynamics display evidences of geographical and ecological conservatism in *A. sphaerocephala* group the dynamics is clearly divergent (Figures 5 and 6).

Discussion

Evolutionary dynamics in time and space of *Gravatarum* and *A. sphaerocephala* group

The last cycle of Andean uplift is the mainstream explanation to diversification processes and irradiation of many taxonomic groups in South America (Antonelli *et al.* 2009, Antonelli & Sanmartín 2011). Genera and families, which has richness center in Atlantic Forest, are among these taxa. However, taxa endemics to the Brazilian Atlantic Forest have Plio-Pleistocene temperature decreases and the last tectonic pulse of Serra do Mar as geoclimatic proxys to explain evolutionary histories (Antonelli *et al.* 2010, Givnish *et al.* 2011, 2014, Perret *et al.* 2006, 2013). Evolutionary histories of *Gravatarum* and *A. sphaerocephala* group seem to be connected to Plio-Pleistocene climatic changes and recent evolution of Serra do Mar.

Brazilian southeastern experienced along Pliocene a tectonic pulse, which originated the modern topography of Serra do Mar region (Almeida 1976, Almeida & Carneiro 1998). Givinish *et al.* (2011, 2014) reinforced this event as the most relevant to Bromelioideae speciation in Atlantic Forest. As suggested by Crisp *et al.* (2011), the pattern found here cannot refuse the hypothesis of last tectonic pulse in Serra do Mar acted as triggering event to speciation in *Gravatarum* and *A. sphaerocephala* group.

Speciation process of both groups occurred along the Pleistocene, a geological period with cycles of climatic changes affecting rainfall regimes and sea level variation (Ehlers & Poulsen 2009, Haq *et al.* 1987, Miller *et al.* 2005, Ravelo *et al.* 2004, Zachos *et al.* 2001). Changes in sea level are the main causes of several marine transgressions recorded to east Brazilian coast, even on Jequitinhonha and São Francisco rivers (Arai 2006, Rossetti *et al.* 2013). However, the last bigger marine transgressions recorded to the Brazilian rivers took place 5Ma ago (Rossetti *et al.* 2013) before the time of origin indicated for both groups by time divergence analysis.

Notwithstanding, sea level had been shifted from -2 up to +12 meters in relation to current level since late Pleistocene according to data of marine terrace from Brazilian northeastern (Barreto *et al.* 2002, Bezerra *et al.* 2003, Suguio *et al.* 2011). The sea level variation influenced the mouths of these rivers and also could play a role on watercourses and floodplains (Arai 2006, Dominguez *et al.* 1981, 1987, Dominguez & Martin 1982, Rossetti *et al.* 20013). Thus, marine transgressions have potential to turn these rivers on geographical barriers in speciation processes, as reported for Atlantic Forest (Carnaval & Moritz 2008, Grazziotin *et al.* 2006, Turchetto-Zolet *et al.* 2013). Many evidences of genetic diveristy in plant taxa from Brazilian eastern reinforce the importance of these rivers barriers in past environmental changes (Carnaval *et al.* 2014, Cazé *et al.*, 2016, Menezes *et al.* 2016). Despite these evidences, some authors had been criticized the importance of eastern Brazilian rivers as barriers to plant species (see revision in Turchetto-Zolet *et al.* 2013)

Heller *et al.* (2015) for the first time demonstrated the Jequitinhonha River is the meridional limit for many Atlantic Forest species in *Aechmea* (*Gravisia* complex). The results show the Jequitinhonha River acting as a probable geographical barrier in one speciation process of *Gravatarum*, which colonized the south of Bahia and Espirito Santo region. These two regions show expressive relevance for biodiversity in Atlantic Forest owing to high levels of endemism and richness (Carnaval & Moritz 2008, Fontoura & Santos 2010, Maciel *et al.* 2015).

The temporal and spatial segregations in diversification processes are indicatives of interaction between clades (Silvestro *et al.* 2015). Competition between distantly related clades is important for biodiversity generation (Silvestro *et al.* 2015). In addition, the diversification taxa equilibrium is only unsettled between competitor clades if one of them suffers extinction process (Benton 2009, Brusatte et al. 2008, Rosenzweig & MacCord 1991). *Gravatarum* and *A. sphaerocephala* group share the same geographical area and evolved in the same time frame. They also show diversification equilibrium that point out some stability in diversification process allowing coexistence of two convergent groups in Atlantic Forest. This equilbrium might be a cause of low diversity in *Gravatarum* and *A. sphaerocephala* group because they are competing for the same environmental and morphological spaces.

Niche and habitat evolution of *Gravatarum* and *A. sphaerocephala* group

Evolution of niche and habitat in *Gravatarum* and *A. sphaerocephala* group reveal the conservatism suggested for morphological convergence histories (Losos 2008, Pearman *et al.* 2008, Peterson *et al.* 1999, Peterson 2011, Wiens *et al.* 2010). Our results show both groups originated in ombrophilous Atlantic Forest. This kind of forest is featured by lesser climatic seasonality, evergreen, taller canopy and lesser salinity influence from the sea. Ombrophilous forest covers, mainly, the center and south part of Atlantic Forest (Thomas & Barbosa 2008).

