



Universidade Federal de Uberlândia

Instituto de Biologia

Programa de Pós-Graduação em Ecologia, Conservação e Biodiversidade

Espécies anemocóricas no cenário de mudanças climáticas: história natural
e consequências funcionais

Larissa Alves de Lima

Uberlândia – Minas Gerais

Março, 2024

Larissa Alves de Lima

Espécies anemocóricas no cenário de mudanças climáticas: história natural
e consequências funcionais

Tese apresentada à Universidade Federal
de Uberlândia, como parte das exigências
do Programa de Pós-Graduação em
Ecologia, Conservação e Biodiversidade
para a obtenção do título de doutor.

Orientadora: Helena Maura Torezan Silingardi

Coorientador: Diego Anjos

Uberlândia – Minas Gerais

Março, 2024

Dados Internacionais de Catalogação na Publicação (CIP)
Sistema de Bibliotecas da UFU, MG, Brasil.

L732e
2023

Lima, Larissa Alves de, 1995-

Espécies anemocóricas no cenário de mudanças climáticas [recurso eletrônico] : história natural e consequências funcionais / Larissa Alves de Lima. - 2023.

Orientadora: Helena Maura Torezan Silingardi.

Coorientador: Diego Anjos.

Tese (Doutorado) - Universidade Federal de Uberlândia, Programa de Pós-graduação em Ecologia, Conservação e Biodiversidade.

Modo de acesso: Internet.

Disponível em: <http://doi.org/10.14393/ufu.te.2024.5002>

Inclui bibliografia.

Inclui ilustrações.

I. Ecologia. I. Silingardi, Helena Maura Torezan, 1968-, (Orient.). II. Anjos, Diego, 1989-, (Coorient.). III. Universidade Federal de Uberlândia. Programa de Pós-graduação em Ecologia, Conservação e Biodiversidade. IV. Título.

CDU: 574

André Carlos Francisco
Bibliotecário Documentalista - CRB-6/3408



UNIVERSIDADE FEDERAL DE UBERLÂNDIA

Coordenação do Programa de Pós-Graduação em Ecologia,
Conservação e Biodiversidade

Av. Pará, 1720, Bloco 2D, Sala 26 - Bairro Umuarama, Uberlândia-MG, CEP 38405-320
Telefone: (34) 3225-8641 - www.pggeco.ib.ufu.br - ecologia@umuarama.ufu.br



ATA DE DEFESA - PÓS-GRADUAÇÃO

Programa de Pós-Graduação em:	Ecologia, Conservação e Biodiversidade				
Defesa de:	Tese, número 92, PPGEGB				
Data:	vinte e seis de março de dois mil e vinte e quatro	Hora de início:	14:00	Hora de encerramento:	18:20
Matrícula do Discente:	12013ECR005				
Nome do Discente:	Larissa Alves de Lima				
Título do Trabalho:	Espécies anemocóricas no cenário de mudanças climáticas: história natural e consequências funcionais				
Área de concentração:	Ecologia				
Linha de pesquisa:	Ecologia de comunidades e biodiversidade				
Projeto de Pesquisa de vinculação:	Resiliência em redes de interações ecológicas no cerrado: impacto do fogo intenso na biodiversidade interativa				

Reuniu-se por videoconferência a Banca Examinadora designada pelo Colegiado do Programa de Pós-graduação em Ecologia, Conservação e Biodiversidade assim composta pelos doutores: Elisa Queiroz Garcia - UFU; Drielly da Silveira Queiroga - University of Cincinnati; Denise Lange - UTFPR; Jean Carlos Santos - UFS e Helena Maura Torezan Silingardi - INBIO/UFU, orientador(a) do(a) candidato(a).

Iniciando os trabalhos o(a) presidente da mesa, Dr(a). Helena Maura Torezan Silingardi, apresentou a Comissão Examinadora e o(a) candidato(a), agradeceu a presença do público e concedeu ao(à) Discente a palavra para a exposição do seu trabalho. A duração da apresentação do(a) Discente e o tempo de arguição e resposta foram conforme as normas do Programa.

A seguir o(a) senhor(a) presidente concedeu a palavra, pela ordem sucessivamente, aos(às) examinadores(as) que passaram a arguir o(a) candidato(a). Ultimada a arguição, que se desenvolveu dentro dos termos regimentais, a Banca, em sessão secreta, atribuiu o resultado final, considerando o(a) candidato(a):

Aprovado(a).

Esta defesa faz parte dos requisitos necessários à obtenção do título de Doutor.

O competente diploma será expedido após cumprimento dos demais requisitos, conforme as normas do Programa, a legislação pertinente e a regulamentação interna da UFU.

Nada mais havendo a tratar foram encerrados os trabalhos. Foi lavrada a presente ata que após lida e achada conforme foi assinada pela Banca Examinadora.



Documento assinado eletronicamente por **Helena Maura Torezan Silingardi, Professor(a) do Magistério Superior**, em 26/03/2024, às 18:21, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Drielly da Silveira Queiroga, Usuário Externo**, em 01/04/2024, às 17:40, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Jean Carlos Santos, Usuário Externo**, em 01/04/2024, às 18:47, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Elisa Queiroz Garcia, Usuário Externo**, em 02/04/2024, às 08:14, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Denise Lange, Usuário Externo**, em 02/04/2024, às 14:06, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



A autenticidade deste documento pode ser conferida no site https://www.sei.ufu.br/sei/controlador_externo.php?acao=documento_conferir&id_orgao_acesso_externo=0, informando o código verificador **5239972** e o código CRC **90966977**.

Agradecimentos

Agradeço à Fapemig pelo auxílio financeiro, ao Programa de Pós-Graduação em Ecologia, Conservação e Biodiversidade, e à Universidade Federal de Uberlândia por todo conhecimento adquirido e estrutura física que permitiram a realização deste trabalho.

Agradeço aos meus pais, que nunca mediram esforços para que meus sonhos se tornassem realidade, que sempre me apoiaram e que me criaram na base do diálogo, sendo grande amigos e confidentes. Agradeço à minha irmã por todas as palavras de apoio e pela cumplicidade.

Agradeço à minha orientadora, Helena Maura Torezan Silingardi, e ao meu coorientador, Diego Anjos. Obrigada pela dedicação! Obrigada por contribuírem tanto para o meu crescimento profissional, quanto pessoal. O mundo, com certeza, precisa de mais pessoas como vocês!

Agradeço do fundo do meu coração, aos meus dois grandes amigos, Letícia Rodrigues Novaes e Marcos Lima de Oliveira, que sempre me apoiaram e tanto contribuíram para essa tese. Não existem palavras capazes de expressar meu carinho por vocês.

*Dedico este trabalho ao meu avô, Vicente Barbosa de Lima,
que sempre será a minha grande inspiração.*

Sumário

Introdução geral	1
Referencias.....	5
Capítulo 1 - How much are phenological events phylogenetically related in the tropical savanna?.....	8
Abstract	9
Introduction.....	10
Materials and methods	12
Study site	12
Plant species	12
Data analysis.....	13
Congeneric species will present the same phenological patterns	14
Species phenophases are intensely related to climate variables	14
Unfavorable abiotic conditions decrease potential reproductive success by affecting characteristics such as inflorescences, floral buds, flowers, and young and ripe fruits.....	15
Results.....	17
Congeneric species will present the same phenological patterns	17
Species phenophases are intensely related to climate variables	26
Unfavorable abiotic conditions decrease potential reproductive success by affecting characteristics such as inflorescences, floral buds, flowers, and young and ripe fruits.....	30
Discussion	33
Acknowledgment	36
References.....	36
Capítulo 2 - Biology and reproductive ecology of <i>Qualea multiflora</i> Mart. (Vochysiaceae) in a Brazilian Savanna	43
Abstract	44
Resumo	45
Introduction.....	46
Materials and methods	48
Study site	48
Plant specie	48
Specie phenology.....	49
Floral display and resources	51

Breeding system	52
Floral visitor	53
Results.....	54
Species phenology	54
Floral phenology.....	58
Floral display and resources	61
Breeding system	63
Floral visitors.....	64
Discussion	91
Species phenology	92
Floral phenology.....	93
Floral display and resources	94
Breeding system	95
Floral visitors.....	95
Final remarks	97
Acknowledgment	97
References.....	98
Capítulo 3 - Predicting the impact of global climate change in the geographic distribution of anemochoric species	111
Introduction.....	113
Results.....	115
How to evaluate the model?	115
Which bioclimatic variables best explained the geographic distribution for each species?.....	118
What is the current distribution of the species?.....	120
What changes will occur?.....	125
Which conservation unit will have the greatest potential for species richness?...	126
Discussion	131
Materials and Methods.....	133
Species data	133
Environmental data.....	135
How to evaluate the model?	136
Which bioclimatic variables best explained the geographic distribution for each species?.....	136
What changes will occur?.....	137
Which conservation unit will have the greatest potential for species richness?...	138

References.....	142
Supplementary	148

Introdução geral

Nos últimos 150 anos, como resultado das atividades antrópicas, como a queima de combustível fósseis e a conversão de áreas naturais para atividades agropecuárias e extensão de áreas urbanas, as concentrações de dióxido de carbono (CO₂) na atmosfera quase duplicaram, aumentando a temperatura média do planeta em aproximadamente 3°C (Arrhenius 1896; Artaxo 2020). As projeções futuras mostram que até o final do século XXI, a temperatura média mundial poderá aumentar mais 3°C (Moss et al. 2010). Para a América do Sul, as projeções mostram um aumento de até 4°C e suas áreas de savana, ou Cerrado, a temperatura média aumentará até 6°C (Marengo 2006; Bustamante et al. 2012).

O aumento da temperatura também traz mudanças na precipitação, umidade e velocidade do vento, estando interligadas, uma variável alterada leva a mudanças em outra (Dore 2005). Há mudanças notáveis na distribuição, intensidade e frequência das chuvas (Coelho et al. 2016; Pepin et al. 2022; Cao et al. 2022). Locais úmidos estão ficando mais úmidos, enquanto locais áridos ficam mais secos a cada dia (Dore 2005; Trenberth 2011). À medida que a temperatura aumenta ocorre um aumento na evaporação da água disponível no ambiente, fazendo com que as chuvas sejam mais intensas em áreas úmidas, enquanto que as áreas mais secas que não possuem umidade suficiente para a formação de nuvens para precipitação acabam se tornando mais áridas ainda (Trenberth 2011), o que acarreta mudanças na umidade do solo e do ar (Trenberth 2011).

As mudanças nos fatores climáticos afetam direta e indiretamente a biodiversidade, influenciando na sobrevivência, manutenção e reprodução dos indivíduos (Hughes 2000; Correa-Lima et al. 2019; Miranda et al. 2019; Simões et al. 2020), e consequentemente interferindo na dinâmica das populações e das comunidades (Brooker 2006; Del-Claro and Torezan-Silingardi 2012; Vilela et al. 2017; Lawson and Rands

2019; Hamann et al. 2021). Os trabalhos descritivos de dados biológicos básicos são fundamentais para entendermos tais mudanças, envolvendo a fenologia, o sistema reprodutivo e as interações biológicas (Goettsch *et al.* 2015).

O futuro da biodiversidade é uma grande preocupação para o mundo pois, devido às limitações fisiológicas de cada espécie muitas delas correm o risco de serem extintas à medida que o aquecimento global avança (Oliveira et al. 2015; Atwater et al. 2018; Correa-Lima et al. 2019). Com o avanço das tecnológicas, hoje é possível prever o futuro das espécies a partir de modelos confiáveis. Modelos matemáticos vêm sendo aplicados para determinar o potencial reprodutivo das espécies diante das mudanças climáticas atuais tanto na agricultura como em plantas nativas (Vilela et al. 2017). A modelagem de nicho ecológico tem sido amplamente utilizada para determinar locais climaticamente adequados para a sobrevivência das espécies (Brito et al. 2009; Shcheglovitova and Anderson 2013; Sen et al. 2016; Vaz and Nabout 2016; Peterson et al. 2018).

Para as plantas, as mudanças climáticas influenciam desde a fenologia dos indivíduos (Vilela et al. 2017; Correa-Lima et al. 2019; Calixto et al. 2021), o sucesso reprodutivo, as interações ecológicas e até a distribuição geográfica das espécies (Simões et al. 2020; Atwater and Barney 2021). Novaes et al. (2020) encontrou padrões fenológicos para espécies arbóreas anemocóricas, onde a florada estava positivamente correlacionada com a precipitação, e a frutificação apresentava correlação negativa com a precipitação e correlação positiva com a velocidade do vento. Estas correlações estão ligadas às estações do ano no Cerrado, onde há duas estações bem definidas: uma quente e úmida e outra fria e seca (Coutinho 2002). A chuva favorece a formação de novos tecidos vegetais, aumentando a translocação de nutrientes entre o solo e a planta (Santamaria et al. 2002), enquanto na época seca a dispersão das sementes é facilitada, aumenta as possibilidades de sucesso reprodutivo visto que as sementes alcançariam

distancias maiores, escapando de possíveis predadores próximos a planta mãe e também da competição com coespecíficos (Janzen 1970; Connell 1971). Mudanças nas variáveis climáticas podem acarretar alterações nos padrões já conhecidos e afetar o ciclo de vida destas plantas. Por exemplo, Vilela et al. (2017) observou em 10 anos de estudo que a fenologia de espécies herbáceas anemocóricas mudou, com alterações na frequência e na intensidade das fenofases, afetando também a dinâmica das populações e das interações ecológicas.

É esperado que o futuro dos ecossistemas sofra alterações, por exemplo, estudos mostram que o Cerrado se tornará mais quente e mais seco (Hofmann et al. 2021). O Cerrado ou savana brasileira é a segunda maior formação vegetal nacional, correspondendo originalmente a aproximadamente 24% do território brasileiro (Ratter 1997; Oliveira and Marquis 2002). Devido à aceleração do processo de fragmentação, às perdas de espécies e ao alto grau de endemismo, o Cerrado é considerado umas das 25 áreas prioritárias para a conservação no mundo, ou um *hotspots* segundo Myers et al. (2000). O Cerrado possui aproximadamente 14.000 espécies de plantas (Flora e Funga do Brasil 2023) e aproximadamente 30% delas apresentam dispersão anemocórica (Novaes et al. 2020) ou dispersão pelo vento, esta é a segunda síndrome de dispersão mais comum neste ambiente (Gottsberger and Silberbauer-Gottsberger 1983).

Assim, este trabalho foi dividido em três capítulos brevemente apresentados a seguir:

Capítulo 1 - Os eventos fenológicos estão filogeneticamente relacionados na savana tropical?

No primeiro capítulo, trabalhamos com a influência dos fatores climáticos na fenologia de *Qualea grandiflora* Mart. e *Q. multiflora*. Considerados sete fenofases, cada

uma caracterizada pela presença de determinadas estruturas, como folhas jovens, folhas maduras, caducifolia ou queda foliar, botões florais, flores, frutos jovens e frutos maduros. As hipóteses testadas foram (i) espécies congêneras apresentam os mesmos padrões fenológicos, (ii) as fenofases das espécies estão intensamente relacionadas às variáveis climáticas, e (iii) condições abióticas desfavoráveis diminuem o potencial sucesso reprodutivo, afetando características como inflorescências, botões florais, flores e frutos jovens e maduros.

Capítulo 2 - Biologia e ecologia reprodutiva de *Qualea multiflora* Mart. (Vochysiaceae) na Savana Brasileira

Neste capítulo nós investigamos a biologia e ecologia reprodutiva de *Qualea multiflora* em uma área de Cerrado. Apesar da representatividade da família Vochysiaceae e do gênero *Qualea*, ainda existem lacunas na literatura acerca de dados básicos. Assim, nós descrevemos (i) a fenologia da espécie, (ii) a fenologia floral, (iii) o display e os recursos florais, (iv) o sistema reprodutivo, e (v) os visitantes florais.

Capítulo 3 - Prevendo o impacto das alterações climáticas globais na distribuição geográfica das espécies anemocóricas

Neste capítulo nós trabalhamos com modelagem de nicho ecológico de cinco espécies de plantas anemocóricas de famílias representativas do Cerrado brasileiro: *Aspidosperma tomentosum* Mart. & Zucc., *Kielmeyera coriacea* Mart. & Zucc., *Peixotoa tomentosa* A. Juss., *Qualea multiflora* Mart. e *Senna velutina* (Vogel) H.S. Irwin & Barneby. Os objetivos deste estudo foram: (i) avaliar os modelos de nicho ecológico, (ii) determinar quais variáveis bioclimáticas melhor explicam a distribuição geográfica das espécies, (iii) avaliar a distribuição atual dessas espécies, (iv) prever mudanças sob distintos cenários climáticos futuros, e (v) analisar a riqueza potencial de espécies dentro dos parques nacionais brasileiros.

Referências

- Arrhenius S (1896) XXXI On the influence of carbonic acid in the air upon the temperature of the ground. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science* 41:237–276. <https://doi.org/10.1080/14786449608620846>
- Artaxo P (2020) As três emergências que nossa sociedade enfrenta: saúde, biodiversidade e mudanças climáticas. *Estudos Avançados* 34:53–66. <https://doi.org/10.1590/s0103-4014.2020.34100.005>
- Atwater DZ, Barney JN (2021) Climatic niche shifts in 815 introduced plant species affect their predicted distributions. *Global Ecology and Biogeography*, geb 13342:
- Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. *Nat Ecol Evol* 2:34–43
- Brito JC, Acosta AL, Álvares F, Cuzin F (2009) Biogeography and conservation of taxa from remote regions: An application of ecological-niche based models and GIS to North-African Canids. *Biol Conserv* 142:3020–3029
- Brooker RW (2006) Plant-plant interactions and environmental change. *New Phytologist* 171:271–284
- Bustamante M, Nardoto G, Pinto A, et al (2012) Potential impacts of climate change on biogeochemical functioning of Cerrado ecosystems. *Brazilian Journal of Biology* 72:655–671. <https://doi.org/10.1590/S1519-69842012000400005>
- Calixto ES, Novaes LR, dos Santos DFB, et al (2021) Climate seasonality drives ant–plant–herbivore interactions via plant phenology in an extrafloral nectary-bearing plant community. *Journal of Ecology* 109:639–651. <https://doi.org/10.1111/1365-2745.13492>
- Cao D, Zhang J, Han J, et al (2022) Projected Increases in Global Terrestrial Net Primary Productivity Loss Caused by Drought Under Climate Change. *Earths Future* 10:. <https://doi.org/10.1029/2022EF002681>
- Coelho CAS, Cardoso DHF, Firpo MAF (2016) Precipitation diagnostics of an exceptionally dry event in São Paulo, Brazil. *Theor Appl Climatol* 125:769–784. <https://doi.org/10.1007/s00704-015-1540-9>
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) *Dynamics of Populations*. Centre for Agricultural Publishing and Documentation, Wageningen. Wageningen, The Netherlands, p 312
- Correa-Lima APA, Varassin IG, Barve N, Zwiener VP (2019) Spatio-temporal effects of climate change on the geographical distribution and flowering phenology of hummingbird-pollinated plants. *Ann Bot* 124:389–398. <https://doi.org/10.1093/aob/mcz079>

- Coutinho LM (2002) O bioma do cerrado. In: KLEIN AL (ed) *Eugen Warming e o cerrado brasileiro*. Editora UNESP, São Paulo, pp 77–92
- Del-Claro K, Torezan-Silingardi HM (2012) *Ecologia das interações plantas-animais: Uma abordagem ecológico-evolutiva*. Technical Books Editora
- Dore MHI (2005) Climate change and changes in global precipitation patterns: What do we know? *Environ Int* 31:1167–1181. <https://doi.org/10.1016/j.envint.2005.03.004>
- Gottsberger G, Silberbauer-Gottsberger I (1983) Dispersal and distribution in the cerrado vegetation of Brazil. *Sonderbd Naturwiss Ver Hamburg* 7:315–352
- Hamann E, Blevins C, Franks SJ, et al (2021) Climate change alters plant--herbivore interactions. *New Phytologist* 229:1894–1910
- Hofmann GS, Cardoso MF, Alves RJ V., et al (2021) The Brazilian Cerrado is becoming hotter and drier. *Glob Chang Biol* 27:4060–4073. <https://doi.org/10.1111/gcb.15712>
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol* 15:56–61
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Lawson DA, Rands SA (2019) The effects of rainfall on plant--pollinator interactions. *Arthropod Plant Interact* 13:561–569
- Marengo JA (2006) *Mudanças climáticas globais e seus efeitos sobre a biodiversidade; caracterização do clima atual e definição das alterações climáticas para o território brasileiro ao longo do século 21., Ministério. Ministério do Meio Ambiente, Brasília, Distrito Federal, Brasil*
- Miranda LS, Imperatriz-Fonseca VL, Giannini TC (2019) Climate change impact on ecosystem functions provided by birds in southeastern Amazonia. *PLoS One* 14:e0215229
- Moss RH, Edmonds JA, Hibbard KA, et al (2010) The next generation of scenarios for climate change research and assessment. *Nature* 463:747–756
- Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/doi.org/10.1038/35002501>
- Novaes LR, Calixto ES, Oliveira ML, et al (2020) Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: A new wind-based approach. *Science of The Total Environment* 730:139039
- Oliveira G, Lima-Ribeiro MS, Terribile LC, et al (2015) Conservation biogeography of the Cerrado's wild edible plants under climate change: Linking biotic stability with agricultural expansion. *Am J Bot* 102:870–877. <https://doi.org/10.3732/ajb.1400352>
- Oliveira PS, Marquis RJ (2002) *The cerrados of Brazil*. Columbia University Press New York

- Pepin NC, Arnone E, Gobiet A, et al (2022) Climate Changes and Their Elevational Patterns in the Mountains of the World. *Reviews of Geophysics* 60:. <https://doi.org/10.1029/2020RG000730>
- Peterson AT, Cobos ME, Jiménez-García D (2018) Major challenges for correlational ecological niche model projections to future climate conditions. *Ann N Y Acad Sci* 1429:66–77. <https://doi.org/10.1111/nyas.13873>
- Ratter J (1997) The Brazilian Cerrado Vegetation and Threats to its Biodiversity. *Ann Bot* 80:223–230. <https://doi.org/10.1006/anbo.1997.0469>
- Santamaria P, Elia A, Serio F (2002) Effect of solution nitrogen concentration on yield, leaf element content, and water and nitrogen use efficiency of three hydroponically-grown rocket salad genotypes. *J Plant Nutr* 25:245–258. <https://doi.org/10.1081/PLN-100108833>
- Sen S, Gode A, Ramanujam S, et al (2016) Modeling the impact of climate change on wild *Piper nigrum* (Black Pepper) in Western Ghats, India using ecological niche models. *J Plant Res* 129:1033–1040
- Shcheglovitova M, Anderson RP (2013) Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecol Modell* 269:9–17
- Simões S dos S, Zappi D, Costa GM da, et al (2020) Spatial niche modelling of five endemic cacti from the Brazilian Caatinga: Past, present and future. *Austral Ecol* 45:35–47
- Trenberth K (2011) Changes in precipitation with climate change. *Clim Res* 47:123–138. <https://doi.org/10.3354/cr00953>
- Vaz ÚL, Nabout JC (2016) Using ecological niche models to predict the impact of global climate change on the geographical distribution and productivity of *Euterpe oleracea* Mart.(Arecaceae) in the Amazon. *Acta Bot Brasilica* 30:290–295
- Vilela AA, Del-Claro VTS, Torezan-Silingardi HM, Del-Claro K (2017) Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. *Arthropod Plant Interact* 12:215–227. <https://doi.org/10.1007/s11829-017-9572-y>

Capítulo 1

How much are phenological events phylogenetically related in the tropical savanna?