The similarity of environmental spaces occupied by both groups in Atlantic Forest is a consequence of same habitat origins, according to our results from niche similarity analysis. Many authors had stated niche conservatism as a pertinent feature of evolution in several biological groups (Losos 2008, Pearman *et al.* 2008, Peterson *et al.* 1999, Peterson 2011, Wiens *et al.* 2010). Peterson (2011) showed niche conservatism is more pronounced in short time lapse. Therefore, it is expected high level of niche conservatism in *Gravatarum* and *A. sphaerocephala* group due to their recent evolutionary history.

Also, niche conservatism had been claimed to explain convergent evolution and morphological similarities among species of different groups (Harmon *et al.* 2005, Losos 2011, Ord & Summers 2015, Patterson & Givnish 2011). Indeed, one of the features of convergent evolution is habitat similarity, which would cause the same selective pressure under two taxa albeit Losos (2011) had proposed that convergent evolution is not always result of natural selection.

Our results confirm geographical conservatism in Bromelioideae as a result of evolution on same environmental niche, as established by Sass & Specht (2010). Despite that, there are strong evidences that niches of *Gravatarum* and *A. sphaerocephala* group are not equivalent, which means niche overlapping of these two groups does not have statistical support in a random sampling in distributional data (Broennimann *et al.* 2012, Warren *et al.* 2008). It happens because niche similarities in both groups are superficial and environmental spaces occupation in different ways by them points out distinct evolutionary dynamics.

There is a physiological support to explain these distinct dynamics environmental space occupation between both groups. Crayn *et al.* (2015) shows *A. sphaerocephala* group has typically CAM physiology strategy, while in *Gravatarum* has evidences of transitional stage to C_3 mechanism. To reinforce this observation, some species of *A. sphaerocephala* group (*A.*

leucolepis and *A. perforata*) have foliar anatomy typical of C_4 physiology (Sousa *et al.* 2005). The CAM or C_4 physiology allow species to tolerate water stress and light overexposure, while C_3 strategy is more typical of species from mesic environments (Benzing 2000). The variety of physiological strategies in *A. sphaerocephala* group might explain its ability to spread in a higher number of open habitats than *Gravatarum*. In contrast, the C_3 mechanism exclusiveness in *Gravatarum* could highlight why its species is almost limited to the same habitat.

Adaptive meaning of morphological spaces of *Gravatarum* and *A. sphaerocephala* group

Advantages that large bodies gives to species of *A. multiflora* and *A. sphaerocephala* groups to occupy Atlantic Forest habitats, it is not clear. Some species of different genera in Bromelioideae from Atlantic Forest have the same growth form pattern, although *Gravatarum* and *A. sphaerocephala* group are the most speciose groups in this morphological space (Smith & Downs 1979). Additionally, other groups with smaller bodies volumes are more speciose in Atlantic Forest than *Gravatarum* and *A. sphaerocephala* group (Heller *et al.* 2015, Goetze *et al.* 2016, Smith & Downs 1979).

Low species richness of the two groups could be imposed by competition for space. Usually, bromeliads communities in Atlantic Forest have one species of *Gravatarum* and *A. sphaerocephala* group (Canela *et al.* 2003, Maciel *et al.* 2015, Sousa 2004). Only three areas in Atlantic Forest have three or more species of them (Maciel *et al.* 2015, Fontoura & Santos 2010, Wendt *et al.* 2008). In one of these areas, population size of species from *Gravatarum* and *A. sphaerocephala* group are the smallest in community (Wendt *et al.* 2008). In addition, few areas where populations of these species are dominant are known (for example, *A. multiflora* in Marau, south of Bahia, Brazil).

Atlantic Forest deforestation process reduced drastically the space to population establishment of these species and, in some cases, population size (Siqueira-Filho & Tabarelli 2006). Our modeling studies identified potential distribution areas to species of *Gravatarum* and *A. sphaerocephala* group where nowadays are urbanized areas or crop fields (Maciel *et al.*, chapter four of this thesis). So, some inferences about community of these groups based only on landscape analysis must be careful. Despite that, very well preserved areas in Atlantic Forest and large fragments show bromeliads communities poorly represented by *Gravatarum* and *A. sphaerocephala* group (Melo *et al.* 2016, Siqueira *et al.* 2014), which suggests low population density as a natural pattern in these groups.

Recent advances in studies about ecological interaction between bromeliads and invertebrate communities give us some clues on advantages of a big body in tank Bromeliaceae. Carrias *et al.* (2012) and Céreghino *et al.* (2011) found that individual size and number of flowers in *Aechmea mertensii* can depend on which ant species colonize the ant garden. It happens because behavior of each ant species induces differences in composition of invertebrate communities in phytotelma leading to more or less nutrients allocation by plants.

Understanding why species of *Gravatarum* and *A. sphaerocephala* group share large, compact and multiflowered inflorescences is possible now. Also, it is possible to realize based on species descriptions of *Aechmea* subg. *Macrochordion*, *A.* subg. *Pothuava* and *A.* subg. *Ortigiesia* that simple inflorescences in these subgenera are often smaller e less flowered than inflorescences of *Gravatarum* and *A. sphaerocephala* group (Canella *et al.* 2003, Faria *et al.* 2010, Leme 2010, Leme & Kollman 2009, Leme & Kollman 2011, Leme *et al.* 2014, Maciel *et al.* 2014, Smith & Downs 1979, Sousa *et al.* 2009, Sousa 2004, Sousa & Wanderley 2014, Wendt 1997).

However, it is particularly difficult to define or hypothesize the adaptive meaning of these large and multiflowered inflorescences against compact and often inconspicuously inserted in rosettes. Specially because there is no clear influence of this kind of inflorescence in pollination inasmuch as studies in floral biology proves there is no spatio-temporal separation of species during blooming period and no differences of visitor's guild in bromeliad communities (Wendt *et al.* 2008) even among species of *Gravatarum* and *A. sphaerocephala* group (Sousa 2004, Wendt *et al.* 2008).

Despite this, Canela & Sazima (2003) stated large clumps of *Aechmea pectinata* individuals are more effective in fruit production than isolated plants. *Aechmea pectinata* also has compact and densely flower inflorescences (Wendt 1997). According Canela & Sazima (2003), this spatial distribution in dense clumps reinforces the territorialism behavior of hummingbirds which pollinate species. Compact inflorescence associated with dense clumps of individuals from *Gravatarum* and *A. sphaerocephala* group could be a plausible way to keep the pollinators around the plants during blooming periods, whereas the hummingbirds would spend less energy with numerous offers of flowers. While species of *Gravatarum* and *A. sphaerocephala* group lost in power of exhibition of its inflorescence, they could gain in fidelity of pollinator behaviors.

Finally, according Losos (2011) sometimes morphological convergence does not also mean adaptive advantage and it is not a result of selective pressure. Then, it is acceptable that morphological convergence in *Gravatarum* and *A. sphaerocephala* group has not any adaptive meaning and it could be generated as result of random process.

Conclusions

Clearly, differences in spatial and environmental evolutionary dynamics of both groups allow them to occupy similar habitats, environmental and geographical spaces in Atlantic Forest. This study brings out an illustrative and rich example of morphological convergence within an adaptive irradiation history. Moreover, it allows understand processes that increase biodiversity in an evolutionary historical hotspot, the Atlantic Forest.

Table 10.1. Result of time divergence, ancestral area reconstructions and ancestral habitat reconstructions. Conventions: Ma = millions of years; DEC = ancestral area and habitat estimated on Dispersion-Extinction-Cladogenesis analysis, DIV = ancestral area and habitat estimated on Statistical-Dispersal Vicariance analysis, PP = probability, p-v = p value of S-DIVA. Geographical areas categories: A = northeastern of São Francisco river, B = central corridor of Atlantic Forest, C = south of Jequitinhonha river. Habitats categories: A = ombrophilous forest, B = restinga, C = semi-decidual forest, D = Caatinga. The group names represent the two groups analyzed and in details are node names with vicariant events identified (orange dots in Figure 2 and with the name of basal species in the Table 1). For best understanding, compare the results of this table with Figure 2.

	Time (Ma)		**Ancentral area reconstruction**					**Ancestral habitat reconstruction**				
Node	**Mean**	**95% HPD**	**DEC**	**PP**	**DIV**	**PP**	**p-v**	**DEC**	**PP**	**DIV**	**PP**	**p-v**
Gravatarum	2.03	3.22-1.02	B	0.74	B	0.76	1	A	1	A	1	1
Gravatarum-node	1.54	2.43-0.69	BC	1	BC	1	0.48	A	1	A	1	1
A. sphaerocephala group	2.41	3.27-1.37	A	0.74	ABC	0.25	0.00	A	0.7	A	1	0.00
A. muricata-node	1.72	2.40-0.91	AC	1	AC	1	0.00	A	0.9	A	1	0.00
A. serragrandensis-node	0.77	1.42-0.23	AB	1	AB	1	1	A	1	A	1	1