Larissa Alves-de-Lima¹, Diego Vinicius Anjos¹, Letícia Rodrigues Novaes ², Marcos
Lima de Oliveira ³, and Helena Maura Torezan- Silingardi ^{1, 3*}

¹Universidade Federal de Uberlândia, Instituto de Biologia, Bloco 2D, Rua Ceará 1084,
Campus Umuarama, Uberlândia, MG, 38405-315

² Departamento de Biología Vegetal y Ecología, Universidad de Sevilla. Sevilla, Spain.

³ Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Departamento de Biologia,
Universidade de São Paulo, Avenida Bandeirantes 3900, Monte Alegre, Ribeirão
Preto, SP, 14040-901

*e-mail: hmtsilingardi@gmail.com ; torezan.silingardi@ufu.br

Seguindo as normas de edição da revista Brazilian Journal of Botany.

Abstract

Phenology is the study of recurrent biological seasonal events resulting from abiotic, biotic and phylogenetic factors. The abiotic factors influencing phenophases both directly and indirectly are climatic variables, such as rainfall, humidity and temperature. Faced with climate change, plants have been adapting their life cycle, influencing the entire ecosystem. Thus, we worked with three hypotheses: (i) congeneric species will present the same phenological patterns; (ii) species phenophases are intensely related to climate variables; and (iii) unfavorable abiotic conditions decrease potential reproductive success by affecting characteristics such as inflorescences, floral buds, flowers, and young and ripe fruits. We carried out our study in a cerrado *sensu stricto* vegetation area, with *Qualea grandiflora* Mart. and *Q. multiflora* Mart. (Vochysiaceae), between August/2018 and July/2023. To define phenological patterns, we analyzed seven phenophases: sprouting leaves, developed leaves, deciduousness, floral buds, flowers, and young and ripe fruits. The phenological patterns were analyzed using circular statistics. To investigate the best relationship between phenophases and climate variables, we performed a Redundancy Analysis (RDA). To analyze the changes that each species undergoes, we performed comparisons with a 'glmmTMB' function. Our three hypotheses were supported. This five-year study demonstrates the importance of long-term phenological observations to our understanding of the future effects of rising global temperature and its potential consequent effects on fire frequency and intensity.

Key words: Anemochorous species, phenological patterns, reproductive success.

Introduction

Phenology is the study of recurrent biological seasonal events (Forrest and Miller-Rushing 2010). Phenology is fundamental to ecology and evolution, being an important characteristic of the life history of many organisms, including insects (Davies 2019; Buckley 2022), amphibians, reptiles (Prodon et al. 2020), birds (Gordo and Sanz 2006), mammals (Boutin and Lane 2014; Beltran et al. 2019) and plants (Lange et al. 2013a; Lacerda et al. 2018; Novaes et al. 2020; Calixto et al. 2021b). Plant phenology investigates the timing and duration of each phenophase, like the formation of fruit, as well as their synchrony between individuals (Newstrom et al. 1994; Mariano et al. 2016; Novaes et al. 2020). Long-term investigations considering vegetal phenology are fundamental to the comprehension of plant development and the main factors affecting it. Plant phenology is a result of abiotic, biotic and phylogenetic factors (Gilman et al. 2010).

The abiotic factors influencing phenophases both directly and indirectly are climatic variables, such as rainfall, humidity and temperature (Morellato et al. 2000; Vilela et al. 2017; Abernethy et al. 2018; Leão-Araújo et al. 2019; Novaes et al. 2020; Santos et al. 2022). Rain and humidity are important triggers to determine vegetal phenology. For Cerrado plants they influence leaf fall and the formation of new plant tissues, such as leaf buds, flowers and consequent fruit formation. In addition, for plant species with wind-dispersed fruits, or anemochorous species, wind is also an essential variable, directly influencing the fitness of these species through the efficacy of seed dispersal (Novaes et al. 2020). Faced with climate change, plants have been adapting their life cycle (Cleland et al. 2007; Vilela et al. 2014, 2017; Correa-Lima et al. 2019; Piao et al. 2019). These adaptations influence ecosystem services, such as nutrient

cycling, seed dispersal, reproductive success, and biological interactions (Brody 1997; Forrest and Miller-Rushing 2010; Forrest 2016; Vilela et al. 2017).

Climate change is making the Brazilian Cerrado hotter and drier (Hofmann et al. 2021), affecting individuals, populations and communities (Vilela et al. 2014, 2017; Velasque and Del-Claro 2016a), and facilitating the occurrence of fires (Jones et al. 2022). Vilela *et al.* (2017) showed variation in 10 years of studies in the timing and synchrony of flowering of four Malpighiaceae species in a Cerrado area, affecting the interaction of plants and their herbivores and pollinators. Future projections also showed that, overall, more Cerrado plants tend to reduce their reproductive success than maintain or increase it, due to reductions in suitable climate for flowering (Correa-Lima et al. 2019). In Cerrado areas, fire is also an important factor for plant phenology (Neves and Damasceno-Junior 2011; Valentin-Silva et al. 2021a). With climate change, fires are becoming more frequent and more intense, affecting the structure and composition of species in the woody forest community of the Cerrado (Miranda et al. 2009) and postponing part of the phenological events of the species (Valentin-Silva et al. 2021b). Cerrado plants have different strategies to overcome fire. Some species flower immediately after the fires, but some species reallocate energy and flower in the following season or after two years (Fidelis and Zironi 2021; Gomes et al. 2021a). Fire also affects the seasonality of fruits (Valentin-Silva et al. 2021b)

Thus, our objective was to investigate the phenology of two common species of Vochysiaceae over five years. Our hypotheses were: (i) congeneric species will present the same phenological patterns; (ii) species phenophases are intensely related to climate variables; and (iii) unfavorable abiotic conditions decrease potential reproductive success by affecting characteristics such as inflorescences, floral buds, flowers, and young and ripe fruits.

Materials and methods

Study site

We carried out our study in an area of Cerrado *sensu stricto* vegetation (18°58'59" S; 48°17'53" W) in the natural reserve of Clube Caça e Pesca Itororó de Uberlândia, Minas Gerais, Brazil. The climate has two well-defined seasons: warm and wet from October to March (rainy season) and cold and dry from April to September (dry season), being classified as Aw according to the Köppen climate classification (Alvares et al. 2013; Velasque and Del-Claro 2016b). The study site experiences a mean annual temperature of 22°C and mean rainfall of 1.500 mm (Alvares et al. 2013; Velasque and Del-Claro 2016b). The area suffered an intense fire in September 2021 (Barbosa 2021). Observations were carried out monthly from August/2018 up to July/2023, with 15 adult and healthy individuals analyzed per species, each with a minimum height of 1m and at least 10m apart. The observations were made by the same person (LAL) so as not to bias the results.

Plant species

Qualea grandiflora Mart. and *Q. multiflora* Mart. (Vochysiaceae) are native to Brazil and easily found in Cerrado areas (Ratter et al. 2003), including in the chosen natural reserve (Lange et al. 2013b, 2017; Calixto et al. 2015, 2020; Appolinario and Schiavini 2018; Novaes et al. 2020), where Vochysiaceae was the most representative plant family. *Qualea parviflora* and *Q. multiflora* present the highest Importance Value Index, and are frequently found together with *Q. grandiflora* and *Vochysia cinamomea* (Appolinario & Schiavini 2002). *Qualea grandiflora* and *Q. multiflora* flowers (Fig. 1) are reduced to just one petal, one carpel, one stamen, and four sepals (Gonçalves et al.

2013; Shimizu and Gonçalves 2017). Dried fruits are capsular with three locules (Barroso et al. 2004).

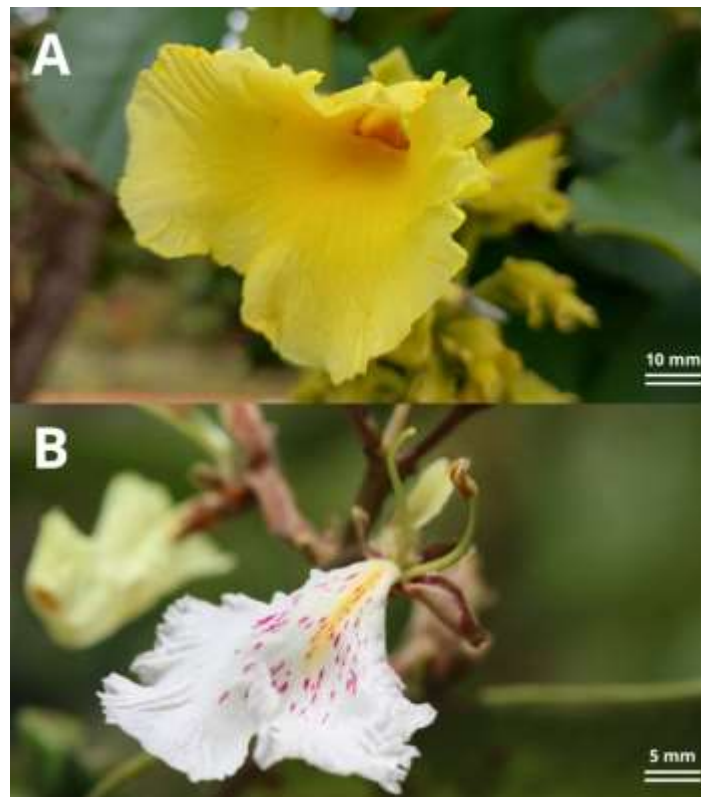


Figure 1. Flower of *Qualea grandiflora* (A) and *Q. multiflora* (B) observed at the natural reserve of Clube de Caça e Pesca Itororó de Uberlândia, Brazil.

Data analysis

We considered August/2018 to July/2019 as the first flowering period or year 1, August/2019 to July/2020 as year 2, August/2020 to July/2021 as year 3, August/2021 to July/2022 as year 4 and August/2022 to July/2023 as year 5. All analyses were performed using R 4.0.0 software.

Congeneric species will present the same phenological patterns

To define phenological patterns, we analyzed seven phenophases: sprouting leaves, developed leaves, deciduousness, floral buds, flowers, young fruits and ripe fruits, as Novaes et al. (2020). We assigned values to each individual by phenophase for each observed month, with 0 – non-existent event; 1 – discrete event observed in just a few branches (1-25%), 2 – frequent event observed in several branches (26-75%), and 3 – intense event observed in almost all branches, adapted from Fournier (1974) and Riberio & Castro (1986). The phenological patterns were analyzed from circular statistics with the circular package in R (Agostinelli & Lund 2017). We calculated the mean vector, mean vector length, median, standard deviation, Rayleigh Z test, Rayleigh p test, Rao U test and Rao p test. For the Rayleigh test and the Rao test, we used $p < 0.05$.

Species phenophases are intensely related to climate variables

To investigate the best relationship between phenophases and climate variables, we performed a Redundancy Analysis (RDA) (Novaes et al. 2020), using the “vegano” package (Oksanen et al. 2019). We considered as predictive environmental variables: the average of each variable, temperature, humidity, wind speed and precipitation, for each month. Climatic data were obtained at the Geography Institute of the Federal University of Uberlândia. The phenophases analyzed as response were: sprouting leaves, developed leaves, deciduousness, floral buds, flowers, young fruits and ripe fruits. We analyzed the multicollinearity between the climatic variables through the Variance Inflation Factor ($VIF > 10$) (Novaes et al. 2020). The statistical significance of each variable was confirmed with 999 permutations at a significance of 5%, using the “envfit” function (Liu et al. 2011). The significance of the model was checked using the “anova” function of the “stats” package. The results were presented in an ordination diagram (biplot), with

variables represented by arrows. We interpreted the results considering three factors to determine which variable influences each phenophase: (i) the size of the angle between the vector of the climatic variable and the vector of phenophase, where values close to 0° indicate a positive correlation, values close to 90° indicate no correlation and values close to 180° indicate a negative correlation, (ii) the direction of the arrows, where arrows pointing in the same direction indicate a positive correlation and in opposite directions a negative correlation, and (iii) the length of vector (Buttigieg and Ramette 2014).

Unfavorable abiotic conditions decrease potential reproductive success by affecting characteristics such as inflorescences, floral buds, flowers, and young and ripe fruits

To analyze the changes reproductive traits that occurred in each species over the four years of observations, we used the reproductive phenophases: floral buds, flowers, young fruits, and ripe fruits. Floral buds were assessed by tallying the number of inflorescences per plant and then tallying the number of floral buds on three of the inflorescences per plant. Floral buds were counted before the flowers opened. To analyze changes in the number of flowers, we assessed the total *floral display*, counting the number of open flowers per day. The number of open flowers per day was assessed at the beginning, middle, and end of the flowering period that totaled about three months, so one observation was carried out per plant, per month of flowering. Young fruits were counted in the second month after flowering and ripe fruits were counted in the fourth month after flowering. All comparison models between years were performed with the ‘glmmTMB’ package, following Table 1 (Brooks et al. 2017).

Table 1. Performed statistical models to compare floral resources and attractiveness between *Qualea grandiflora* Mart. and *Q. multiflora* Mart.

	N/species/year	Model	Distribution	Variable response	Fixed predictor variable	Random predictor variable
Inflorescences	15 plants	GLM	Poisson	Number of inflorescences	Year	1 Plant ID
Floral buds per inflorescence	45 inflorescences	GLMM	Poisson	Quantity of flower buds per inflorescence	Year	1 Plant ID/Inflorescence
Open flowers per day	15 plants	GLMM	Poisson	Number of flowers opened by inflorescence per day in each flowering month	Year	1 Plant ID/Month
Young fruits	15 plants	GLM	Poisson	Number of young fruits	Year	1 Plant ID
Ripe fruits	15 plants	GLM	Poisson	Number of ripe fruits	Year	1 Plant ID

Results

Congeneric species will present the same phenological patterns

Qualea grandiflora and *Q. multiflora* displayed a similar phenological pattern supporting our first hypothesis. Both species showed leaf sprouting as the dry season ended and the rainy season began. The species were deciduous as leaves fall in the dry season. In the rainy season, we observed the flowering, which lasts about 90 days. The populations displayed a similar annual flowering pattern. Young fruits appeared at the end of the rainy season and matured throughout the dry season, where we observed a greater number of ripe fruits.

All analyzed phenophases were significant as to seasonality (Tab. 2; Figs. 2; 3). In *Qualea grandiflora* leaf sprouting activity peaked in September with maximum intensity occurring between September and October (Figs. 2; 4a). Developing leaves were observed throughout the year, except in August and September, with a peak of activity in February (Fig. 2) and maximum intensity between November and April (Fig. 4b). Deciduousness peaked in July and August (Fig. 2) with maximum intensity in August (Fig. 4c). Floral budding displayed peak activity between October and November (Fig. 2) with higher intensity in November (Fig. 4d). The flowering activity peaked between October and December (Fig. 2) with maximum intensity observed between November and January (Fig. 4e). Young fruit development peaked in March and May (Fig. 2) with maximum intensity in July (Fig. 4f). Ripe fruits had their peak activity in June (Fig. 2) and higher intensity between March and July (Fig. 4g). In year 4, after the intense fire, there was a change in the patterns found. Sprouting leaves showed peak activity in November, developed leaves peaked in March and deciduousness in September (Fig. 2). The peak intensity of sprouting leaves occurred in December, developed leaves between

December and April, and deciduousness between August and November (Figs. 4a; b; c). Due to the damage, we had no flowering and consequently no fruits.

Individuals of *Qualea multiflora* showed sprouting leaves with peak activity in August and September (Fig. 3), and maximum intensity between August and November (Fig. 4a). Developed leaves were observed throughout the year, except in August and September, with peak activity between February and March (Fig. 3) and maximum intensity between October and May (Fig. 4b). Deciduousness peaked in July and August (Fig. 3), with maximum intensity between July and September (Fig. 4c). Floral budding showed peak activity between October and December (Fig. 3) with higher intensity in November (Fig. 4d). Flowering activity peaked in November and December (Fig. 3 and 4e). Development of young fruits peaked in March and May (Fig. 3) with maximum intensity in March and April (Fig. 4f). The ripening of fruit peaked in April, May and June (Fig. 3) with higher intensity between April and August (Fig. 4g). In year 4, sprouting leaves showed peak activity in November, developed leaves in March and deciduousness in September (Fig. 3). The peak intensity of sprouting leaves occurred in November, developed leaves between December and June and deciduousness between August and October (Fig. 4a; b; c). Just like *Q. grandiflora*, in year 4 we had no flowers or fruits for *Q. multiflora*.

Table 2. Circular statistical analysis testing of phenological patterns over five years (year 1: August/2018 to July/2019; year 2: August/2019 to July/2020; year 3: August/2020 to July/2021; year 4: August/2021 to July/2022; and year 5: August/2022 to July/2023) of *Qualea grandiflora* Mart. and *Q. multiflora* Mart. in the Cerrado reserve.