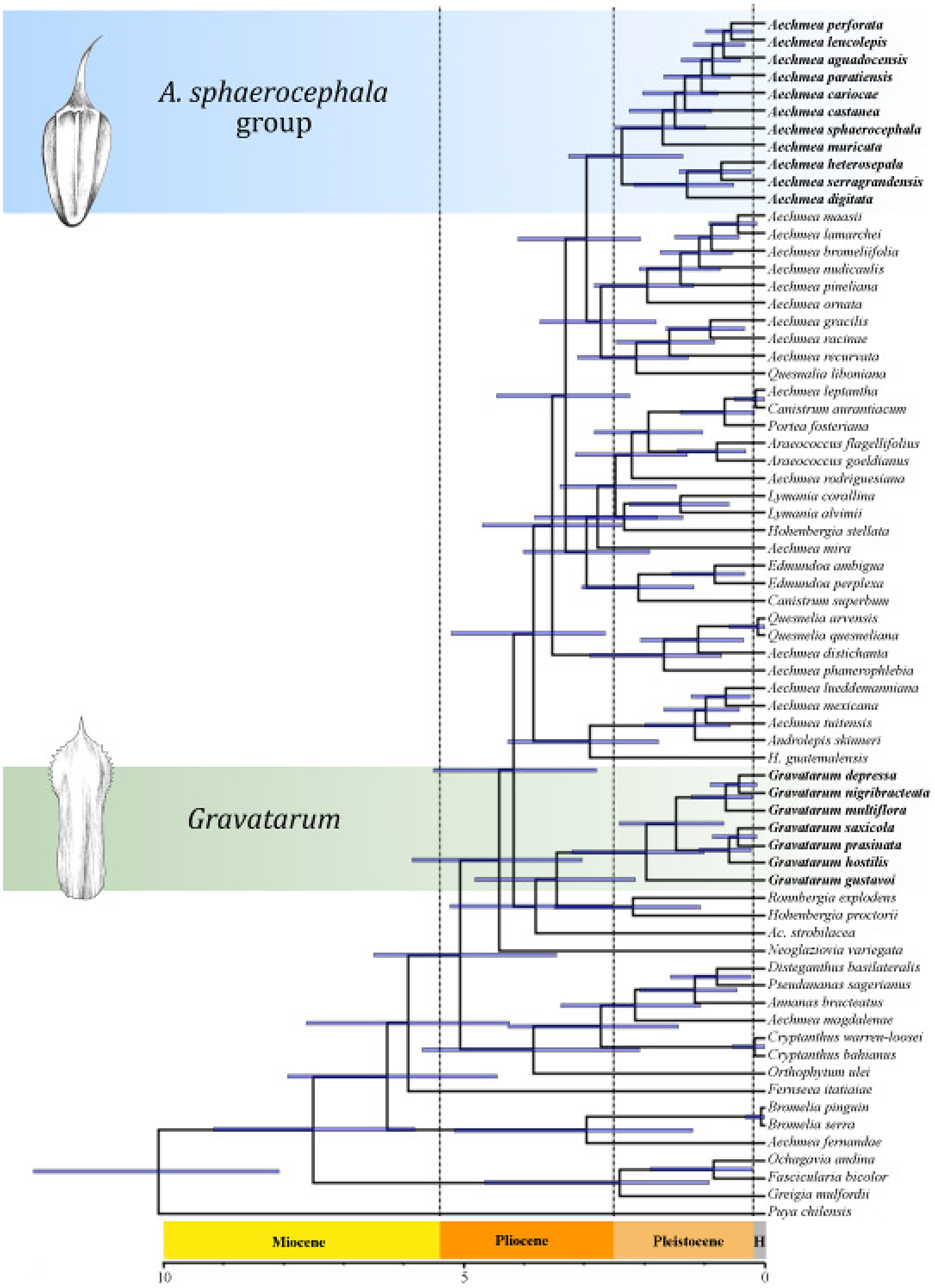

Figure 10.1. Beast chronogram of bayesian analysis of time divergence in Bromelioideae. In bold are highlighted *Gravatarum* and *A. sphaerocephala* group. The bars represent 95% confidence interval. The avatars represent the floral bract, one of the main difference between the two groups.