	Mean vector (μ)	Month	Length of mean vector (r) <u>RHO</u>	Median	Circular standard deviation	Rayleigh test (Z)	Rayleigh test (p)	Rao test (U)	Rao test (p)
Year 1									
<i>Qualea grandiflora</i>									
Sprouting leaves	2661.573	Sep	0.945	270.000	340.797	0.945	<0.001	322.759	<0.001
Developed leaves	57.439	Feb	0.119	60.019	118.189	0.119	0.104	335.094	<0.001
Deciduousness	199.203	Jul	0.657	209.925	307.429	0.657	<0.001	302.857	<0.001
Floral buds	308.236	Nov	0.949	300.001	341.443	0.949	<0.001	310.909	<0.001
Flowers	332.059	Dec	0.920	330.011	336.634	0.920	<0.001	324.000	<0.001
Young fruits	131.331	May	0.528	120.039	64.726	0.529	<0.002	322.597	<0.001
Ripe fruits	185.503	Aug	0.576	180.115	299.552	0.576	<0.002	323.478	<0.001
<i>Qualea multiflora</i>									
Sprouting leaves	262.376	Sep	0.946	269.943	340.916	0.946	<0.001	321.429	<0.001
Developed leaves	63.115	Mar	0.115	60.019	119.261	0.115	0.119	335.404	<0.001
Deciduousness	194.045	Jul	0.817	209.924	323.496	0.816	<0.000	324.706	<0.001
Floral buds	306.287	Nov	0.941	299.981	340.013	0.941	<0.001	322.757	<0.001
Flowers	329.268	Nov	0.912	329.985	335.361	0.912	<0.001	335.455	<0.001
Young fruits	129.841	May	0.335	120.038	84.805	0.335	<0.001	327.600	<0.001
Ripe fruits	172.318	Jun	0.665	180.115	51.925	0.663	<0.001	325.714	<0.001

Year 2									
<i>Qualea grandiflora</i>									
Sprouting leaves	244.834	Sep	0.981	239.961	348.836	0.9812	<0.001	320.000	<0.001
Developed leaves	45.023	Feb	0.193	45.023	103.949	0.193	0.004	336.000	<0.001
Deciduousness	194.045	Jul	0.799	194.904	321.692	0.799	<0.001	320.000	<0.001
Floral buds	298.376	Oct	0.951	299.981	340.602	0.951	<0.001	303.158	<0.001
Flowers	293.618	Oct	0.944	299.981	341.829	0.944	<0.001	315.000	<0.001
Young fruits	66.726	Mar	0.683	60.02	50.076	0.683	<0.001	329.578	<0.001
Ripe fruits	121.93	May	0.805	120.038	37.715	0.805	<0.001	312.632	<0.001
<i>Qualea multiflora</i>									
Sprouting leaves	248.388	Sep	0.972	239.961	346.405	0.814	<0.01	325.714	<0.001
Developed leaves	30.015	Feb	0.139	30.015	113.712	0.145	<0.01	334.777	<0.001
Deciduousness	217.719	Aug	0.911	209.923	335.242	0.495	<0.01	302.4	<0.001
Floral buds	285.535	Oct	0.876	299.98	330.601	0.228	<0.01	310.344	<0.001
Flowers	301.987	Nov	0.922	299.98	337.016	0.367	<0.01	325.161	<0.001
Young fruits	85.643	Mar	0.719	90.057	46.551	0.265	<0.01	318.461	<0.001
Ripe fruits	131.847	May	0.671	120.038	51.301	0.163	<0.01	310.588	<0.001
Year 3									
<i>Qualea grandiflora</i>									
Sprouting leaves	245.658	Sep	0.981	239.961	348.836	0.981	<0.01	320	<0.001
Developed leaves	30.015	Feb	0.263	30.015	93.771	0.262	<0.01	334.285	<0.001
Deciduousness	200.464	Jul	0.771	209.923	318.613	0.771	<0.01	306.383	<0.001
Floral buds	306.286	Nov	0.941	299.891	340.012	0.941	<0.01	322.758	<0.001
Flowers	333.183	Dec	0.919	329.984	336.436	0.919	<0.01	322.307	<0.001
Young fruits	83.579	Mar	0.813	90.057	34.607	0.833	<0.01	316.097	<0.001
Ripe fruits	126.515	May	0.833	120.038	36.824	0.813	<0.01	317.142	<0.001

<i>Qualea multiflora</i>									
Sprouting leaves	239.961	Aug	1	239.961	360	1	<0.01	315	<0.001
Developed leaves	38.814	Feb	0.225	30.015	98.931	0.225	<0.001	336	<0.001
Deciduousness	220.757	Aug	0.887	209.923	331.981	0.887	<0.001	335.172	<0.001
Floral buds	337.356	Dec	0.974	329.984	346.985	0.974	<0.01	324	<0.001
Flowers	350.558	Dec	0.971	360	345.971	0.971	<0.01	327.272	<0.001
Young fruits	119.292	Apr	0.834	90.057	34.454	0.834	<0.01	313.846	<0.001
Ripe fruits	90.745	Apr	0.833	120.038	34.64	0.833	<0.01	305.454	<0.001
Year 4									
<i>Qualea grandiflora</i>									
Sprouting leaves	318.043	Nov	0.796	356.998	345.22	0.967	<0.01	331.2	<0.001
Developed leaves	70.968	Mar	0.523	60.019	65.196	0.523	<0.01	332.307	<0.001
Deciduousness	246.267	Sep	0.754	239.961	316.954	0.754	<0.01	328.235	<0.001
Floral buds	-	-	-	-	-	-	-	-	-
Flowers	-	-	-	-	-	-	-	-	-
Young fruits	-	-	-	-	-	-	-	-	-
Ripe fruits	-	-	-	-	-	-	-	-	-
<i>Qualea multiflora</i>									
Sprouting leaves	317.338	Nov	0.966	329.984	345.091	0.966	<0.001	332.307	<0.001
Developed leaves	79.911	Mar	0.598	90.057	58.074	0.598	<0.001	333.473	<0.001
Deciduousness	259.796	Sep	0.669	269.942	308.603	0.669	<0.001	334.588	<0.001
Floral buds	-	-	-	-	-	-	-	-	-
Flowers	-	-	-	-	-	-	-	-	-
Young fruits	-	-	-	-	-	-	-	-	-
Ripe fruits	-	-	-	-	-	-	-	-	-

Year 5									
<i>Qualea grandiflora</i>									
Sprouting leaves	246.668	Sep	0.947	239.961	341.081	0.947	<0.02	317.142	<0.001
Developed leaves	33.919	Feb	0.262	30.015	93.197	0.262	<0.001	320	<0.001
Deciduousness	217.662	Aug	0.835	209.923	325.669	0.835	<0.01	334.285	<0.001
Floral buds	291.439	Oct	0.88	291.439	331.092	0.88	<0.03	321.081	<0.001
Flowers	325.536	Nov	0.867	325.536	329.712	0.869	<0.04	325.714	<0.001
Young fruits	78.191	Mar	0.795	75.038	38.773	0.795	<0.05	312.631	<0.001
Ripe fruits	108.573	Apr	0.878	120.038	29.174	0.878	<0.06	311.351	<0.001
<i>Qualea multiflora</i>									
Sprouting leaves	245.063	Sep	0.936	239.961	339.273	0.936	<0.001	324.000	<0.001
Developed leaves	33.070	Feb	0.270	30.015	92.727	0.270	<0.001	334.101	<0.001
Deciduousness	208.547	Jul	0.805	209.923	322.263	0.805	<0.001	328.421	<0.001
Floral buds	288.114	Oct	0.862	299.98	328.816	0.862	<0.001	325.714	<0.001
Flowers	325.473	Nov	0.864	329.984	329.094	0.854	<0.001	329.361	<0.001
Young fruits	75.840	Mar	0.836	75.038	34.242	0.836	<0.001	322.105	<0.001
Ripe fruits	97.050	Apr	0.849	90.057	32.719	0.849	<0.001	317.142	<0.001

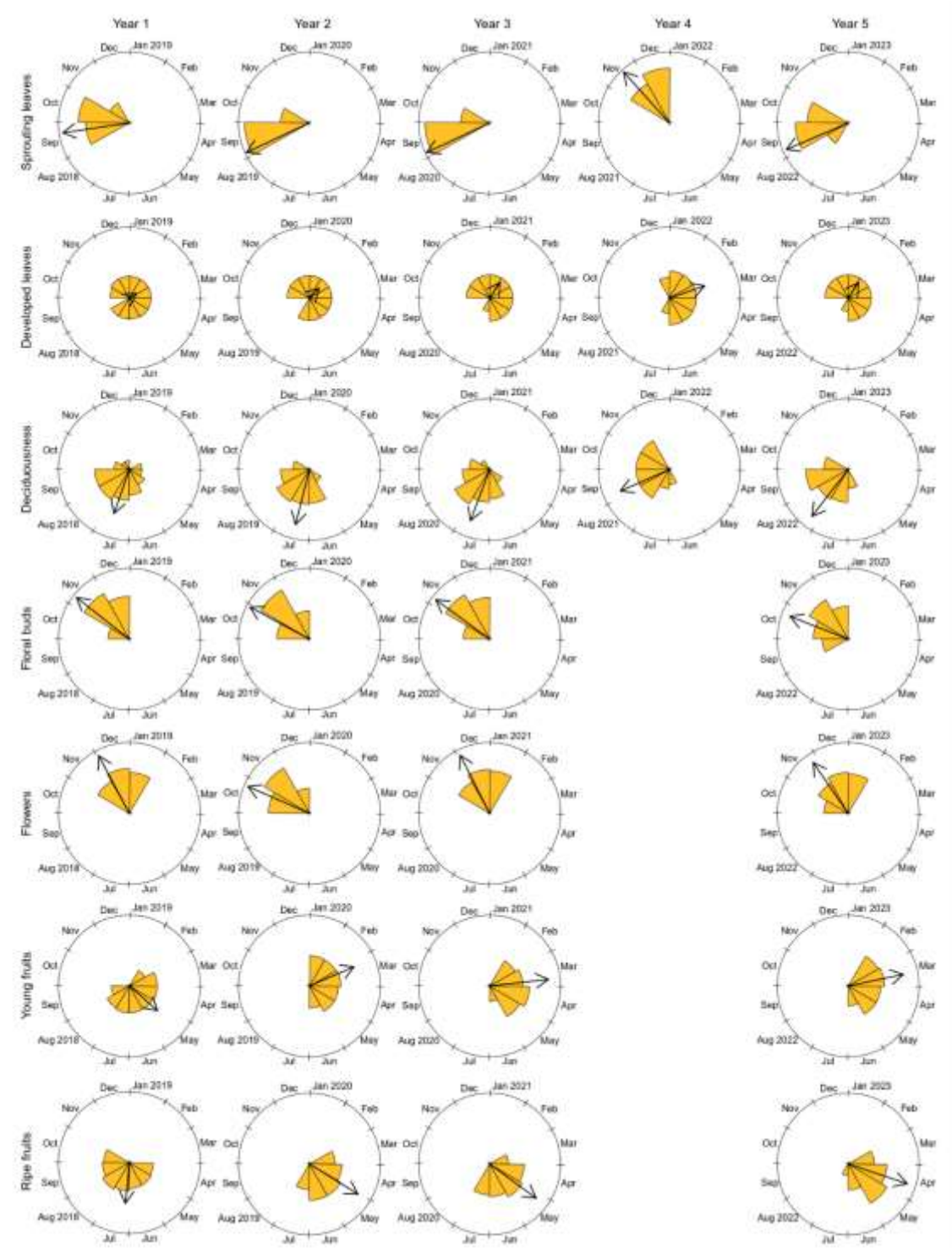


Figure 2. *Qualea grandiflora* phenology over five years (year 1: August/2018 to July/2019; year 2: August/2019 to July/2020; year 3: August/2020 to July/2021; year 4: August/2021 to July/2022; and year 5: August/2022 to July/2023) in the Cerrado reserve. The arrow position represents the mean angle (mean month) and the arrow length represents the length of the mean vector (r). Rainy season – October to March; Dry season – April to September. Statistical results are depicted in Table 2.

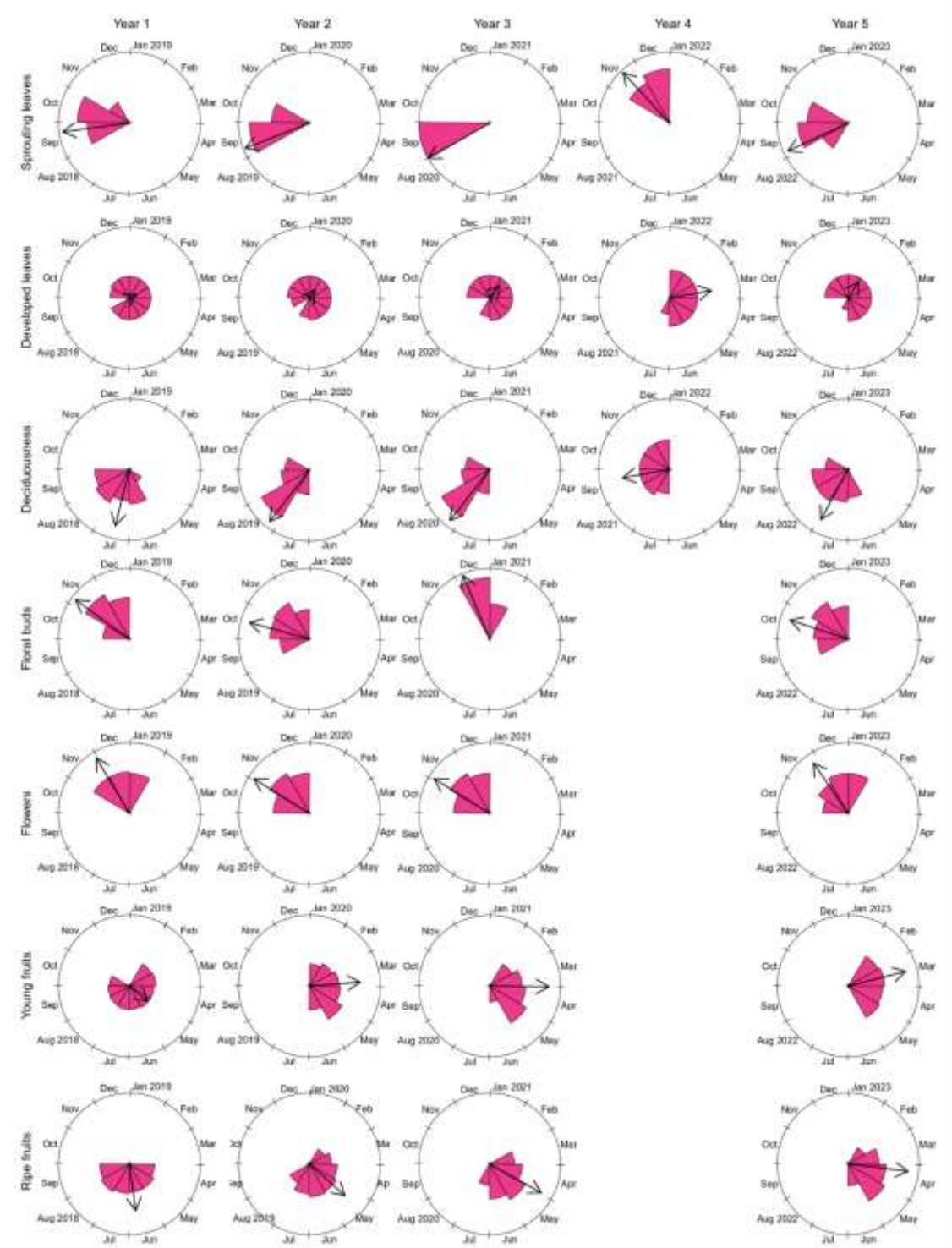


Figure 3. *Qualea multiflora* phenology over five years (year 1: August/2018 to July/2019; year 2: August/2019 to July/2020; year 3: August/2020 to July/2021; year 4: August/2021 to July/2022; and year 5: August/2022 to July/2023) in the Cerrado reserve. The arrow position represents the mean angle (mean month) and the arrow length represents the length of the mean vector (r). Rainy season – October to March; Dry season – April to September. Statistical results are depicted in Table 2.

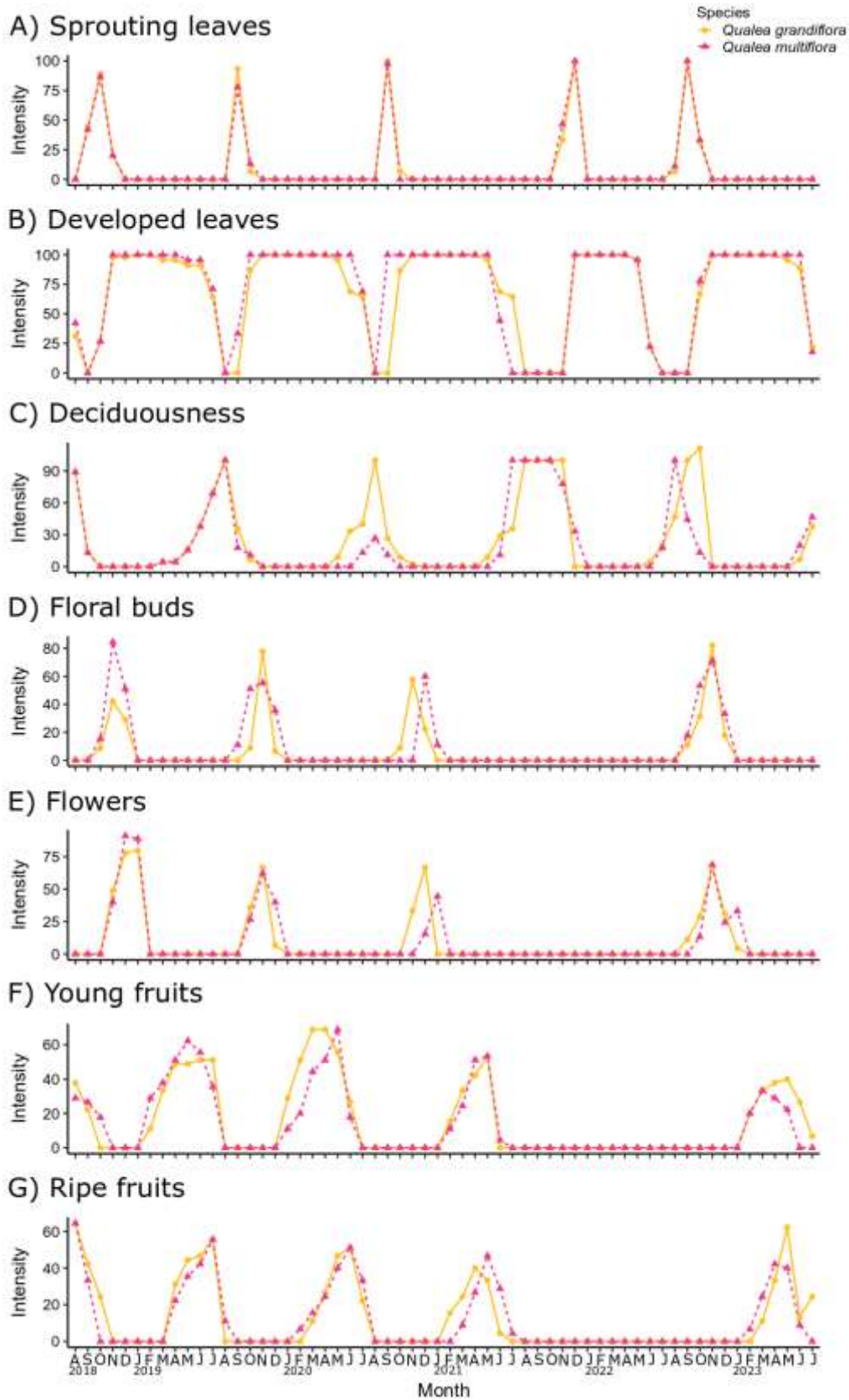


Figure 4. Phenophase intensity of *Qualea grandiflora* Mart. and *Q. multiflora* Mart from the Cerrado reserve between August/2018 to July/2023: (a) sprouting leaves; (b) developed leaves; (c) deciduousness; (d) floral buds; (e) flowers; (f) young fruits and (g) ripe fruits

Species phenophases are intensely related to climate variables

The second hypothesis was also supported as *Q. grandiflora* and *Q. multiflora* phenophases were intensely related to climate variables. In general, these species have similar relationships between phenophases and climatic variables (Tabs 3 and 4). The presence and higher intensity of leaf sprouting were positively correlated with rainfall and wind speed. Developed leaves were positively correlated to rainfall and negatively correlated to wind speed, whereas deciduousness was negatively correlated to rainfall and positively correlated to wind speed. The number of both floral buds and flowers was positively correlated with rainfall and negatively with wind. Young fruits were positively correlated to humidity and mature fruits negatively correlated to rainfall and positively correlated to wind speed.

The climate variables analyzed appear to have significantly influenced the phenophases of *Q. grandiflora* over the years (year 1: $F_{3,8}=2.59$, $p<0.05$; year 2: $F_{4,7}=4.31$, $p<0.05$; year 3: $F_{4,7}=6.44$, $p<0.05$; and year 5: $F_{4,7}=6.74$, $p<0.05$), except during year 4 (year 4: $F_{4,7}=0.44$, $p=0.85$). The accumulated constrained eigenvalues of the first two RDA axes accounted for 93% for year 1, 89% for year 2, 86% for year 3, 97% for year 4, and 90% for year 5. The adjusted bi-multivariate redundancy statistic (R^2 adjusted) was 24% for year 1, 55% for year 2, 66% for year 3, 0% for year 4, and 57% for year 5. Phenophase variation was better explained in year 1 by humidity ($r^2=0.64$) and temperature ($r^2=0.63$). For year 2 and year 3, all climate variables were significant: wind speed (year 2: $r^2=0.89$; year 3: $r^2=0.94$), temperature (year 2: $r^2=0.84$; year 3: $r^2=0.85$), humidity (year 2: $r^2=0.75$; year 3: $r^2=0.88$) and rainfall (year 2: $r^2=0.70$; year 3: $r^2=0.85$). For year 4, the variables were not significant. For year 5, the most important variables were temperature ($r^2=0.73$), wind speed ($r^2=0.69$) and humidity ($r^2=0.67$).

For *Qualea multiflora*, the climatic variables influenced the phenophases over the five years (year 1: $F_{3,8}=2.09$, $p=0.05$; year 2: $F_{4,7}=4.25$, $p<0.05$; year 3: $F_{4,7}=6.44$, $p<0.05$; year 4: $F_{4,7}=14.41$, $p>0.05$; year 5: $F_{4,7}=4.62$, $p<0.05$). The accumulated constrained eigenvalues of the first two RDA axes accounted for 93% for year 1, 89% for year 2, 86% for year 3, 99% for year 4, and 87% for year 5. The adjusted bi-multivariate redundancy statistic (R^2 adjusted) was 28% for year 1, 54% for year 2, 66% for year 3, 83% for year 4, and 57% for year 5. Phenophase variation was better explained in year 1 by temperature ($r^2=0.74$), wind speed ($r^2=0.69$) and humidity ($r^2=0.69$). For year 2, the most important variables were wind speed ($r^2=0.72$) and temperature ($r^2=0.60$). For year 3, all climate variables were significant: wind speed ($r^2=0.94$), humidity ($r^2=0.88$), rainfall ($r^2=0.85$) and temperature ($r^2=0.85$). For year 4, the variables were not significant. For year 5, the most important variables were temperature ($r^2=0.75$), wind speed ($r^2=0.72$) and humidity ($r^2=0.65$).

Table 3. Relationship between phenophases of *Qualea grandiflora* and abiotic variables in the natural reserve of Clube de Caça e Pesca de Uberlândia, Brazil. Positive relationship: +, Negative relationship: -; Absent or weak relationship: /; Non-applicable: NA).

<i>Qualea grandiflora</i>	Rainfall	Wind speed	Temperature	Humidity
Sprouting leaves				
year 1	/	/	/	/
year 2	+	/	/	/
year 3	/	+	+	/
year 4	NA	NA	NA	NA
year 5	/	+	/	/
Developed leaves				
year 1	/	/	/	/
year 2	+	/	/	/
year 3	+	-	-	/
year 4	/	/	/	/
year 5	+	/	-	/
Deciduousness				
year 1	/	+	+	+

year 2	-	+	+	+
year 3	-	+	+	+
year 4	NA	NA	NA	NA
year 5	/	+	+	+
Floral buds				
year 1	/	-	-	-
year 2	+	-	-	-
year 3	+	/	/	-
year 4	NA	NA	NA	NA
year 5	/	-	-	-
Flowers				
year 1	/	-	-	-
year 2	+	-	-	-
year 3	+	-	-	-
year 4	NA	NA	NA	NA
year 5	/	-	-	-
Young fruits				
year 1	/	/	/	+
year 2	/	/	/	/
year 3	/	/	/	+
year 4	NA	NA	NA	NA
year 5	/	/	/	+
Ripe fruits				
year 1	/	+	+	+
year 2	/	/	/	+
year 3	/	/	/	+
year 4	NA	NA	NA	NA
year 5	/	+	+	+

Table 4. Relationship between phenophases of *Qualea multiflora* and abiotic variables in the natural reserve of Cerrado in Clube de Caça e Pesca de Uberlândia, Brazil. Positive relationship: +, Negative relationship: -; Absent or weak relationship: /; Non-applicable: NA).

<i>Qualea multiflora</i>	Rainfall	Wind speed	Temperature	Humidity
Sprouting leaves				
year 1	+	/	/	-
year 2	+	/	/	/
year 3	/	+	+	/
year 4	NA	NA	NA	NA
year 5	/	+	/	/
Developed leaves				
year 1	/	-	-	/

year 2	+	-	-	/
year 3	+	-	-	/
year 4	NA	NA	NA	NA
year 5	+	-	/	/
Deciduouness				
year 1	-	+	+	+
year 2	/	+	+	+
year 3	-	+	+	+
year 4	NA	NA	NA	NA
year 5	-	+	+	+
Floral buds				
year 1	+	-	-	-
year 2	+	/	/	-
year 3	+	/	/	-
year 4	NA	NA	NA	NA
year 5	+	-	-	-
Flowers				
year 1	+	-	-	-
year 2	+	-	-	-
year 3	+	-	-	-
year 4	NA	NA	NA	NA
year 5	+	-	-	-
Young fruits				
year 1	-	/	/	+
year 2	/	/	/	/
year 3	/	/	/	+
year 4	NA	NA	NA	NA
year 5	/	/	/	+
Ripe fruits				
year 1	-	+	+	+
year 2	-	+	+	+
year 3	-	/	/	+
year 4	NA	NA	NA	NA
year 5	/	/	/	+

Unfavorable abiotic conditions decrease potential reproductive success by affecting characteristics such as inflorescences, floral buds, flowers, and young and ripe fruits

The third hypothesis was also supported, as the production of inflorescences, floral buds, flowers, young fruits, and ripe fruits from both species decreased as unfavorable abiotic conditions intensified (Tab. 5, Figs. 5). Regarding the number of floral buds per inflorescence, a decrease was observed over the four years in *Q. grandiflora*, whereas in *Q. multiflora*, we observed a decrease in the first three years and then an increase in the fifth year.

Table 5. Reproductive structures produced by *Qualea grandiflora* and *Q. multiflora* in the natural reserve of Cerrado in Clube de Caça e Pesca de Uberlândia, Brazil.

Species	Phenophase	Year 1	Year 2	Year 3	Year 5	χ^2	<i>p</i>
<i>Qualea grandiflora</i>	Inflorescences	133.066±54.992	97.000±70.916	84.066±44.425	41.133±18.707	678.25	<0.001
	Floral buds	27.111±6.634	23.556±4.789	18.622±4.992	20.444±4.947	82.845	<0.001
	Flowers per day	32.533±32.371	30.888±49.256	29.111±31.484	24.451±19.437	75.496	<0.001
	Young Fruits	117.600±41.071	123.867±155.848	91.733±48.786	82.133±46.687	172.760	<0.001
	Ripe Fruits	105.400±44.143	85.066±53.427	80.400±42.637	72.733±41.028	101.300	<0.001
<i>Qualea multiflora</i>	Inflorescences	16.333±6.229	11.800±3.895	11.133±5.139	10.133±3.067	27.029	<0.001
	Floral buds	24.200±6.771	20.088±5.264	19.155±3.044	22.600±4.653	33.340	<0.001
	Flowers per day	23.488±6.864	17.577±15.191	13.711±8.228	17.489±10.090	184.83	<0.001
	Young Fruits	42.800±20.747	33.400±14.773	31.133±14.715	25.667±12.904	68.177	<0.001
	Ripe Fruits	36.866±19.014	28.800±13.831	26.267±12.197	21.866±11.903	61.881	<0.001

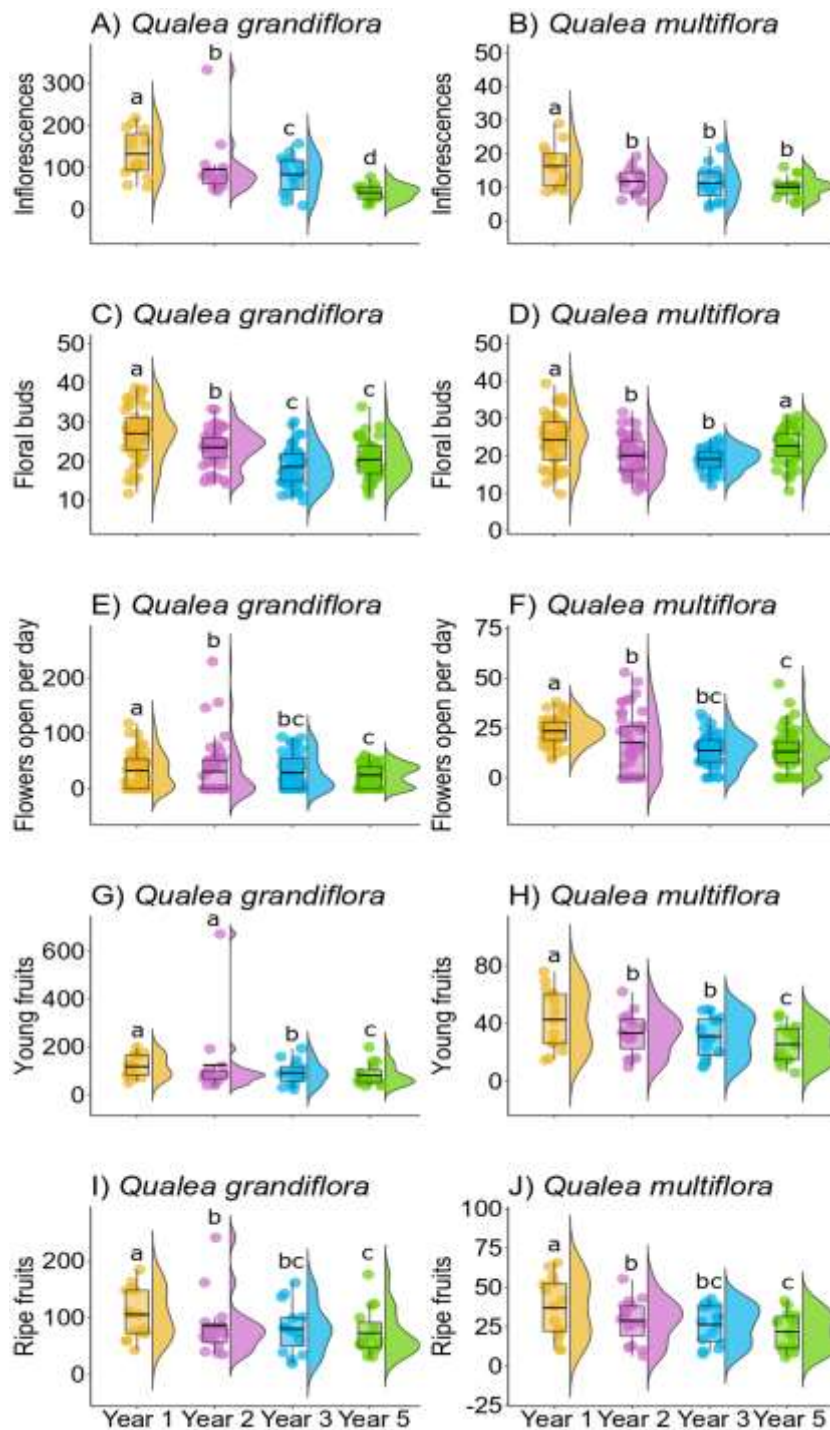


Figure 5. Inflorescences of (A) *Qualea grandiflora* ($\chi^2=678.25$, $p<0.001$) and (B) *Q. multiflora* ($\chi^2=27.029$, $p<0.001$), floral bus of (C) *Qualea grandiflora* ($\chi^2=82.845$, $p<0.001$) and (D) *Q. multiflora* ($\chi^2=33.340$, $p<0.001$), flowers open per day of (E) *Qualea grandiflora* ($\chi^2=75.496$, $p<0.001$) and (F) *Q. multiflora* ($\chi^2=184.83$, $p<0.001$), young fruits of (G) *Qualea grandiflora* ($\chi^2=172.760$, $p<0.001$) and (H) *Q. multiflora* ($\chi^2=68.177$, $p<0.001$), and ripe fruits of (I) *Qualea grandiflora* ($\chi^2=101.300$, $p<0.001$) and (J) *Q. multiflora* ($\chi^2=61.881$, $p<0.001$) in the Cerrado reserve during year 1 (August/2018 to July/2019), year 2 (August/2019 to July/2020), year 3 (August/2020 to July/2021), and year 5 (August/2022 to July/2023).

Discussion

The number of sprouting leaves produced at the end of the dry season and the beginning of the rainy season was positively related to rainfall and wind speed, but the wind speed acted as a secondary influence. Rain increases the translocation of nutrients between the soil and the plant, facilitating the differentiation of plant tissues (Santamaria et al. 2002; Silva et al. 2011). At the end of the dry season and the beginning of the rainy season there is an increase in wind speed, coinciding with the appearance of young leaves (Novaes et al. 2020). *Qualea grandiflora* and *Q. multiflora* showed sprouting leaves during the same period in other studies (Silvério and Lenza 2010; Novaes et al. 2020; Silva et al. 2020; Almeida et al. 2021; Calixto et al. 2021b). Other anemochoric species, such as *Aspidosperma tomentosum*, *Dalbergia miscolobium*, *Kielmeyera coriacea* and *Peixotoa tomentosa* also showed patterns of leaf production similar to our species (Novaes et al. 2020).

Both *Q. grandiflora* and *Q. multiflora* showed developed leaves throughout the year, being positively related to rainfall and negatively related to wind speed. However, the species were deciduous, losing many of their leaves at the end of the dry season and the beginning of the rainy season. Deciduousness showed an inverse relationship to developed leaves, being negatively related to rainfall and positively related to wind speed. Deciduousness is a protective action of the plant in the face of low water availability in the environment (Goldstein et al. 2008; Tomlinson et al. 2013). By dropping its leaves, the plant reduces physiological stress incurred by water loss through evapotranspiration (Goldstein et al. 2008; Tomlinson et al. 2013). Other studies also observed deciduate for *Qualea grandiflora* and *Q. multiflora* (Novaes et al. 2020; Silva et al. 2020; Almeida et al. 2021; Calixto et al. 2021b), as well as for other species of the

genus, such as *Q. parviflora* (Ferreira et al. 2017; Calixto et al. 2021a), also common in Cerrado areas (Lacerda et al. 2018).

Floral buds and flowers were observed in the rainy season, between October and January, with rainfall as the main climatic factor present. During periods of increased precipitation, there is a heightened exchange of nutrients between the soil and the plant, which optimizes the plant's photosynthetic capacity and enhances the production and maintenance of new plant tissues (Silva et al. 2011). Flowering during the rainy season was also observed in other populations of *Q. grandiflora* (Potascheff et al. 2020; Almeida et al. 2021) and *Q. multiflora* (Azevedo et al. 2014; Silva et al. 2020), as well as in other species of the genus (Fischer and Gordo 1993; Ferreira et al. 2017). In the Cerrado, other anemochoric species such as *Digitaria insularis*, *Galeandra montana*, *Heteropteris umbellat*, *Polypodium latipe*, *Securidaca tomentosa*, *Serjania erecta*, and *Vernonia polyanthes* also bloom in the rainy period (Batalha and Mantovani 2000). *Qualea grandiflora* and *Q. multiflora* displayed an annual flowering pattern, being the most frequent pattern observed among tropical species (Newstrom et al. 1994; Silvério and Lenza 2010; Calixto et al. 2021b), including the Vochysiaceae (Silvério and Lenza 2010; Ferreira et al. 2017; Novaes et al. 2020; Calixto et al. 2021b).

Young fruits showed maximum activity between March and May, with maximum intensity for *Q. grandiflora* in March and April and for *Q. multiflora* in July. Young fruits were positively correlated with humidity due to the greater amounts of water and nutrients required for the development of new tissues. Ripe fruits in *Q. grandiflora* had maximum activity in June and maximum intensity in March and July, while in *Q. multiflora* maximum activity was observed between April and June, with maximum intensity in April and August, both during the dry season. Ripe fruits had a negative correlation with rainfall and a positive correlation with wind speed. The wind speed is correlated with the

reproductive success of anemochoric species, as it allows diaspores to be transported through greater distances, both reducing the risk of predators and pathogens that are usually more frequent near the mother plant and facilitating establishment in suitable areas removed from competition with conspecifics close to the mother plant (Levin et al. 2003; Soons and Bullock 2008). Similar fruit patterns have also been observed in other studies of *Q. grandiflora* and *Q. multiflora* (Silvério and Lenza 2010; Lacerda et al. 2018; Silva et al. 2020; Almeida et al. 2021), and for other species from the genus (Rodríguez and Satoja 2008; Ferreira et al. 2017).

In year 4, due to the intense fire, the plants suffered changes in their phenological cycle. Plants in the Cerrado have morphological and physiological adaptations to survive fire, as well as phenological ones (Simon et al. 2009). Once the rainy season began, the nutrients freed from the burned leaves became available in the soil increasing leaf sprouting in a response similar to a drought response (Gomes et al. 2021b). However, the flowering was compromised as the resources accumulated in the roots were used to grow new branches and leaves and not for reproduction, an adaptive mechanism to overcome the stress (Miller et al. 2019). Similar patterns were observed in an experiment with controlled fire, where the group of burned plants invested more energy in vegetative phases than in reproductive phases, allocating energy to maintain individual survival (Gomes et al. 2021b). Phylogenetically close to *Q. grandiflora* and *Q. multiflora*, *Q. parviflora* showed similar phenological behavior post-fire, producing no flowers until the following year (Palermo and Miranda 2012).

The number of inflorescences, flowers opened by day, young fruits, and ripe fruits over the years decreased in both species (Figure 5). Regarding the number of floral buds per inflorescence, a decrease was observed throughout our study in the first three years for both species (Table 5). After the fire in the fourth year they did not reproduce, but in

the fifth year both had more floral buds and *Q. multiflora* had more flowers than before the fire, despite the fact that the flowering period of the fifth year was not observed completely. Other studies also observed variations in plant phenology in Cerrado species over the last few years. For example, after 10 years of study, Vilela *et al.* (2017) showed variation in the timing, intensity and synchrony of flowering of four species of the Malpighiaceae family in the same Cerrado area. They observed three species decreased their period of flowering, whereas just one increased. These changes affected the interaction of these species with herbivores and pollinators and, therefore, their ability to fructify and maintain their population sizes in the area.

In conclusion, we consider our three hypotheses confirmed. Congeneric species of *Qualea* presented similar phenological patterns, which patterns were closely tied to climate variables. Further, unfavorable abiotic conditions decreased the production of all reproductive structures assessed, which may compromise the maintenance of both populations in the field area. This five-year study demonstrates the importance of long-term phenological observations to our understanding of the future effects of rising global temperature and its potential consequent effects on fire frequency and intensity.

Acknowledgment

We thank the staff of Clube de Caça e Pesca Itororó de Uberlândia for letting us use their natural area. We also thank Gregory Hocutt for improving the language.

References

Abernethy K, Bush ER, Forget P-M, et al (2018) Current issues in tropical phenology: a synthesis. *Biotropica* 50:477–482. <https://doi.org/10.1111/btp.12558>

- Almeida SE da S, Silva PO da, Oliveira TCS de, et al (2021) Aspectos fenológicos reprodutivos de *Qualea grandiflora* Mart. em Cerrado. *Ciência Florestal* 31:920–934. <https://doi.org/10.5902/1980509839037>
- Alvares CA, Stape JL, Sentelhas PC, et al (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22:711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Appolinario V, Schiavini I (2018) Levantamento fitossociológico de espécies arbóreas de cerrado (stricto sensu) em Uberlândia-Minas Gerais. *Boletim do Herbário Ezechias Paulo Heringer* 10:
- Azevedo IFP, Nunes YRF, Ávila MA, et al (2014) Phenology of riparian tree species in a transitional region in southeastern Brazil. *Revista Brasileira de Botânica* 37:47–59. <https://doi.org/10.1007/s40415-014-0046-5>
- Barbosa L (2021) Incêndio destrói quase 600 hectares de reserva no Clube Caça e Pesca. *Diário de Uberlândia*. *Diário de Uberlândia*
- Barroso GM, Morim MP, Peixoto AL, Ichaso CLF (2004) Frutos e sementes: morfologia aplicada à sistemática de dicotiledôneas. UFV, Viçosa
- Batalha MA, Mantovani W (2000) Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. *Rev Bras Biol* 60:129–145
- Beltran RS, Kirkham AL, Breed GA, et al (2019) Reproductive success delays moult phenology in a polar mammal. *Sci Rep* 9:5221. <https://doi.org/10.1038/s41598-019-41635-x>
- Boutin S, Lane JE (2014) Climate change and mammals: evolutionary versus plastic responses. *Evol Appl* 7:29–41. <https://doi.org/10.1111/eva.12121>
- Brody AK (1997) Effects of pollinators, herbivores, and seed predators on flowering phenology. *Ecology* 78:1624–163
- Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400
- Buckley LB (2022) Temperature-sensitive development shapes insect phenological responses to climate change. *Curr Opin Insect Sci* 52:100897. <https://doi.org/10.1016/j.cois.2022.100897>
- Buttigieg PL, Ramette A (2014) A guide to statistical analysis in microbial ecology: a community-focused, living review of multivariate data analyses. *FEMS Microbiol Ecol* 90:543–550. <https://doi.org/10.1111/1574-6941.12437>
- Calixto ES, Lange D, Bronstein J, et al (2020) Data from: Optimal Defense Theory in an ant-plant mutualism: extrafloral nectar as an induced defense maximized in the most valuable plant structures. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.stqjq2c0x>

- Calixto ES, Lange D, Bronstein J, et al (2021a) Optimal Defense Theory in an ant-plant mutualism: extrafloral nectar as an induced defense is maximized in the most valuable plant structures. *Journal of Ecology* 109:167–178. <https://doi.org/10.1111/1365-2745.13457>
- Calixto ES, Lange D, Del-Claro K (2015) Foliar anti-herbivore defenses in *Qualea multiflora* Mart. (Vochysiaceae): Changing strategy according to leaf development. *Flora* 212:19–23. <https://doi.org/10.1016/j.flora.2015.02.001>
- Calixto ES, Novaes LR, dos Santos DFB, et al (2021b) Climate seasonality drives ant–plant–herbivore interactions via plant phenology in an extrafloral nectary-bearing plant community. *Journal of Ecology* 109:639–651. <https://doi.org/10.1111/1365-2745.13492>
- Cleland EE, Chuine I, Menzel A, et al (2007) Shifting plant phenology in response to global change. *Trends Ecol Evol* 22:357–365
- Correa-Lima APA, Varassin IG, Barve N, Zwiener VP (2019) Spatio-temporal effects of climate change on the geographical distribution and flowering phenology of hummingbird-pollinated plants. *Ann Bot* 124:389–398. <https://doi.org/10.1093/aob/mcz079>
- Davies WJ (2019) Multiple temperature effects on phenology and body size in wild butterflies predict a complex response to climate change. *Ecology* 100:. <https://doi.org/10.1002/ecy.2612>
- Ferreira KR, Fina BG, Rêgo NH, et al (2017) Fenologia de *Qualea parviflora* Mart. (Vochysiaceae) em um remanescente de Cerrado sensu stricto. *Journal of Neotropical Agriculture* 4:15–22. <https://doi.org/10.32404/rean.v4i3.1534>
- Fidelis A, Zironi HL (2021) And after fire, the Cerrado flowers: A review of post-fire flowering in a tropical savanna. *Flora* 280:151849. <https://doi.org/10.1016/j.flora.2021.151849>
- Fischer E, Gordo M (1993) *Qualea cordata*: pollination by the territorial bee *Centris tarsata* in the Campos Rupestres. *Cienc Cult* 45:144–147
- Forrest J, Miller-Rushing AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3101–3112. <https://doi.org/10.1098/rstb.2010.0145>
- Forrest JRK (2016) Complex responses of insect phenology to climate change. *Curr Opin Insect Sci* 17:49–54
- Gilman SE, Urban MC, Tewksbury J, et al (2010) A framework for community interactions under climate change. *Trends Ecol Evol* 25:325–331. <https://doi.org/10.1016/j.tree.2010.03.002>
- Goldstein G, Meinzer FC, Bucci SJ, et al (2008) Water economy of Neotropical savanna trees: six paradigms revisited. *Tree Physiol* 28:395–404. <https://doi.org/10.1093/treephys/28.3.395>