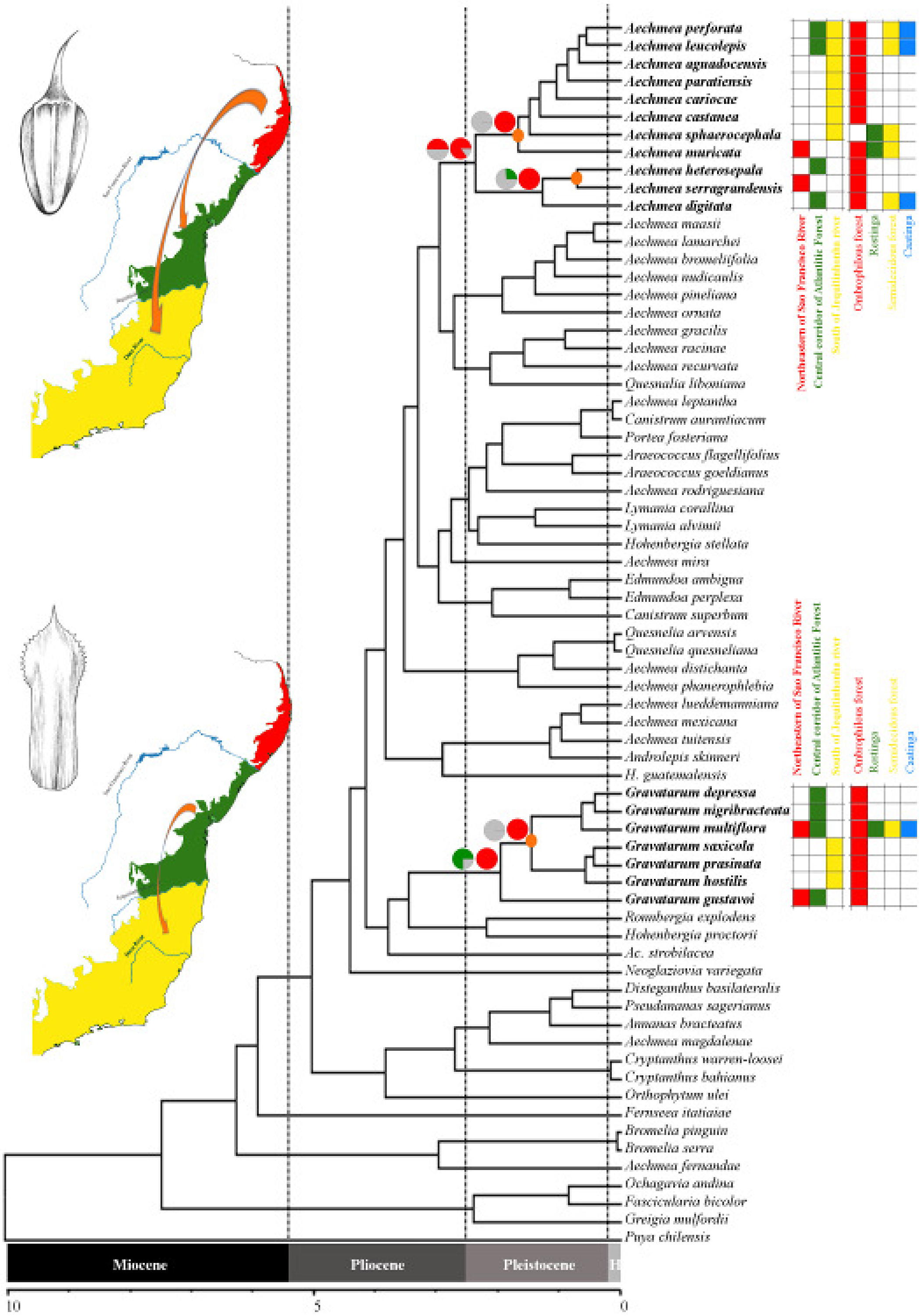

Figure 10.2. Time dynamics of environmental and geographical spaces occupations by *Gravatarum* and *A. sphaerocephala* group, highlighted in bold. Beast chronogram with mean ages and geological scale. Left maps and dots in nodes represent vicariant events estimated in S-DIVA, DEC and combined analysis. Pie graphs above branches represent the probability of ancestral area (right) and ancestral habitat (left). Next to the species names is the distribution on geographical areas and habitats. For more details, see Table 1.

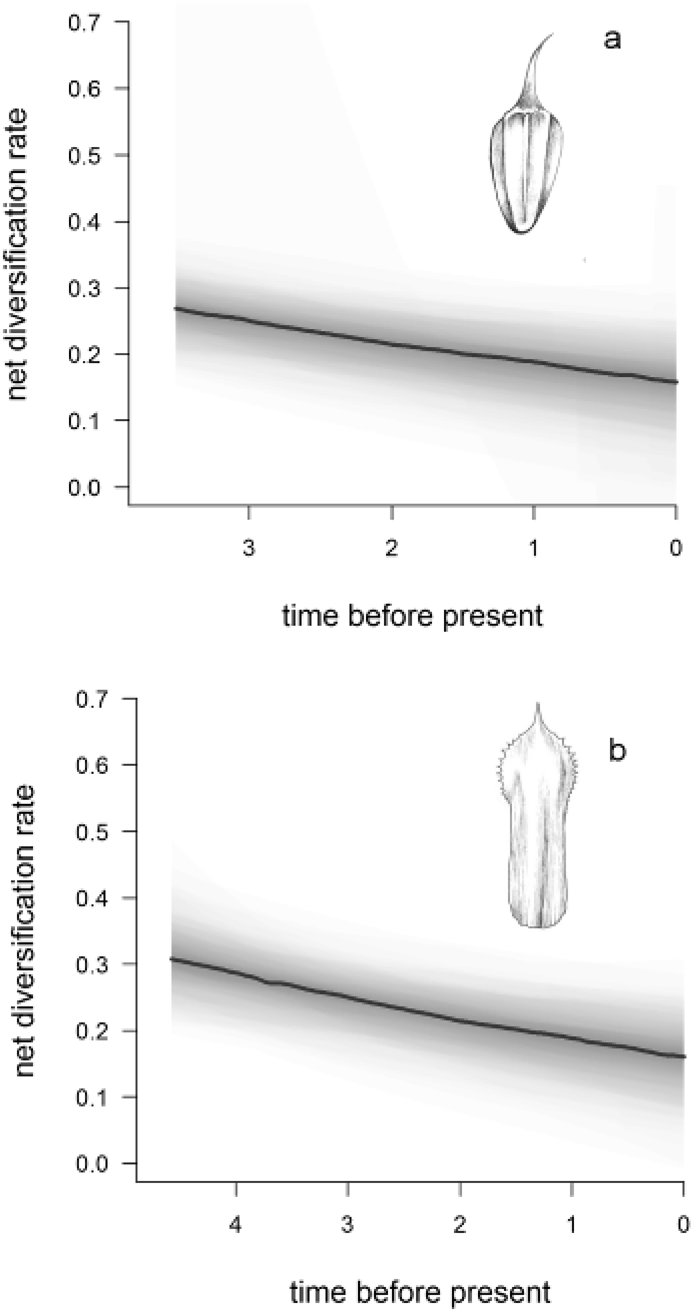

Figure 10.3. Rates-through-time plots of net diversification utilizing BAMM analysis for *A. sphaerocephala* group (a) and *Gravatarum*(b). Dark line represent the median values and the shaded area means the 95% interval of confidence.

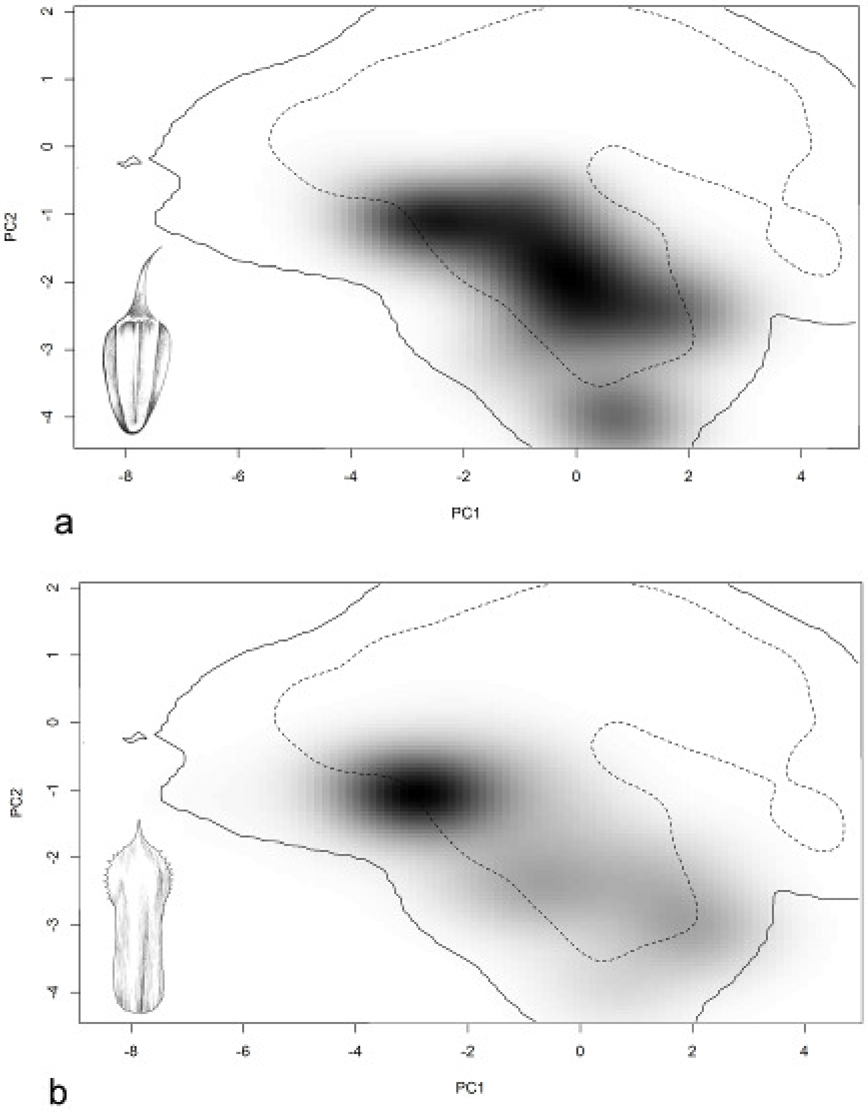

Figure 10.4. Environmental space occupied by *Gravatarum* (a) and *A. sphaerocephala* group (b) in Atlantic Forest. This graph is a result from niche similarity and overlap analysis carried out on R using the package ecospat. Shaded polygons represent the density of occurrences of species occupied by cell in a gray scale from 0 to 100%, where black one is the densest cells. Solid contour line represents 100% of all environmental available (background) in Atlantic Forest for the two groups and the dashed line the 50%.