- Gomes L, Lenza E, Souchie FF, et al (2021a) Long-term post-fire resprouting dynamics and reproduction of woody species in a Brazilian savanna. *Basic Appl Ecol* 56:58–71. <https://doi.org/10.1016/j.baae.2021.06.005>
- Gomes L, Lenza E, Souchie FF, et al (2021b) Long-term post-fire resprouting dynamics and reproduction of woody species in a Brazilian savanna. *Basic Appl Ecol* 56:58–71. <https://doi.org/10.1016/j.baae.2021.06.005>
- Gonçalves DJP, Romero R, Yamamoto K (2013) Vochysiaceae no Parque Nacional da Serra da Canastra, Minas Gerais, Brasil. *Rodriguésia* 64:863–875
- Gordo O, Sanz JJ (2006) Climate change and bird phenology: a long-term study in the Iberian Peninsula. *Glob Chang Biol* 12:1993–2004. <https://doi.org/10.1111/j.1365-2486.2006.01178.x>
- Hofmann GS, Cardoso MF, Alves RJ V., et al (2021) The Brazilian Cerrado is becoming hotter and drier. *Glob Chang Biol* 27:4060–4073. <https://doi.org/10.1111/gcb.15712>
- Jones MW, Abatzoglou JT, Veraverbeke S, et al (2022) Global and Regional Trends and Drivers of Fire Under Climate Change. *Reviews of Geophysics* 60:. <https://doi.org/10.1029/2020RG000726>
- Lacerda DMA, Rossatto DR, Ribeiro-Novaes ÉKMD, Almeida-Júnior EB (2018) Reproductive phenology differs between evergreen and deciduous species in a Northeast Brazilian savanna. *Acta Bot Brasilica* 32:367–375. <https://doi.org/10.1590/0102-33062017abb0343>
- Lange D, Calixto ES, Del-Claro K (2017) Variation in extrafloral nectary productivity influences the ant foraging. *PLoS One* 12:1–13. <https://doi.org/10.1371/journal.pone.0169492>
- Lange D, Dáttilo W, Del-Claro K (2013a) Influence of extrafloral nectary phenology on ant-plant mutualistic networks in a neotropical savanna. *Ecol Entomol* 38:463–469. <https://doi.org/10.1111/een.12036>
- Lange D, Dáttilo W, Del-Claro K (2013b) Influence of extrafloral nectary phenology on ant-plant mutualistic networks in a neotropical savanna. *Ecol Entomol* 38:463–469. <https://doi.org/10.1111/een.12036>
- Leão-Araújo ÉF, Souza ERB de, Naves RV, Peixoto N (2019) Phenology of *Campomanesia adamantium* (Cambess.) O. Berg in Brazilian Cerrado. *Rev Bras Frutic* 41:. <https://doi.org/10.1590/0100-29452019121>
- Levin SA, Muller-Landau *Helene C., Nathan *Ran, Chave *Jérôme (2003) The Ecology and Evolution of Seed Dispersal: A Theoretical Perspective. *Annu Rev Ecol Evol Syst* 34:575–604. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132428>
- Liu Y-F, Qi H-Y, Bai C-M, et al (2011) Grafting Helps Improve Photosynthesis and Carbohydrate Metabolism in Leaves of Muskmelon. *Int J Biol Sci* 7:1161–1170. <https://doi.org/10.7150/ijbs.7.1161>

- Mariano GC, Morellato LPC, Almeida J, et al (2016) Modeling plant phenology database: Blending near-surface remote phenology with on-the-ground observations. *Ecol Eng* 91:396–408. <https://doi.org/10.1016/j.ecoleng.2016.03.001>
- Miller RG, Tangney R, Enright NJ, et al (2019) Mechanisms of Fire Seasonality Effects on Plant Populations. *Trends Ecol Evol* 34:1104–1117. <https://doi.org/10.1016/j.tree.2019.07.009>
- Miranda HS, Sato MN, Neto WN, Aires FS (2009) Fires in the cerrado, the Brazilian savanna. In: *Tropical Fire Ecology*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 427–450
- Morellato LPC, Talora DC, Takahasi A, et al (2000) Phenology of Atlantic Rain Forest Trees: A Comparative Study1. *Biotropica* 32:811–823. <https://doi.org/10.1111/j.1744-7429.2000.tb00620.x>
- Neves DRM, Damasceno-Junior GA (2011) Post-fire phenology in a campo sujo vegetation in the Urucum plateau, Mato Grosso do Sul, Brazil. *Brazilian Journal of Biology* 71:881–888. <https://doi.org/10.1590/S1519-69842011000500009>
- Newstrom LE, Frankie GW, Baker HG (1994) A New Classification for Plant Phenology Based on Flowering Patterns in Lowland Tropical Rain Forest Trees at La Selva, Costa Rica. *Biotropica* 26:141. <https://doi.org/10.2307/2388804>
- Novaes LR, Calixto ES, Oliveira ML, et al (2020) Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: A new wind-based approach. *Science of The Total Environment* 730:139039
- Oksanen J, Blanchet FG, Friendly M, et al (2019) *vegan: Community Ecology Package* (R package Version 2.5-5)
- Palermo AC, Miranda HS (2012) Efeito do fogo na produção de frutos de *Qualea parviflora* Mart. (Vochysiaceae) em cerrado sensu stricto. *Revista Árvore* 36:685–693. <https://doi.org/10.1590/S0100-67622012000400010>
- Piao S, Liu Q, Chen A, et al (2019) Plant phenology and global climate change: Current progresses and challenges. *Glob Chang Biol* 25:1922–1940
- Potascheff CM, Brito VLG, Galetto L, et al (2020) Nectar features, diurnal and nocturnal pollinators, and male fitness in *Qualea grandiflora* (Vochysiaceae). *Plant Systematics and Evolution* 306:1–12. <https://doi.org/10.1007/s00606-020-01646-y>
- Prodou R, Geniez P, Cheylan M, Besnard A (2020) Amphibian and reptile phenology: the end of the warming hiatus and the influence of the NAO in the North Mediterranean. *Int J Biometeorol* 64:423–432. <https://doi.org/10.1007/s00484-019-01827-6>
- Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the Floristic Composition of the Brazilian Cerrado Vegetation Iii: Comparison of the Woody Vegetation of 376 Areas. *Edinb J Bot* 60:57–109. <https://doi.org/10.1017/s0960428603000064>
- Rodríguez L, Satoja E (2008) Fenología, Biología floral y de Polinización de especies de la familia Vochysiaceae en la Guayana Venezolana. *Acta Bot Venez* 31:331–366

- Santamaria P, Elia A, Serio F (2002) Effect of solution nitrogen concentration on yield, leaf element content, and water and nitrogen use efficiency of three hydroponically-grown rocket salad genotypes. *J Plant Nutr* 25:245–258. <https://doi.org/10.1081/PLN-100108833>
- Santos M de O, Almeida BV de, Campos NB, et al (2022) Vegetative and reproductive phenology of *Copaifera langsdorffii* Desf. in different phytophysiognomies. *Research, Society and Development* 11:e41011427288. <https://doi.org/10.33448/rsd-v11i4.27288>
- Shimizu GH, Gonçalves DJP (2017) Flora das cangas da Serra dos Carajás, Pará, Brasil: Vochysiaceae. *Rodriguesia* 68:1159–1164. <https://doi.org/10.1590/2175-7860201768351>
- Silva PO da, Almeida SE da S, Oliveira TCS, et al (2020) Fenologia reprodutiva e vegetativa de *Qualea multiflora* Mart. em Cerradão. *Oecologia Australis* 24:127–140. <https://doi.org/10.21826/2446-82312019v74e2019013>
- Silva IA, da Silva DM, de Carvalho GH, Batalha MA (2011) Reproductive phenology of Brazilian savannas and riparian forests: environmental and phylogenetic issues. *Ann For Sci* 68:1207–1215. <https://doi.org/10.1007/s13595-011-0071-5>
- Silvério DV, Lenza E (2010) Fenologia de espécies lenhosas em um cerrado típico no Parque Municipal do Bacaba, Nova Xavantina, Mato Grosso, Brasil. *Biota Neotrop* 10:205–216. <https://doi.org/10.1590/s1676-06032010000300024>
- Simon MF, Grether R, de Queiroz LP, et al (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences* 106:20359–20364. <https://doi.org/10.1073/pnas.0903410106>
- Soons MB, Bullock JM (2008) Non-Random Seed Abscission, Long-Distance Wind Dispersal and Plant Migration Rates. *British Ecological Society* 98:581–590
- Tomlinson KW, Poorter L, Sterck FJ, et al (2013) Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *Journal of Ecology* 101:430–440. <https://doi.org/10.1111/1365-2745.12056>
- Valentin-Silva A, Alves VN, Tunes P, Guimarães E (2021a) Fire does not change sprouting nor flowering, but affects fruiting phenology in a Neotropical savanna community. *Flora* 283:151901. <https://doi.org/10.1016/j.flora.2021.151901>
- Valentin-Silva A, Alves VN, Tunes P, Guimarães E (2021b) Fire does not change sprouting nor flowering, but affects fruiting phenology in a Neotropical savanna community. *Flora* 283:151901. <https://doi.org/10.1016/j.flora.2021.151901>
- Velasque M, Del-Claro K (2016a) Host plant phenology may determine the abundance of an ecosystem engineering herbivore in a tropical savanna. *Ecol Entomol* 41:421–430. <https://doi.org/10.1111/een.12317>
- Velasque M, Del-Claro K (2016b) Host plant phenology may determine the abundance of an ecosystem engineering herbivore in a tropical savanna. *Ecol Entomol* 41:421–430

Vilela AA, Del-Claro VTS, Torezan-Silingardi HM, Del-Claro K (2017) Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. *Arthropod Plant Interact* 12:215–227.
<https://doi.org/10.1007/s11829-017-9572-y>

Vilela AA, Torezan-Silingardi HM, Del-Claro K (2014) Conditional outcomes in ant-plant-herbivore interactions influenced by sequential flowering. *Flora: Morphology, Distribution, Functional Ecology of Plants* 209:359–366.
<https://doi.org/10.1016/j.flora.2014.04.004>

Capítulo 2

Biology and reproductive ecology of *Qualea multiflora* Mart. (Vochysiaceae) in a Brazilian Savanna

Larissa Alves-de-Lima¹, Eduardo Soares Calixto^{2,3}, Leticia Rodrigues Novaes⁴, Marcos Lima de Oliveira^{1,3}, Helena Maura Torezan-Silingardi^{1,3*}

¹ Universidade Federal de Uberlândia, Instituto de Biologia, Programa em Pós-graduação em Ecologia, Conservação e Biodiversidade, Rua Ceará 1084, Uberlândia, MG, 38.405-315, Brazil.

² Entomology and Nematology Department. University of Florida, 1881, Natural Area Dr, Gainesville, FL, 32608, USA.

³ Universidade de São Paulo, Programa de Pós-graduação em Entomologia, Faculdade de Filosofia, Ciências e Letras, Av. Bandeirantes, 3900, Ribeirão Preto, SP, 14.040-901, BRAZIL

⁴ Universidad de Sevilla, Departamento de Biología Vegetal y Ecología, Avenida Reina Mercedes, 6, CP 41012, Sevilla, España.

*Author for correspondence: hmtsilingardi@gmail.com and torezan.silingardi@ufu.br

Seguindo as normas de edição da revista Acta Botânica Brasileira.

Abstract

The genus *Qualea* Aublet has approximately 50 species and is the second largest in the Vochysiaaceae A.St.-Hil. Family, with around 240 species. However, even with its numerous and widely distributed species, there are still gaps in its biology and reproductive ecology. Thus, the objective of this work was to describe the phenology of *Qualea multiflora*, its floral phenology. Floral display and resources, the reproductive system and floral visitors, in an area of Cerrado *sensu stricto* in Minas Gerais from August/2018 to January/2021. Reproductive phenology showed that flowering occurred in the summer, between November/2018 and January/2019, for around 80 days. The flowers showed diurnal anthesis lasting about two days, during which there were changes in color. The floral display was composed of 18 ± 7.79 (mean $\pm$ standard error) inflorescences, each with an average of 1.20 ± 0.80 open flowers per day. Each flower had only one anther that produced pollen grains (9958.40 ± 344.81) with high viability ($91.29 \pm 7.62\%$).

Keywords: Cerrado, Flowers, Phenology, Pollinators, Alogamy.

Resumo

O gênero *Qualea* Aublet tem aproximadamente 50 espécies e é o segundo maior da família Vochysiaceae A.St.-Hil., com cerca de 240 espécies. No entanto, mesmo com suas numerosas espécies amplamente distribuídas, ainda existem lacunas acerca da biologia e ecologia reprodutiva. Assim, o objetivo deste trabalho foi descrever a fenologia de *Qualea multiflora*, sua fenologia floral, o display e recursos florais, o sistema reprodutivo e os visitantes florais, numa área de Cerrado *sensu stricto* de Minas Gerais de agosto/2018 a janeiro/2021. A fenologia reprodutiva mostrou que a florada ocorreu no verão, entre novembro/2018 até janeiro/2019, por cerca de 80 dias. As flores apresentaram antese diurna e com duração de cerca de dois dias, ao longo dos quais houve mudanças na coloração. O display floral foi composto por $18 \pm 7,79$ (média $\pm$ erro padrão) inflorescências, cada uma com média de $1,20 \pm 0,80$ flores abertas por dia. Cada flor teve apenas uma antera que produziu grãos de pólen ($9958,40 \pm 344,81$) com alta viabilidade ($91,29 \pm 7,62\%$). The nectar was produced for two days and its quantity and concentration of sugars decreased over time. The reproductive system was self-incompatible and non-agamospermic, with dependence on medium to large bees, wasps and hummingbirds for fruiting. 386 visits from 43 species were recorded in 2019, and 264 visits from 32 species in 2020.

Palavras chaves: Cerrado, Fenologia, Flores, Polinizadores, Alogamia.

Introduction

The most diverse of the tropical savannas is located in Brazil, where it is called Cerrado. It comprised originally around 22% of the Brazilian territory with about 2,000,000 km² (Coutinho 2002). Nowadays Cerrado is restricted to small remnants due to human activity, it is estimated that only 600,000 km² remain, a loss of around 70% of the original area (Oliveira-Filho and Ratter 2002). Within it is many phytophysiognomies, Cerrado show a wide floristic diversity composed mainly of angiosperms from about 150 families (Souza and Lorenzi 2008) with around 4000 endemic species. The high level of endemism and the fast destruction of its natural areas characterize Cerrado as a hotspot for conservation (Myers et al. 2000).

One of Cerrado's most abundant families is the Vochysiaceae A.St.-Hil. family, comprising 240 species distributed across eight genera (Shimizu and Yamamoto 2012a) and primarily inhabiting tropical regions (Negrelle et al. 2007). In Brazil, this family is represented by six genera encompassing approximately 163 species, distributed across various Brazilian phytophysionomies (Flora do Brasil 2023). Vochysiaceae species exhibit a sub-shrub to arboreal habit, simple leaves with opposite or whorled phyllotaxis, and zygomorphic bisexual flowers with only one fertile stamen (Kawasaki 2006). *Qualea* Aublet is the second largest genus within Vochysiaceae, comprising about 50 species that produce simplified flowers, consisting of five united sepals forming a spur to hold nectar, a single petal, one stamen and one pistil (Shimizu and Yamamoto 2012b; Gonçalves et al. 2017; Shimizu and Gonçalves 2017). Phenological variations in flower anthesis are observed among *Qualea* species, with some species displaying nocturnal opening, such as *Q. grandiflora* (Potascheff et al. 2020), while others exhibit daytime opening, as seen in *Q. paviflora* (REF). Additionally, there are variations in the duration of the flowers,

ranging from single-day blooms to those lasting up to three days (Barbosa 1983; Rodríguez and Satoja 2008).

Qualea species have a variable floral display, since the number of open flowers depends on some elements, as abiotic and biotic factors, structural and physiological characteristics of each individual available in the area (Ohashi and Yahara 2001), and the proximity between them. Floral display defines the number of floral resources available that directly influences the attraction of pollinators and floral visitors, being fundamental for self-incompatible species (Ohashi and Yahara 2001). Floral resources produced by *Qualea* species include pollen and nectar (Rodríguez and Satoja 2008; Morais et al. 2020) supplemented by extrafloral nectar produced in the leaves (Calixto et al. 2015, 2021a), which aids in attracting visitors.

Genus *Qualea* show late self-incompatibility, a characteristic widely distributed within the family (Oliveira, 1998; Oliveira e Gibbs, 2000; Custódio et al., 2014). Self-incompatibility makes species dependent on pollinators to transfer pollen between plants. There are records of pollination by bees, wasps, moths and hummingbirds within the genus (Machado and Oliveira 2015; Morais et al. 2020; Potascheff et al. 2020; Alves-de-Lima et al. 2023). Flowers play a vital role in ecosystem maintenance, serving as a source of food and shelter for various invertebrates, such as bees (Rodríguez and Satoja 2008; Morais et al. 2020), wasps (Barbosa 1983), ants (Del-Claro et al. 1996; Raupp et al. 2020; Calixto et al. 2021a), beetles (Del-Claro et al. 1996), spiders (Nahas et al. 2012), and also vertebrates, such as hummingbirds (Machado and Oliveira 2015). Moreover, the extrafloral nectaries present on the leaves of *Qualea* species attract mutualistic ants (Del-Claro et al. 1996; Calixto et al. 2015, 2021a, c, b; Lange et al. 2017) and spiders (Nahas et al. 2012; Lange et al. 2021), positioning the genus as a representative contributor to biodiversity in Cerrado (Bronstein 2021).

Despite a substantial increase in studies focusing on *Qualea* species, particularly in Cerrado areas, the biology and reproductive ecology of certain *Qualea* species remain inadequately explored (Ponte et al. 2020). Investigations into the biology and reproductive ecology are crucial as they provide fundamental data for the conservation of populations (Goettsch et al. 2015). Consequently, this study aims to describe the (i) species phenology, (ii) floral phenology, (iii) floral display and resources, (iv) breeding system, and (v) floral visitors within a population of *Q. multiflora* in a Cerrado area from central Brazil.

Materials and methods

Study site

Fieldwork was carried out from August 2018 to January 2021 in an area of cerrado *sensu stricto* vegetation (Del-Claro et al. 2019), located within the natural reserve area of the Clube de Caça e Pesca Itororó in the city of Uberlândia, Minas Gerais state, South-eastern Brazil (18°58'59" S; 48°17'53" W). The climate is characterized by two distinct seasons, a dry/cold season from April to September and a wet/warm season from October to March, classified as Aw according to the Köppen-Geiger system. The area presents average annual temperature of 22°C, and precipitation totaling 1.500 mm in the year (Alvares et al. 2013; Novaes et al. 2020; Calixto et al. 2021c). Vochysiaceae is the second most representative tree family within the area (Silva et al. 2022).

Plant specie

Qualea multiflora Mart. (Vochysiaceae) trees can reach up to 10 meters height (Shimizu and Yamamoto 2012b) and are notably common in Cerrado areas (Ratter et al. 2003), including our study area (Novaes et al. 2020; Calixto et al. 2021a, c), where its

population exhibits a density of approximately 73 individuals per hectare (Del-Claro et al. 1996). A distinctive feature of *Q. multiflora* flowers is its single white petal with magenta spots observed on the first day of opening, turning from the second day on to yellow petal with purple spots (Shimizu and Yamamoto 2012b). The dried fruits are capsules with three locules and many flying seeds (Barroso et al. 1999), similar to *Q. cordata*, *Q. grandiflora* and *Q. parviflora* (Gonçalves et al. 2017).

A total of 65 individuals of *Q. multiflora* were employed in this study: 20 for species phenology observations, 10 for floral phenology, floral display and floral resources investigations, 15 for breeding system tests, and 20 for floral visitors observations. Selected individuals met the criterion of a minimum height of 1 meter and were positioned at least 10 meters apart. To ensure result impartiality, all observations were consistently conducted by a single person (LAL).

Specie phenology

Qualea multiflora individuals were observed monthly from August 2018 to July 2019 to assess seven phenophases, each characterized by the presence of specific structures: sprouting leaves, developed leaves, deciduousness, floral buds, flowers, young fruits and ripe fruits (Novaes et al. 2020). The phenophase activity index was calculated based on the presence or absence of these phenophases following Bencke and Morellato (2002) and circular statistics were employed to evaluate the activity of each phenophase. Months were converted into angles, with each month corresponding to 30°. The frequency of individuals presenting each phenophase was utilized to estimate the following parameters: the mean vector (μ), the mean month, the mean length of the vector (r), the median, the circular standard deviation, the Rayleigh test Z and Rayleigh test p for data uniformity (Morellato et al. 2010; Novaes et al. 2020; Lange et al. 2021; Calixto et al.

2021c). Prior to the analyzes, the normality of the circular data was assessed using the Watson quality adjustment test. To determine the intensity of each phenophase, we categorized each individual based on the intensity of the event, where 0 represented a non-existent event, 1 indicated a discrete event in about 1-25% of the tree branches, 2 denoted a frequent event (26–75%), and 3 represented an intense event (76–100%) (Fournier 1974; Ribeiro and Castro 1986; Torezan-Silingardi and Oliveira 2004; Novaes et al. 2020; Alves-de-Lima et al. 2023).

Floral phenology

We characterized floral phenology by observing 20 pre-bagged floral buds, equally distributed among 10 individuals. The observation spanned from the floral opening to the fall of all structures. Additionally, in another set of 30 pre-bagged flowers distributed equally in the same 10 individuals, three flowers per individual, we assessed stigma receptivity using the 3% hydrogen peroxide test (Kearns and Inouye 1993; Torezan-Silingardi and Oliveira 2004)). The formation of bubbles after contact with 3% hydrogen peroxide indicated that the stigma was receptive (Kearns and Inouye 1993). In a subsequent set of 30 flowers, also pre-bagged and evenly distributed equally among the 10 selected individuals, we determined the moment of the pollen grains release by gently touching the anther onto a black and slightly rough surface (Alves-de-Lima et al. 2023). The release of pollen grains into the structure was analyzed with the naked eye (Torezan-Silingardi and Oliveira 2004; Wu et al. 2005).

Floral display and resources

The analysis of floral display and resources was conducted on the same 10 individuals employed for floral phenology. To assess floral display, we quantified the total number of inflorescences, inflorescence size, total number of floral buds, and the average daily number of open flowers. The evaluation of floral resources encompassed the examination of pollen, nectar and scent. The total number of inflorescences was quantified by directly counting the them before the flowers opened. Three medium sized inflorescences devoid of open flowers were randomly chosen for each individual plant, and their sizes were measured using a digital caliper. Additionally, the total number of floral buds in each of these three inflorescences was quantified. Subsequently, we conducted daily monitoring of the same three inflorescences, counting the number of flowers opened over a period of 10 consecutive days. This observation spanned from the tenth to the nineteenth day of flowering, allowing us to estimate the average daily number of flowers that opened.