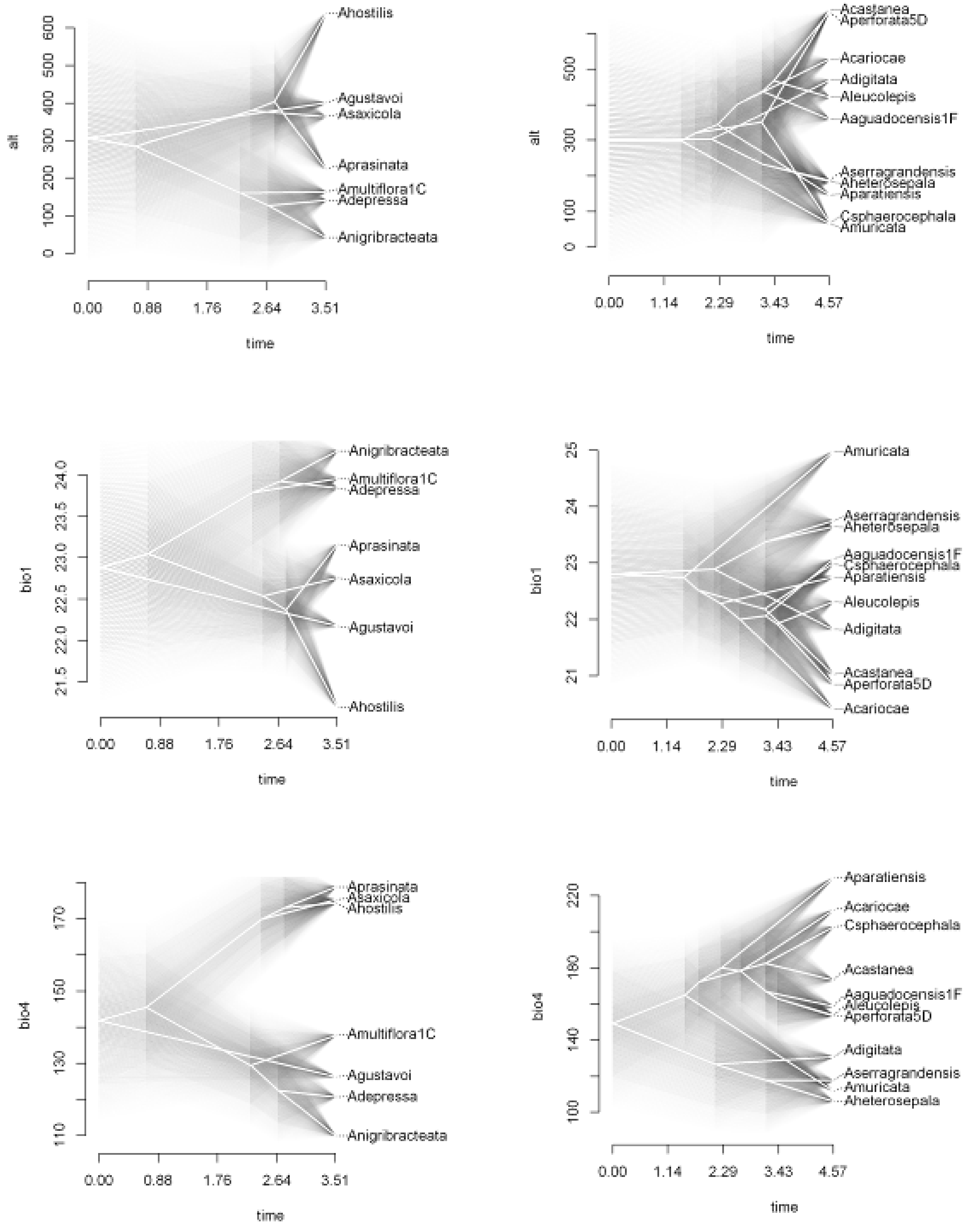

Figure 10.5. Reconstruction of trait evolution of niche space (bioclimatic and altitudinal traits) and evolutionary time since the root of *Gravatarum* (first column) and *A. sphaerocephala* group (second column). Blue shade represents the confidence interval of 95% of the analysis. This figures show the evolution of altitude (alt), annual mean temperature (bio1) and temperature seasonality (bio4).