The total number of pollen grains and the pollen viability were examined in one flower per individual, from the same 10 plants. These flowers were previously bagged and collected promptly after floral opening, and subsequently transported to the Laboratório de Morfologia, Microscopia e Imagem at Universidade Federal de Uberlândia. For transportation, each flower was placed in individual Falcon tubes and stored in polystyrene boxes with ice to prevent dehydration of the pollen grains (Munique and Calixto 2018). In the laboratory, we stained all the pollen grains obtained from the single anther of each flower with acetic carmine and subjected them to microscopic analysis (Kearns and Inouye 1993). Pollen viability was estimated by dividing the number of viable pollen grains obtained by the total number of grains present in the anthers.

To quantify nectar volume and sugar concentration, we examined 10 flowers on their first day of opening (white petal) and 10 flowers on the second day after opening (yellow petal), flowers were examined every two hours, spanning from 06:00 to 18:00 hours. This procedure involved selecting one white flower and one yellow flower per individual per hour. Nectar was collected using 10 μ L capillaries, and the proportion of sugar (% Brix) was analyzed with a handheld refractometer (Eclipse model) (Raupp et al. 2020; Calixto et al. 2021a).

The floral scent was examined in 30 flowers, with three flowers assessed per individual. This analysis involved evaluating the presence and intensity of scent throughout the floral longevity, commencing at the floral opening and concluding with the fall of the flower. Each observation of floral scent was performed by a single person (LAL) to avoid bias, and was assigned a numerical note per flower, with the following scale: 0 for no scent, 1 for mild, 2 for moderate, and 3 for strong.

Breeding system

The breeding system was investigated in additional 20 individuals. Thirty floral buds were marked per individual, and these were evenly distributed across five treatments, resulting 120 floral buds per treatment and 600 floral buds in total. The treatments applied were as follow: (i) agamospermy, where buds were emasculated in the pre-anthesis phase with partial removal of the sepal and petal; (ii) spontaneous self-pollination, with pollination occurring without interference from any pollen vector; (iii) manual self-pollination, involving manual pollination within the same flower by touching the dehiscent anther on the stigma to transfer pollen grains; (iv) manual cross-pollination, conducted manually between flowers of individuals with a minimum distance of 20 meters from each other; and (v) natural pollination (control), allowing flowers to be freely

contacted by visitors (Torezan-Silingardi and Oliveira 2004). In spontaneous self-pollination the floral buds were enclosed in bags and left in place until fruit formation or floral abortion. For agamospermy, manual self-pollination, and manual cross-pollination, floral buds were similarly bagged before treatment and reseeded afterward to safeguard the buds. Polyester mesh bags were employed for bagging the buds, allowing light and gas exchange while protecting the flowers from contact with animals or external pollen (Boyd et al. 2011; Medan et al. 2015; Suinyuy and Johnson 2021). The treatments were weakly monitored to observe outcomes. The Reproductive Efficiency Index was computed as the ratio between the number of fruits resulting from natural pollination and manual cross-pollination following Ruiz and Arroyo (1978).

Floral visitor

Floral visitors were identified using additional 15 plants, each with a minimum of eight newly opened flowers. Observations were conducted during two flowering periods of 2018/2019 and 2019/2020, spanning a total of 40 hours per year and accumulating an overall sampling effort of 80 hours. In the first flowering period the observations took place from 5:00 to 19:00 h, comprising 30 hours in the morning and 10 hours in the afternoon. In the second flowering period the observations occurred from 5:00 to 3:00h, encompassing 20 hours in the morning, 10 hours in the afternoon, and 10 hours in the night.

To evaluate visitation frequency, we treated flowers of the same individual as dependent. Vertebrate identification was achieved through direct observations, photographs and expert consultations. Arthropods were collected, identified with the assistance of experts, and subsequently deposited in the entomological collection of the Laboratório de Ecologia Comportamental e de Interações at the Biology Institute of the

Federal University of Uberlândia. Taxonomic identification was consistently pursued at the most precise taxonomic level possible, with classifications ranging from family to genus and species.

We categorized floral visitors into six groups: (i) effective pollinators - those who actively contributed to pollination by frequently contacting both anther and stigma; (ii) occasional pollinators - those promoting low pollination rates by visiting flowers less frequently, or touching reproductive parts occasionally; (iii) pollen thieves - individuals collecting pollen without facilitating pollination; (iv) nectar thieves - individuals collecting nectar without promoting pollination; (v) floral herbivores - animals causing damage to floral buds and flowers when feeding on their parts; (vi) predators - individuals feeding on insects within the flowers; and (vii) non-interacting visitors - those having contact with petal and sepals, without collecting floral resources or causing damage, and not exhibiting aggressive behavior (Del-Claro and Torezan-Silingardi 2012).

Results

Species phenology

All phenophases were significantly unimodal, except for the development of leaves (Table. 1). *Qualea multiflora* exhibited continuous leaf production throughout the year, except in September, with maximum intensity (100%) observed between November 2018 and April 2019 (Fig. 1a) and the peak activity occurring in March (Table 1; Fig. 2a). Deciduousness, or leaf loss, occurred from May to December, reaching maximum intensity in August (86.6%) (Fig. 1a) and peaking in July (Table 1; Fig. 2b). Leaf sprouting had its maximum intensity in October (86.6%) (Fig. 1a) and peak activity in September (Table 1; Fig. 2c). The first floral buds appeared in October 2018, with maximum intensity and peak activity in November, achieving an intensity of 84.4%

(Table 1; Figs. 1b; 2d). The population flourished from November 2018 to January 2019 for approximately 80 days. The analyzed population exhibited an annual flowering pattern, with the highest flowering intensity observed in December at 91.1% (Fig. 1b) and peak activity in November (Table 1; Fig. 2e). Young fruits reached maximum intensity (62.2%) in May, coinciding with peak activity (Table 1; Figs. 1b; 2f). The maximum intensity of ripe fruits occurred in August at 64.4% (Fig. 1b), with peak activity in June (Table 1; Fig. 2g).

Table 1 Phenology of *Qualea multiflora* from August 2018 to July 2019 in a Cerrado vegetation at the reserve area of the Clube de Caça e Pesca Itororó de Uberlândia, in South-Eastern Brazil, presented as Circular statistics results.

Phenophases	N	Mean vector (μ)	Month	Length of mean vector (r)	Median	Circular standard deviation	Rayleigh test (Z)	Rayleigh test (p)
Developed leaves	20	63.115	Mar	0.115	60.019	119.261	0.115	0.119
Deciduousness	20	194.045	Jul	0.817	209.924	323.496	0.816	<0.000
Sprouting leaves	20	262.376	Sep	0.946	269.943	340.916	0.946	<0.001
Flower buds	20	306.287	Nov	0.941	299.981	340.013	0.941	<0.001
Flowers	20	329.268	Nov	0.912	329.985	335.361	0.912	<0.001
Young fruits	20	129.841	May	0.335	120.038	84.805	0.335	<0.001
Ripe fruits	20	172.318	Jun	0.665	180.115	51.925	0.663	<0.001

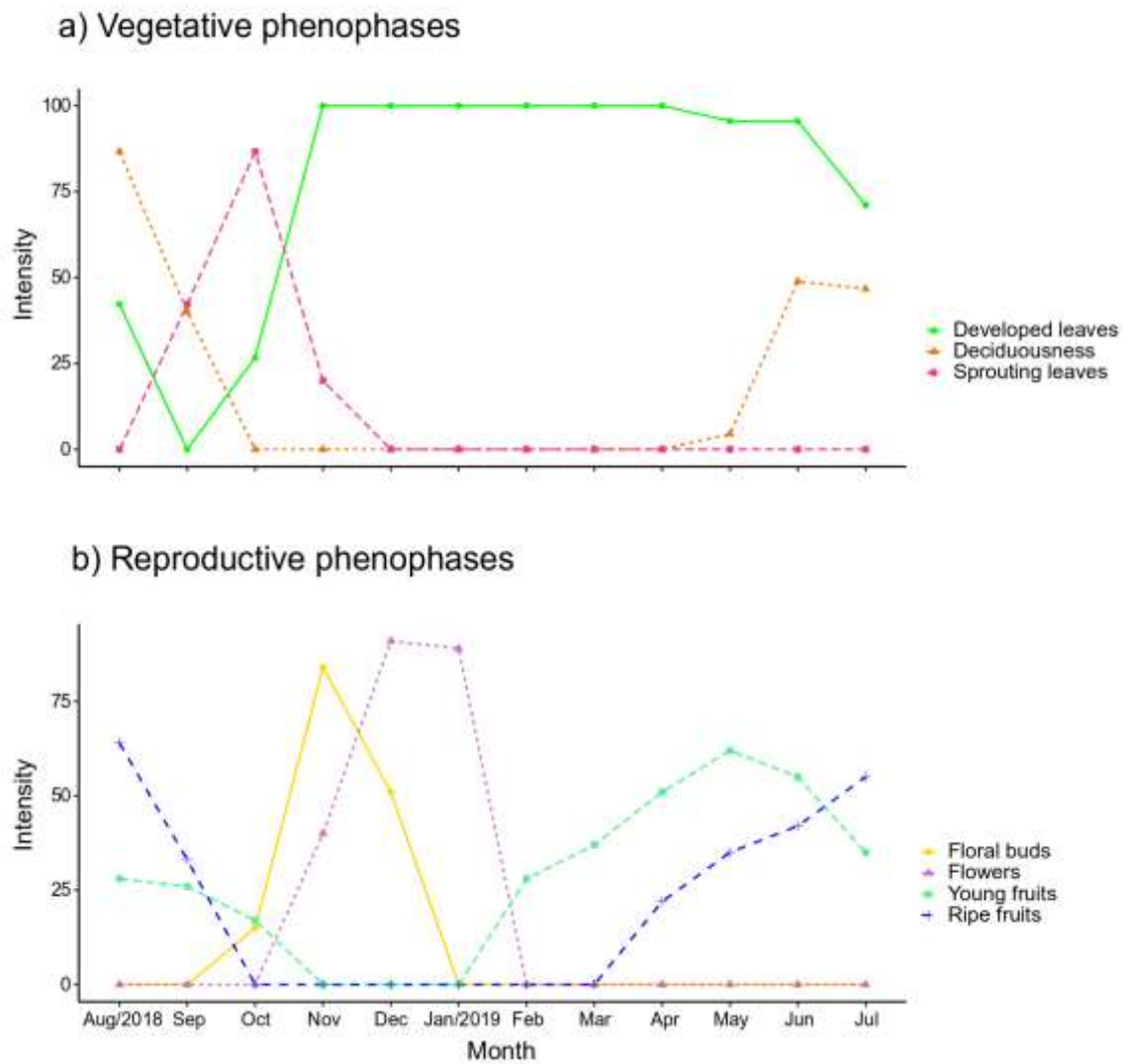


Fig. 1 *Qualea multiflora* phenophases from August 2018 to July 2019 in a Cerrado vegetation at the Clube de Caça e Pesca Itororó de Uberlândia, in South-Eastern Brazil. Vegetative (a) and reproductive (b) phenophases.

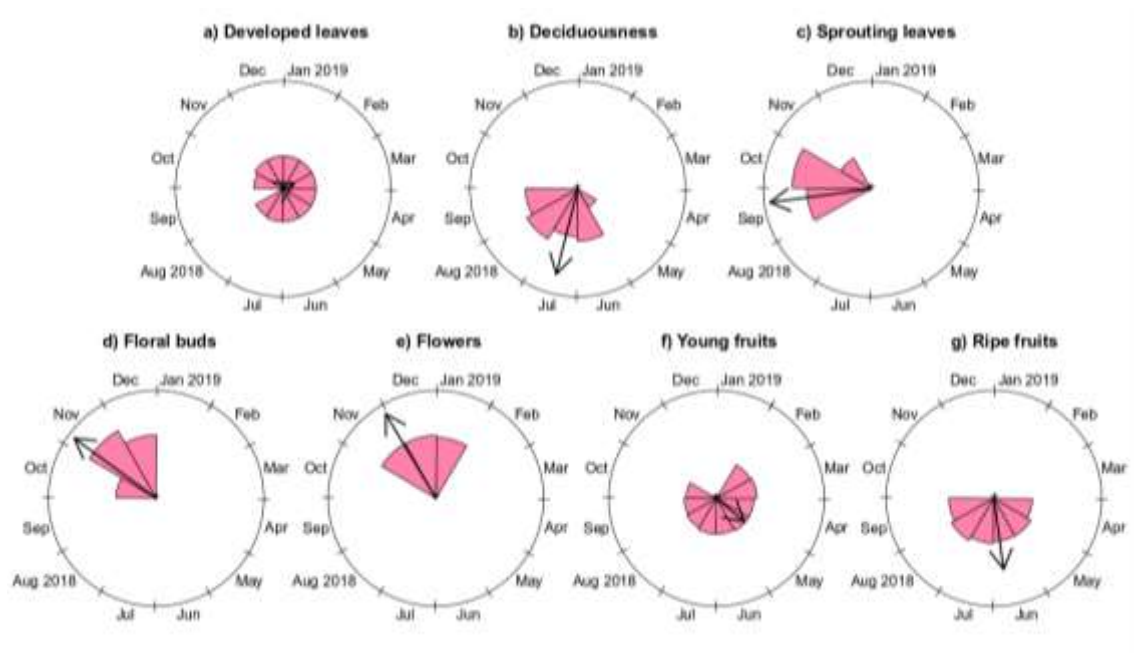


Fig. 2 *Qualea multiflora* phenology in a Cerrado vegetation at Clube de Caça e Pesca Itororó de Uberlândia, in South-Eastern Brazil. Arrow position represents the mean angle (mean month) and arrow length represents the length of mean vector (r). Rainy season occurred from October to March and the dry season from April to September. Statistical results are depicted in Table 1.

Floral phenology

Qualea multiflora floral buds commenced opening at approximately 4:30h (Fig. 3a). The process of floral opening spanned about 3 hours. The flower displays a single white petal with a yellow central stripe and various pink and irregular patches, a central style with a greenish hue and green stigma, and just one stamen with a yellow anther (Fig. 3b). Anther dehiscence initiated around 5:00 hours, followed shortly by receptivity of the stigma. At the end of the first day, the petal transitioned to yellow, and the pink spots darkened, the stamen and the stylet start to lost their initial homogeneous greenish tones (Fig. 3c). The anther began to darken but still released a small amount of pollen. The stigmatic surface became darker and less receptive. The petal darkened and slowly twisted

until the end of the second day or the beginning of the third when it fell, along with the stamen (Fig. 3d, e), leaving only the pistil attached to the floral receptacle (Fig. 3f).

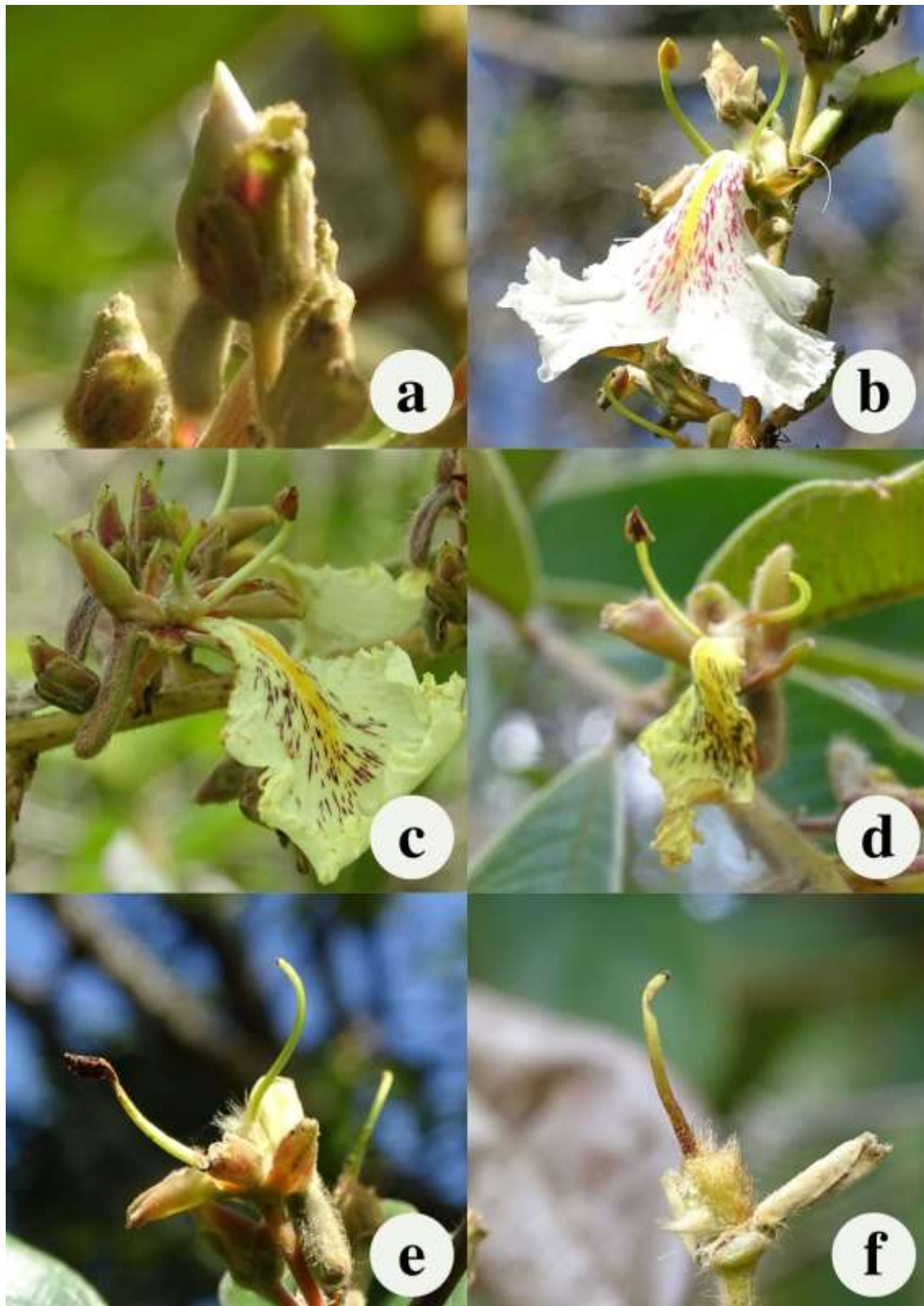


Fig. 3 *Qualea multiflora* ontogenetic stages. Pre-anthesis phase (a), flower just after anthesis (b), second day flower (c), twisted and darkened petal in the end of the second or beginning of the third day (d), total browning of the anther (e) and, the brown colored pistil and darkened stigmatic surface.

Floral display and resources

Qualea multiflora produced an average of 18 ± 7.79 (mean $\pm$ standard error) inflorescences per plant, each measuring 28.45 ± 11.25 cm in length and bearing 26.04 ± 10.43 floral buds per inflorescence. On average, each inflorescence had 1.20 ± 0.80 open flowers per day and each individual plant had 21,6 new flowers per day. The flowers produced 9958.40 ± 344.81 pollen grains, with a viability of 91.29 ± 7.62 %.

In the first day of opening *Q. multiflora* flowers exhibited a bigger amount of nectar (4.9 ± 0.8 μ L) than in the second day (1.8 ± 0.8 μ L) (Fig. 4a). There was a decay in the mean volume nectar throughout the day, ranging from 5.83 to 3.86 μ L in the first day flowers, and from 2.59 to 0.41 μ L in the second day flowers. The sugar concentration was bigger in the nectar of the first day flowers (38.2 ± 6.3 %Brix) than in the second day ones (16.3 ± 5.4 %Brix) (Fig. 4b). Sugar concentration also decreased over the day, ranging from 46.5 to 33.3 %Brix for the first day flowers, and 21.5 to 6.3 %Brix for the second day flowers.

The scent of *Q. multiflora* flowers was intense and sweet, beginning to be released at 05:00 h (Fig. 5). By 08:00 hour the scent reached its peak and remained constant until 12:00 h. From 12:00 to 19:00 h the scent gradually softened. The scent intensity slowly decreased until 02:00 h and remained constant until the evening of the second day, when it was no longer noticeable.

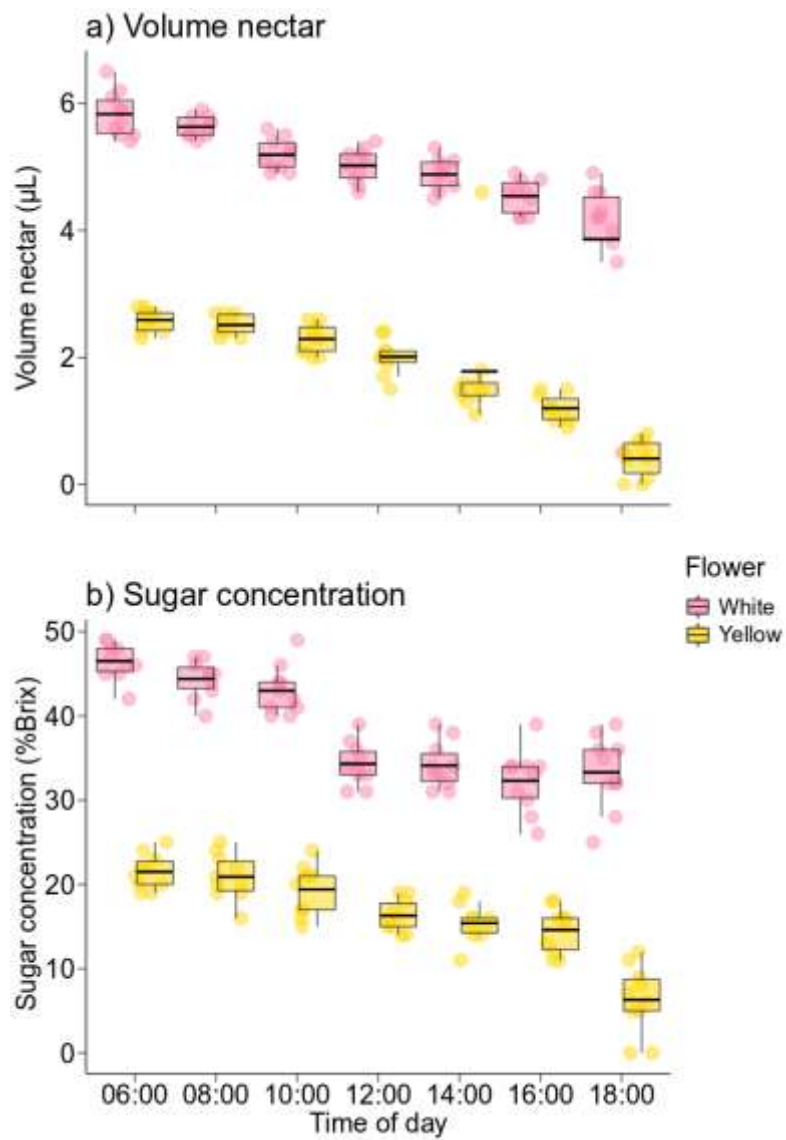


Fig. 4 Daily variation on nectar volume (a) and sugar concentration (b) in first day flowers (white petal) and second day flowers (yellow petal) of *Qualea multiflora* in a Cerrado vegetation at Clube de Caça e Pesca Itororó de Uberlândia, in South-Eastern Brazil.

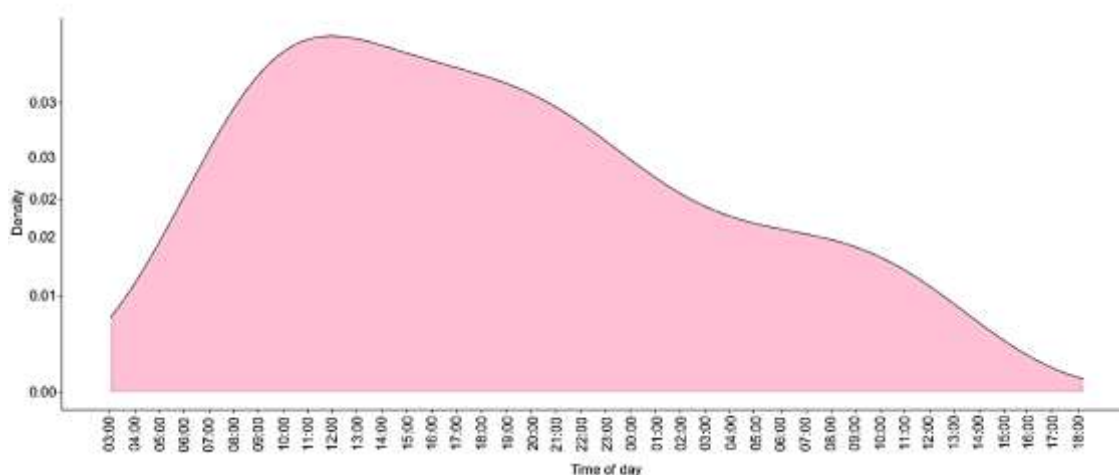


Fig. 5 Scent intensity in *Qualea multiflora* flowers from opening to floral fall.

Breeding system

Qualea multiflora did not yield fruit from the treatments of agamospermy, spontaneous self-pollination and manual self-pollination (Table 2), indicating a non-agamospermic and self-incompatible breeding system. The Reproductive Efficiency Index (0.83) indicates that the pollination services are not adequate in the area, as manual pollination was more effective to promote to fruit formation.

Table 2 *Qualea multiflora* breeding system considering the five treatments realized and the fruit formation.

Treatments	Nº of flowers	Nº of fruits	Fruiting (%)
Agamospermy	120	0	0
Spontaneous self-pollination	120	0	0
Manual self-pollination	120	0	0
Manual cross-pollination	120	18	15
Natural pollination	120	15	12.5

Floral visitors

Qualea multiflora flowers were visited more times and by more animal species in the first flowering period than in the second (386 and 264 visits, and 43 and 32 species, respectively) (Table 3). The visits comprised vertebrates such as hummingbirds, and invertebrates including insects and spiders. These were classified into nine orders: Apodiformes, Araneae, Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera (Fig. 6a), Lepidoptera (Fig. 6b) and Orthoptera. The peak of visitation occurred between 07:00 and 10:00 hours (Fig. 7) and the most frequent order was Hymenoptera, representing 58.70% and 71.59% of visits in the first and second flowerings. *Erinnyis ello*, *Camponotus blandus* and *Macroductylus pumilio* were observed in the night period.

Pollination of flowers occurred exclusively during the day and was carried out by bees, wasps and hummingbirds. Sixteen species were identified as pollinators, of which seven were considered effective pollinators and nine occasional pollinators. The effective pollinators observed in both flowering periods included *Bombus (Fervidobombus) morio*, *Epicharis (Epicharis) bicolor* (Fig. 6c), *E. (Triepicharis) analis*, *E. (Epicharana) flava*, and *Xylocopa (Neoxylocopa) suspecta*. *Xylocopa (Neoxylocopa) frontalis* was observed only in 2018/2019 and *Centris (Trachina) similis* only in 2019/2020 flowering periods. Notably, among the most frequent occasional pollinators were: *Amazilia fimbriata*, *Epicharis (Epicharitides) cockerelli* (Fig. 6d), *Heliomaster squamosus*, *Paratrigona lineata* and *Polistes simillimus*. Thirteen species of thieves were observed, with six species collected pollen, six species collected nectar, and one species collected both resources. Among the pollen thieves, small bees (Fig. 6e) and a Diptera species belonging to the Syrphinae subfamily were present. True bugs (Fig. 6f), ants (Fig. 6g), butterflies, moths and hummingbirds were considered nectar thieves. *Ceratina* sp. was the only species observed stealing both resources.

Coleoptera and Orthoptera (Figs 6h, i) were classified as herbivores. The beetle *Macroductylus pumilio* was the most frequent observed herbivore, more frequent in the first than in the second flowering (7.5% and 4.1%, respectively). Wasps and spiders were considered predators. Non-interacting visitors included Blattodea and flies from Muscidae and Sarcophagidae families, which were seen only resting on the petal. They had no contact with floral resources or other floral visitors and were not observed feeding on floral structures.

Table 3 Visitors of *Qualea multiflora* (Vochisylaceae). Absolute (AF) and relative (RF) frequency of floral visitors; the type of interaction in the flower (INT) is defined as: PO – Pollinators, PT – Pollen Thieves, NT – Nectar Thieves, FH – Floral Herbivore, PR – Predator, NV – Non-interacting Visitor; and the time that it was observed (TIME): D – Day (light time), N – Night.

	2019		2020			
	AF	RF	AF	RF	INT	TIME
INVERTEBRATES						
Blattodea						
Blattodea sp	1	0.259	0	0.000	NV	D
Coleoptera						
Cetoniinae sp	5	1.295	1	0.379	FH	D
<i>Chauliognathus fallax</i> (Germar, 1824)	1	0.259	0	0.000	FH	D
Curculionidae sp	0	0.000	2	0.758	FH	N
Entiminae sp	0	0.000	1	0.379	FH	D
<i>Macroductylus pumilio</i> (Burm., 1855)	29	7.513	11	4.167	FH	D/N
<i>Naupactus</i> sp	1	0.259	0	0.000	FH	D
Diptera						
Muscidae sp	0	0.000	1	0.379	NV	D
<i>Sarcophaga</i> sp	2	0.518	0	0.000	NV	D
Sarcophagidae sp	2	0.518	0	0.000	NV	D
Syrphidae sp1	6	1.554	0	0.000	PT	D

Hymenoptera						
Bees						
<i>Augochlora (Oxystoglossella) sp</i>	1	0.259	2	0.758	PT	D
<i>Bombus (Fervidobombus) morio</i> (Swederus, 1787)	12	3.109	10	3.788	PO	D
<i>Centris (Centris) aenea</i> Lepeletier, 1841	9	2.332	12	4.545	PO	D
<i>Centris (Trachina) similis</i> (Fabricius, 1804)	0	0.000	6	2.273	PO	D
<i>Ceratina sp</i>	13	3.368	7	2.652	PT, NT	D
<i>Dialictus sp</i>	3	0.777	1	0.379	PT	D
<i>Euglossa sp1</i>	1	0.259	0	0.000	PT	D
<i>Epicharis (Epicharis) bicolor</i> Smith, 1854	25	6.477	38	14.394	PO	D
<i>Epicharis (Epicharitides) cockerelli</i> Friese, 1900	12	3.109	35	13.258	PO	D
<i>Epicharis (Triepicharis) analis</i> Lepeletier, 1841	7	1.813	10	3.788	PO	D
<i>Epicharis (Epicharana) flava</i> Friese, 1900	15	3.886	20	7.576	PO	D
<i>Eufriesea auriceps</i> (Friese, 1899)	4	1.036	3	1.136	PO	D
<i>Exomalopsis fulvofasciata</i> Smith, 1879	3	0.777	0	0.000	PT	D
<i>Tetragonisca angustula</i> (Latreille, 1811)	0	0.000	2	0.758	PT	D
<i>Xylocopa (Neoxylocopa) frontalis</i> (Olivier, 1789)	21	5.440	0	0.000	PO	D
<i>Xylocopa (Neoxylocopa) suspecta</i> Moure & Camargo, 1988	45	11.658	9	3.409	PO	D
Wasps						
<i>Polistes simillimus</i> Zikán, 1951	8	2.073	10	3.788	PO	D

<i>Polybia occidentalis</i> (Olivier, 1791)	1	0.259	8	3.030	PT	D
Pompilidae sp	1	0.259	0	0.000	PT	D
<i>Synoeca</i> sp	1	0.259	4	1.515	PT	D
<i>Zethus cylindricus</i> (Fox, 1899)	1	0.259	0	0.000	PT	D
Ants						
<i>Atta laevigata</i> (Smith, 1858)	1	0.259	0	0.000	PR	D
<i>Azteca</i> sp	1	0.259	0	0.000	PR	D
<i>Camponotus blandus</i> (Smith, 1858)	10	2.591	5	1.894	PR	D/N
<i>Camponotus senex</i> (Smith, 1858)	5	1.295	0	0.000	PR	D
<i>Camponotus</i> sp	1	0.259	0	0.000	PR	D
<i>Ectatomma tuberculatum</i> (Olivier, 1792)	3	0.777	4	1.515	PR	D
Hemiptera						
Cydnidae sp	4	1.036	0	0.000	NT	D
Pentatomidae sp	8	2.073	0	0.000	NT	D
Lepidoptera						
<i>Aetilha</i> sp	1	0.259	2	0.758	NT	D
<i>Badecla badaca</i> (Hewitson, 1868)	5	1.295	3	1.136	NT	D
<i>Erinnyis ello</i>	0	0.000	2	0.758	NT	N
Orthoptera						
<i>Cephalocoema</i> sp	1	0.259	0	0.000	FH	D

<i>Hyperbaenus</i> sp	1	0.259	0	0.000	FH	D
<i>Scudderia</i> sp	0	0.000	1	0.379	FH	D
Araneae						
Oxiopidae sp	1	0.259	0	0.000	PR	D
Salticidae sp1	1	0.259	0	0.000	PR	D
Salticidae sp2	1	0.259	0	0.000	PR	D
Salticidae sp3	0	0.000	1	0.379	PR	N
Thomisidae sp	1	0.259	0	0.000	PR	D
VERTEBRATES						
Apodiforme						
<i>Amazilia fimbriata</i> (Gmelin, 1788)	32	8.290	22	8.333	PO	D
<i>Calliphlox amethystina</i> (Boddaert, 1783)	1	0.259	0	0.000	NT	D
<i>Colibri serrirostris</i> (Vieillot, 1816)	1	0.259	0	0.000	NT	D
<i>Eupetomena macroura</i> (Gmelin, 1788)	0	0.000	11	4.167	PO	D
<i>Heliomaster squamosus</i> (Temminck, 1823)	47	12.176	15	5.682	PO	D
Total	386	100	264	100		



Fig. 6 Floral visitors of *Qualea multiflora* in Cerrado vegetation, South-Eastern Brazil. a. *Centris (Trachina) similis*; b. *Badecla badaca*; c. *Epicharis (Epicharis) bicolor*; d. *Epicharis (Epicharitides) cockerelli*; e. *Tetragonisca angustula*; f. Pentatomidae sp; g *Camponotus blandus*; h. *Scudderia* sp; i. *Cephalocoema* sp.

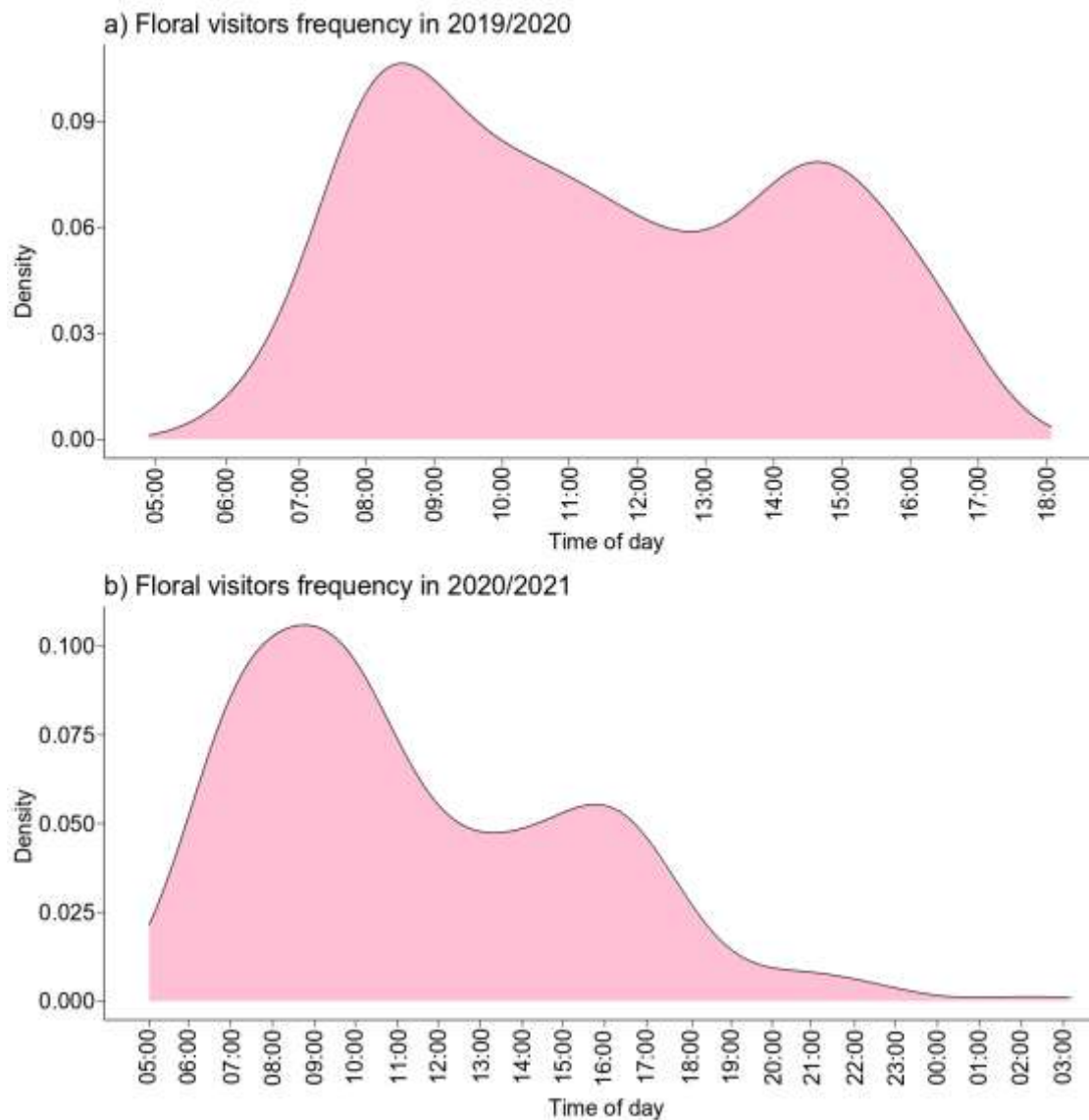


Fig. 7 Floral visitors' frequency in *Qualea multiflora* during the day in 2019/2020 (a) and day and night in 2020/2021 (b).

Discussion

In this study we evaluated the biology and reproductive ecology of *Qualea multiflora*, revealing (i) annual flowering lasting approximately 80 days during the summer; (ii) approximately 21,6 new flowers per day on average in each tree; (iii) flowers with 2-day longevity; (iv) pollen grains average of 9958.40 ± 344.81 per flower,

with $91\pm 7.62\%$ viability, (v) average nectar volume and sugar concentration of 4.9 ± 0.8 μL and 38.2 ± 6.3 %Brix respectively, in first day flowers, and 1.8 ± 0.8 μL and 16.3 ± 5.4 %Brix respectively, in the second day flowers; (vi) self-incompatible reproductive system; and (vii) widespread pollination, involving medium and large bees, wasps and hummingbirds.

Species phenology

Qualea multiflora is a deciduous species, with sprouting leaves occurring between September and November, developing leaves from October to August, and deciduousness between May and September. Deciduousness occurs in the driest period, being a common response among woody species to water stress (Kushwaha and Singh 2005). Sprouting leaves at the end of the dry season and beginning of the rainy season is favored by the availability of remobilized minerals transported by phloem from old leaves to the meristematic areas, and by the increase of humidity, which allows the formation of new plant tissues (Van Schaik et al. 1993). This pattern was also observed for populations of *Q. multiflora* in other studies (Silvério and Lenza 2010, Silva et al. 2020, Novaes et al. 2020; Calixto et al. 2021c) and for congenerous species such as *Q. grandiflora* and *Q. parviflora* (Calixto et al. 2021c).

The annual flowering observed in our *Q. multiflora* population is the most common pattern among tropical species (Newstrom et al. 1994). Floral buds were observed from October to December and flowers from November to January, both in the rainy season. The higher air humidity optimizes pollen fertilization (Omondi et al. 2016) and the formation of new tissues, necessary to fruit and leaf development (Kushwaha and Singh 2005). The flowering period was coincident with the observed by other authors in

the same area (Novaes et al. 2020; Calixto et al. 2021c) or far away (Lacerda et al. 2018; Silva et al. 2020)

Young fruits were observed between February and September, and ripe fruits from April to October, in the end of the rainy season and the complete dry season. Fruit ripening from April to September coincides with the dry season and favors anemochory species as *Q. multiflora* to disperse dry seeds (Novaes et al. 2020), what benefits the reproductive success of the species (Soons & Bullock 2008), since the seeds have a lower potential for survival close to the mother plant (Janzen 1970; Connell 1971). Ripe fruits in the dry season were also reported for *Q. multiflora*, *Q. grandiflora* and *Q. parviflora* (Calixto et al. 2021c).

Floral phenology

Qualea multiflora showed diurnal opening with anthesis occurring at 5:00h. The floral opening is an important factor in determining the community of pollinators. This association is observed in Vochysiaceae since *Q. cordata* and *Q. parviflora* that had a daytime floral opening, permitting them to be visited and pollinated mainly by bees (Fischer and Gordo 1993; Morais et al. 2020), while *Qualea grandiflora* flowers were pollinated by moths just after their night anthesis (Potascheff et al. 2020). *Qualea multiflora* flowers had diurnal anthesis and were pollinated mainly by bees, corroborating Barbosa (1983) observations. Barbosa (1983) also reported changes in color and floral duration of more than one day. The Vochysiaceae species have day-long flowers as *Qualea parviflora* (Barbosa 1983), and flowers lasting two or three days as *Vochysia crassifolia* (Rodríguez and Satoja 2008) and *Qualea grandiflora* (Potascheff et al. 2020).

Floral display and resources

Inflorescences and floral buds are decisive for the floral display, being an important factor in attracting floral visitors (Ohashi and Yahara 2001). The length of the inflorescences and the number of floral buds observed by us were greater than those found for *Q. multiflora*, as well as for congener species (Gonçalves et al. 2013).

The single anther presented in *Qualea multiflora* flowers produced large number of pollen grains with high viability. These values are similar to those described by Morais et al. (2020). Pollen quantity and viability are fundamental for the formation of fruits of the species genus *Qualea*, since they have a non-agamospermic reproductive system, that is, pollen dependent for fertilization (Oliveira 1998a).

Characteristics of nectar, such as volume and sugar concentration, are known as mediators of the plant-pollinator relationship (Galletto et al. 2018; Potascheff et al. 2020). The bigger amount of nectar and sugar concentration in flowers recently opened can attract more pollinators, being favorable to the *fitness* of the species due to the greater receptivity of stigma. However, *Q. grandiflora* (Potascheff et al. 2020) and *Vochysia cinnamomea* (Santos et al. 1997a).

The scent was intense and sweet, being released from floral opening at dawn until the end of the second day. The beginning of the release of the scent coincides with the beginning of the arrival of the pollinators. These adaptations between plants and pollinations are the result of a long evolutionary history (Neff and Simpson 1981). The release of scent optimized the encounter of flowers by pollinators, being an important olfactory guide (Majetic et al. 2009; Faegri and van der Pijl 2013). Thus, the release of scent by second day flowers can benefit the *fitness* of the species by attracting pollinators to receptive flowers just opened.