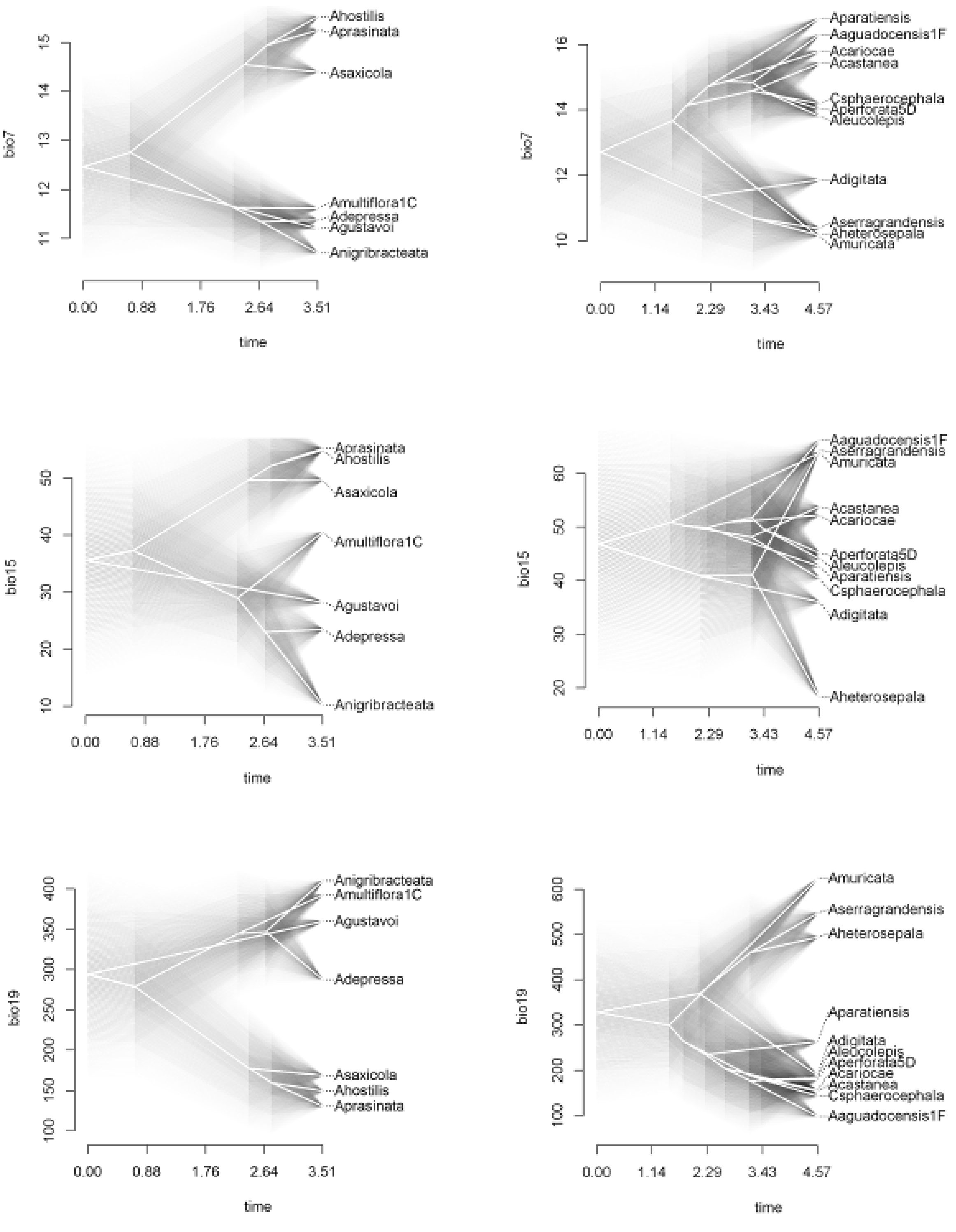

Figure 10.6. Reconstruction of trait evolution of niche space (bioclimatic and altitudinal traits) and evolutionary time since the root of *Gravatarum* (first column) and *A. sphaerocephala* group (second column). Blue shade represents the confidence interval of 95% of the analysis. This figures show the evolution of temperature annual range (bio7), precipitation seasonality (bio15) and precipitation of coldest quarter (bio19).

11 Considerações finais

Com a compilação dos artigos apresentados aqui foi possível traçar um panorama da diversidade de *Aechmea* na Floresta Atlântica ao Norte do Rio São Francisco; da qualidade das informações sobre o habitat dessas espécies; das conexões possíveis que espécies de bromélia com distribuição disjunta entre a Floresta Atlântica e Amazônica podem ter estabelecido no passado; e das dinâmicas evolutivas associadas aos grupos com espécies endêmicas na Floresta Atlântica ao Norte do Rio São Francisco.

O conhecimento taxonômico de *Aechmea* na porção setentrional da Floresta Atlântica parece ter atingido um patamar de estabilidade. O acréscimo de espécies nas listas dos trabalhos recentes e no desenvolvido aqui apresenta uma tendência de redução. Não obstante, ficou claro com os novos registros de ocorrência que o conhecimento sobre a distribuição de alguns táxons pode ainda ser aprimorado com futuros esforços de coleta.

O conhecimento da distribuição tem impactos significativos nos estudos de modelagem, e as premissas decorrentes de nossas conclusões deverão ser ampliadas para outros grupos endêmicos da Floresta Atlântica. É possível concluir que não necessariamente a quantidade de amostras de ocorrências afeta o conhecimento sobre o nicho de uma espécie. Além disso, a causa de lacunas na distribuição e na apreensão do espaço ambiental de alguns táxons deve ser associada também à perda de habitat e à intensa fragmentação experienciada nessa porção da Floresta Atlântica.

A informação da qualidade dos habitats foi fundamental para apoiar as conclusões de que espécies com distribuição disjunta entre a Floresta Atlântica ao norte do Rio São Francisco e a Floresta Amazônica tiveram oportunidades no passado para migrar entre as duas áreas através de um corredor estabelecido ao longo da costa atlântica. Diante do fato de que as mudanças climáticas são cíclicas e os padrões de disjunção são verificados em diversos táxons, nossas conclusões neste tópico ganham maior amplitude. Além disso, os resultados fizeram um acréscimo significativo no paradigma que explica esse tipo disjunção ao deslocar o eixo de importância do interior do Nordeste para o litoral, como possível corredor.

Os resultados da filogenia abriram oportunidades e permitiram resolver outras questões. Pela primeira vez, uma amostragem significativa de *Aechmea* subg. *Chevaliera* foi incluída no contexto filogenético de Bromelioideae. Isso permitiu confirmar que o subg. *Chevaliera* é um grupo polifilético e algumas espécies tradicionalmente classificadas no subgênero na verdade nem pertencem à linhagem core de Bromeliodeae, onde está o gênero *Aechmea*. Além disso, ficou claro que a inflorescência estrobiliforme foi sobrevalorizada como estado de caracter definidor do subgênero levando ao posicionamento sistemático artificial de muitas espécies. Como decorrência, um novo gênero foi proposto e descrito para circunscrever espécies do complexo taxonômico *A. multiflora.* Esse novo gênero, chamado de *Gravatarum*, e circunscreve sete espécies de um grupo monofilético e com forte sustentação estatística.

Dois grupos morfologicamente convergentes e simpátricos que reúnem a maior parte das espécies classicamente atribuídas ao subg. *Chevaliera* foram identificados nas análises. Eles são o gênero *Gravatarum* e o grupo *A. sphaerocephala*. Este achado se mostrou como uma oportunidade de estudar com mais detalhe os processos e forças evolutivas que estão na base de um dos mais bem documentados fenômenos de irradiação adaptativa. O estudo da biogeografia deles também permitiu entender processos de colonização da Floresta Atlântica e em especial concluir que o Centro de Endemismo Pernambuco foi palco de múltiplos e independentes eventos de colonização e especiação.

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