Breeding system

The breeding system of *Q. multiflora* was non-agamospermic and self-incompatible, being therefore dependent on pollen from another individual for fruit formation, so the species requires pollen vectors. The self-incompatible system of *Q. multiflora* was already reported (Morais et al. 2020). Self-incompatibility ensures greater genetic variability when compared to compatible systems (Gibbs 1990). The self-incompatible system has been said to be an ancestral characteristic of angiosperms (Gibbs 1990; Nettancourt 1997). Self-incompatibility is seen in Cerrado plants (Oliveira 1998a; Munin et al. 2008; Silvério and Lenza 2010; Costa et al. 2014) and within the Vochysiaceae family (Oliveira 1998a; Oliveira and Gibbs 2000; Custódio et al. 2014). The fruit formation was very low, with 15% in manual cross-pollination and 12.5% in natural pollination. The Reproductive Efficiency Index obtained (0.83) indicates pollinators effectiveness is inferior than manual pollination, however this index was much smaller in the past for *Q. multiflora* observed in a nearby area by Barbosa (1983) with REI value equal to 0.33.

Floral visitors

Flowers of *Q. multiflora* were visited by invertebrates and vertebrates seeking for resources, shelter and resting area. Pollination was mainly carried out by bees, but also by wasps and hummingbirds. This widespread pollination is common in the Cerrado (Oliveira and Gibbs 2002). Bees were also indicated by Barbosa (1983), Silva et al. (2012) and Morais et al. (2020) as the main pollinators of *Q. multiflora*. Congeneric species as *Q. jundiahy* (Yamamoto et al. 2007), *Q. parviflora* (Silva et al. 2012) and *Q. schomburgkiana* (Rodríguez and Satoja 2008) also have their flowers pollinated by bees,

that are recognized as an important group of pollinators for the Vochysiaceae family (Fischer and Gordo 1993; Santos et al. 1997b; Oliveira 1998b; Gimenes 2007; Yamamoto et al. 2007; Rodríguez and Satoja 2008; Silva et al. 2012; Morais et al. 2020). Wasps were observed on *Q. multiflora* flowers by Barbosa (1983) and pollination by hummingbirds was also reported by Maruyama et al. (2013) and Machado and Oliveira (2015). Other species from the Vochysiaceae have flowers visited by hummingbirds, as *Qualea parviflora* and *Vochysia cinnamomea* (Silva et al. 2012).

Thieves of floral resources within the Vochysiaceae family were not recorded before the present study. Pollen thieves were observed in the flowers collecting resources without promoting pollination, what is a common behavior in many species (Alves-Dos-Santos et al. 2016). Some studies have shown that the indirectly action of thieves can sometimes benefit the plant, forcing pollinators to increase the frequency of visits in searching for floral resources (Milet-Pinheiro and Schlindwein 2009; Irwin et al. 2010; Almeida-Soares et al. 2010).

Beetles, grasshopper, crickets, and katydids were considered floral herbivores by feeding on the floral tissues, especially the petal. *Macrodactylus pumilio* was the most frequent floral herbivore in this study. *Macrodactylus pumilio* already was observed as herbivore of great impact on *Q. multiflora* flowers before (Del-Claro et al. 1996). Ants and spiders were present and protected the flowers of *Q. multiflora* from the action of herbivores, what was observed also by Nahas et al. (2012), thus, ants and spiders were considered as predators. Non-interacting individuals were cockroaches and flies, which only rested on petals.

Final remarks

Studying the biology and reproductive ecology of plant species is essential to better understand ecosystem services, and thus help in decision-making regarding the conservation of populations and ecosystems (Goettsch et al. 2015). *Qualea multiflora* is a source of food, shelter and resting places for different groups of vertebrate and invertebrate organisms. Generalist species, such as *Q. multiflora*, are important for maintaining biodiversity (Bronstein 2021). The self-incompatible and non-agamospermic reproductive system makes *Q. multiflora* a non-recommended species for areas at an early stage of restoration, as it depends on pollinators for its reproduction. But this species can be used on late restoration as it can support interactions with a vast group of animal species, maintaining them. These data are essential for planning the protection and restoration of area (Rodrigues et al. 2009; Menz et al. 2011).

Acknowledgment

We thank Letícia Alves de Lima for her assistance in the field; Eduardo Andrade Botelho de Almeida, Solange Cristina Augusto, Kleber Del-Claro, Bruno de Sousa Lopes, Yuri Campanholo Grandinete and Rogério Botion Lopes for their assistance in identifying floral visitors; Raquel L. Carvalho and Rafaella Teixeira Maciel Oliveira for comments in earlier draft of the manuscript; the Clube de Caça e Pesca Itororó de Uberlândia for allowing the use of its area; the Laboratório de Morfologia, Microscopia e Imagem - UFU for the structure and equipment used. This studied was financed in part by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Code of funding 001 (LAL), and by Conselho Nacional de Desenvolvimento Científico e Tecnológico - Brazil (CNPQ) - Finance code 403647/2021-5 (HMTS).

References

- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology* 43:1223–1232
- Alvares CA, Stape JL, Sentelhas PC, et al (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22:711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Alves-de-Lima L, Calixto ES, Oliveira ML de, et al (2023) Flowering Time Variation in Two Sympatric Tree Species Contributes to Avoid Competition for Pollinator Services. *Plants* 12:3347. <https://doi.org/10.3390/plants12193347>
- Alves-Dos-Santos I, Da Silva CI, Pinheiro M, Kleinert ADMP (2016) Quando um visitante floral é um polinizador? *Rodriguesia* 67:295–307. <https://doi.org/10.1590/2175-7860201667202>
- Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. *Glob Chang Biol* 11:1504–1513
- Arrhenius S (1896) XXXI On the influence of carbonic acid in the air upon the temperature of the ground. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science* 41:237–276. <https://doi.org/10.1080/14786449608620846>
- Artaxo P (2020) As três emergências que nossa sociedade enfrenta: saúde, biodiversidade e mudanças climáticas. *Estudos Avançados* 34:53–66. <https://doi.org/10.1590/s0103-4014.2020.34100.005>
- Atwater DZ, Barney JN (2021) Climatic niche shifts in 815 introduced plant species affect their predicted distributions. *Global Ecology and Biogeography*, geb 13342:
- Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. *Nat Ecol Evol* 2:34–43
- Barbosa AAA (1983) Aspectos da ecologia reprodutiva de tres especies de Qualea (Vochysiaceae) num cerrado de Brasilia-DF. Univerisade de Brasília
- Barroso GM, Morim MP, Peixoto AL, Ichaso CLF (1999) Frutos e sementes: morfologia aplicada à sistemática de dicotiledôneas. Editora Universidade Federal de Viçosa, Viçosa
- Bencke CSC, Morellato LPC (2002) Comparação de dois métodos de avaliação da fenologia de plantas, sua interpretação e representação. 4:269–275
- Bosso L, Rebelo H, Garonna AP, Russo D (2013) Modelling geographic distribution and detecting conservation gaps in Italy for the threatened beetle *Rosalia alpina*. *J Nat Conserv* 21:72–80

- Boyd RS, Teem A, Wall MA (2011) Floral biology of an Alabama population of the federally endangered plant, *Xyris tennesseensis* Kral (Xyridaceae). *Castanea* 76:255–265
- Brambilla M, Ficetola GF (2012) Species distribution models as a tool to estimate reproductive parameters: a case study with a passerine bird species. *Journal of Animal Ecology* 81:781–787
- Brito JC, Acosta AL, Álvares F, Cuzin F (2009) Biogeography and conservation of taxa from remote regions: An application of ecological-niche based models and GIS to North-African Canids. *Biol Conserv* 142:3020–3029
- Broennimann O, Thuiller W, Hughes G, et al (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Glob Chang Biol* 12:1079–1093
- Bronstein JL (2021) The Gift That Keeps on Giving: Why Does Biological Diversity Accumulate Around Mutualisms? In: *Plant-Animal Interactions*. Springer International Publishing, Cham
- Brooker RW (2006) Plant-plant interactions and environmental change. *New Phytologist* 171:271–284
- Bustamante M, Nardoto G, Pinto A, et al (2012) Potential impacts of climate change on biogeochemical functioning of Cerrado ecosystems. *Brazilian Journal of Biology* 72:655–671. <https://doi.org/10.1590/S1519-69842012000400005>
- Buzatti RS de O, Lemos-Filho JP, Bueno ML, Lovato MB (2017) Multiple Pleistocene refugia in the Brazilian cerrado: evidence from phylogeography and climatic nichemodelling of two *Qualea* species (Vochysiaceae). *Botanical Journal of the Linnean Society* 185:307–320
- Calixto ES, Lange D, Bronstein J, et al (2021a) Optimal Defense Theory in an ant-plant mutualism: extrafloral nectar as an induced defense is maximized in the most valuable plant structures. *Journal of Ecology* 109:167–178. <https://doi.org/10.1111/1365-2745.13457>
- Calixto ES, Lange D, Del-Claro K (2015) Foliar anti-herbivore defenses in *Qualea multiflora* Mart. (Vochysiaceae): Changing strategy according to leaf development. *Flora* 212:19–23. <https://doi.org/10.1016/j.flora.2015.02.001>
- Calixto ES, Lange D, Moreira X, Del-Claro K (2021b) Plant species specificity of ant-plant mutualistic interactions: Differential predation of termites by *Camponotus crassus* on five species of extrafloral nectaries plants. *Biotropica* 53:1406–1414. <https://doi.org/10.1111/btp.12991>
- Calixto ES, Novaes LR, dos Santos DFB, et al (2021c) Climate seasonality drives ant-plant-herbivore interactions via plant phenology in an extrafloral nectary-bearing plant community. *Journal of Ecology* 109:639–651. <https://doi.org/10.1111/1365-2745.13492>

- Cao D, Zhang J, Han J, et al (2022) Projected Increases in Global Terrestrial Net Primary Productivity Loss Caused by Drought Under Climate Change. *Earths Future* 10:. <https://doi.org/10.1029/2022EF002681>
- Carvalho RL, Resende AF, Barlow J, et al (2023) Pervasive gaps in Amazonian ecological research. *Current Biology* 33:3495-3504.e4. <https://doi.org/10.1016/j.cub.2023.06.077>
- Coelho CAS, Cardoso DHF, Firpo MAF (2016) Precipitation diagnostics of an exceptionally dry event in São Paulo, Brazil. *Theor Appl Climatol* 125:769–784. <https://doi.org/10.1007/s00704-015-1540-9>
- Colwell RK, Rangel TF (2009) Hutchinson’s duality: the once and future niche. *Proceedings of the National Academy of Sciences* 106:19651–19658. <https://doi.org/https://doi.org/10.1073/pnas.0901650106>
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) *Dynamics of Populations*. Centre for Agricultural Publishing and Documentation, Wageningen. Wageningen, The Netherlands, p 312
- Correa-Lima APA, Varassin IG, Barve N, Zwiener VP (2019) Spatio-temporal effects of climate change on the geographical distribution and flowering phenology of hummingbird-pollinated plants. *Ann Bot* 124:389–398. <https://doi.org/10.1093/aob/mcz079>
- Costa FO, de Lima DCR, Silva ALG (2014) Biologia reprodutiva de *Vatairea macrocarpa* (Benth.) Ducke (Fabaceae-Faboideae) em uma área de Cerrado no município de Chapadinha, MA, Brasil. *Heringeriana* 8:1–19
- Costa MH, Pires GF (2010) Effects of Amazon and Central Brazil deforestation scenarios on the duration of the dry season in the arc of deforestation. *International Journal of Climatology* 30:1970–1979
- Coutinho LM (2002) O bioma do cerrado. In: KLEIN AL (ed) *Eugen Warming e o cerrado brasileiro*. Editora UNESP, São Paulo, pp 77–92
- Custódio LN, Carmo-Oliveira R, Mendes-Rodrigues C, Oliveira PE (2014) Pre-dispersal seed predation and abortion in species of *Callisthene* and *Qualea* (Vochysiaceae) in a Neotropical savanna. *Acta Bot Brasilica* 28:309–320
- Del-Claro K, Berto V, Réu W (1996) Effect of herbivore deterrence by ants on the fruit set of an extrafloral nectary plant, *Qualea multiflora* (Vochysiaceae). *J Trop Ecol* 12:887. <https://doi.org/10.1017/S0266467400010142>
- Del-Claro K, Rodriguez-Marales D, Calixto ES, et al (2019) Ant pollination of *Paepalanthus lundii* (Eriocaulaceae) in Brazilian savanna. *Ann Bot* 123:1159–1165. <https://doi.org/10.1093/aob/mcz021>
- Del-Claro K, Torezan-Silingardi HM (2012) *Ecologia das interações plantas-animais: Uma abordagem ecológico-evolutiva*. Technical Books Editora

- Dore MHI (2005) Climate change and changes in global precipitation patterns: What do we know? *Environ Int* 31:1167–1181. <https://doi.org/10.1016/j.envint.2005.03.004>
- Elith J, Phillips SJ, Hastie T, et al (2011) A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17:43–57
- Evans SE, Wallenstein MD (2014) Climate change alters ecological strategies of soil bacteria. *Ecol Lett* 17:155–164
- Faegri K, van der Pijl L (2013) Principles of pollination ecology. Elsevier
- Ferreira RB, Parreira MR, Nabout JC (2021) The impact of global climate change on the number and replacement of provisioning ecosystem services of Brazilian Cerrado plants. *Environ Monit Assess* 193:. <https://doi.org/10.1007/s10661-021-09529-6>
- Filho IAM, Neves AJ das, Silva GE, Vieira A dos S (2019) Áreas de proteção ambiental e a preservação do bioma cerrado. *Revista Brasileira de Estudos de Segurança Pública* 12:10–19
- Fischer E, Gordo M (1993) *Qualea cordata*: pollination by the territorial bee *Centris tarsata* in the Campos Rupestres. *Cienc Cult* 45:144–147
- Fonseca M, Lamas I, Kasecker T (2010) O papel das unidades de conservação. *Scientific American Brasil* 39:18–23
- Fournier LA (1974) Un método cuantitativo para la medición de características fenológicas en árboles. *Turrialbra (IICA)* 24:422–423
- Freeman EA, Moisen GG (2008) A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecol Modell* 217:48–58
- Frei ER, Ghazoul J, Matter P, et al (2014) Plant population differentiation and climate change: responses of grassland species along an elevational gradient. *Glob Chang Biol* 20:441–455
- Galetto L, Araujo FP, Grilli G, et al (2018) Flower trade-offs derived from nectar investment in female reproduction of two *Nicotiana* species (Solanaceae). *Acta Bot Brasilica* 32:473–478. <https://doi.org/https://doi.org/10.1590/0102-33062018ab0121>
- Gibbs PE (1990) Self-incompatibility in flowering plants: a neotropical perspective. *Revista Brasileira de Botânica* 13:125–136
- Gimenes M (2007) Polinização de *Vochysia lucida* C. Presl (Vochysiaceae) em uma área de restinga na Bahia. *Rev Bras Entomol* 51:465–470. <https://doi.org/10.1590/S0085-56262007000400010>
- Goettsch B, Hilton-Taylor C, Cruz-Piñón G, et al (2015) High proportion of cactus species threatened with extinction. *Nat Plants* 1:1–7. <https://doi.org/10.1038/nplants.2015.142>

- Gonçalves DJP, Romero R, Yamamoto K (2013) Vochysiaceae no Parque Nacional da Serra da Canastra, Minas Gerais, Brasil. *Rodriguésia* 64:863–875
- Gonçalves DJP, Shimizu GH, Yamamoto K, Semir J (2017) Vochysiaceae na região do Planalto de Diamantina, Minas Gerais, Brasil. *Rodriguésia* 68:159–193
- Gottsberger G, Silberbauer-Gottsberger I (1983) Dispersal and distribution in the cerrado vegetation of Brazil. *Sonderbd Naturwiss Ver Hamburg* 7:315–352
- Guisan A, Mod HK, Scherrer D, et al (2019) Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities. *Global Ecology and Biogeography* 28:1384–1392. <https://doi.org/10.1111/geb.12967>
- Hamann E, Blevins C, Franks SJ, et al (2021) Climate change alters plant--herbivore interactions. *New Phytologist* 229:1894–1910
- Harley CDG, Anderson KM, Demes KW, et al (2012) Effects of climate change on global seaweed communities. *J Phycol* 48:1064–1078
- Hernández-Lambrano RE, González-Moreno P, Sánchez-Agudo JÁ (2017) Towards the top: niche expansion of *Taraxacum officinale* and *Ulex europaeus* in mountain regions of South America. *Austral Ecol* 42:577–589
- Hidasi-Neto J, Joner DC, Resende F, et al (2019) Climate change will drive mammal species loss and biotic homogenization in the Cerrado Biodiversity Hotspot. *Perspect Ecol Conserv* 17:57–63
- Hijmans RJ, Cameron SE, Parra JL, et al (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978. <https://doi.org/10.1002/joc.1276>
- Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. *Nature* 470:479–485
- Hofmann GS, Cardoso MF, Alves RJ V., et al (2021) The Brazilian Cerrado is becoming hotter and drier. *Glob Chang Biol* 27:4060–4073. <https://doi.org/10.1111/gcb.15712>
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol* 15:56–61
- Hutchinson GE (1957) Concluding Remarks: animal ecology and demography. . *Cold Spring Harb Symp Quant Biol* 22:415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- Irwin RE, Bronstein JL, Manson J, Richardson LL (2010) Nectar robbing: ecological and evolutionary perspectives. *Annu Rev Ecol Evol Syst* 41:271–292. <https://doi.org/10.1146/annurev.ecolsys.110308.120330>

- Jacobi CM, do Carmo FF, Vincent RC, Stehmann JR (2007) Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodivers Conserv* 16:2185–2200. <https://doi.org/10.1007/s10531-007-9156-8>
- Jacobsen CD, Brown DJ, Flint WD, et al (2020) Vulnerability of high-elevation endemic salamanders to climate change: A case study with the Cow Knob Salamander (*Plethodon punctatus*). *Glob Ecol Conserv* 21:e00883
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Johansson V, Lönnell N, Rannik Ü, et al (2016) Air humidity thresholds trigger active moss spore release to extend dispersal in space and time. *Funct Ecol* 30:1196–1204
- Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol Lett* 8:1010–1020
- Kawasaki ML (2006) Vochysiaceae. In: Kubitzki K (ed) *The families and genera of vascular plants*. Springer, Berlin, pp 480–487
- Kearns CA, Inouye DW (1993) *Techniques for pollination biologists*. University press of Colorado
- Klink CA, Machado RB (2005) Conservation of the Brazilian cerrado. *Conservation biology* 19:707–713
- Kushwaha CP, Singh KP (2005) Diversity of leaf phenology in a tropical deciduous forest in India. *J Trop Ecol* 21:47–56
- Lacerda DMA, Rossatto DR, Ribeiro-Novaes ÉKMD, Almeida-Júnior EB (2018) Reproductive phenology differs between evergreen and deciduous species in a Northeast Brazilian savanna. *Acta Bot Brasilica* 32:367–375. <https://doi.org/10.1590/0102-33062017abb0343>
- Lange D, Calixto ES, Del-Claro K (2017) Variation in extrafloral nectary productivity influences the ant foraging. *PLoS One* 12:1–13. <https://doi.org/10.1371/journal.pone.0169492>
- Lange D, Calixto ES, Del-Claro K, Stefani V (2021) Spatiotemporal niche-based mechanisms support a stable coexistence of ants and spiders in an extrafloral nectary-bearing plant community. *Journal of Animal Ecology* 90:1570–1582. <https://doi.org/10.1111/1365-2656.13477>
- Lawson DA, Rands SA (2019) The effects of rainfall on plant–pollinator interactions. *Arthropod Plant Interact* 13:561–569
- Lira FDA, Amado TF, Moura TA, Riul P (2021) Vulnerable areas to accidents with scorpions in Brazil. *Tropical Medicine and International Health* 00: <https://doi.org/10.1111/tmi.13561>

- Lopes TM, Bailly D, Almeida BA, et al (2017) Two sides of a coin: Effects of climate change on the native and non-native distribution of *Colossoma macropomum* in South America. *PLoS One* 12:e0179684
- Machado AO, Oliveira PE (2015) β -Diversity of hummingbird plants in cerrado areas of Central Brazil. *Rodriguésia* 66:1–19
- Majetic CJ, Raguso RA, Ashman TL (2009) The sweet smell of success: Floral scent affects pollinator attraction and seed fitness in *Hesperis matronalis*. *Funct Ecol* 23:480–487. <https://doi.org/10.1111/j.1365-2435.2008.01517.x>
- Malhi Y, Roberts JT, Betts RA, et al (2008) Climate change, deforestation, and the fate of the Amazon. *Science* (1979) 319:169–172
- Marengo JA (2006) Mudanças climáticas globais e seus efeitos sobre a biodiversidade; caracterização do clima atual e definição das alterações climáticas para o território brasileiro ao longo do século 21., Ministério. Ministério do Meio Ambiente, Brasília, Distrito Federal, Brasil
- Marengo JA, Ambrizzi T, da Rocha RP, et al (2010) Future change of climate in South America in the late twenty-first century: intercomparison of scenarios from three regional climate models. *Clim Dyn* 35:1073–1097. <https://doi.org/10.1007/s00382-009-0721-6>
- Maruyama PK, Oliveira GM, Ferreira C, et al (2013) Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften* 100:1061–1068
- Matricardi EAT, Skole DL, Costa OB, et al (2020) Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science* (1979) 369:1378–1382
- Medan D, Castillo-Campos G, Zarlavsky G (2015) Floral biology of *Adolphia infesta* and the reproductive profile of Colletieae (Rhamnaceae). *J Pollinat Ecol* 16:
- Mendoza-González G, Martínez-Moreno ML, Rojas-Soto OR, et al (2013) Ecological niche modeling of coastal dune plants and future potential distribution in response to climate change and sea level rise. *Glob Chang Biol* 19:2524–2535
- Menz MHM, Phillips RD, Winfree R, et al (2011) Reconnecting plants and pollinators: Challenges in the restoration of pollination mutualisms. *Trends Plant Sci* 16:4–12
- Merow C, Smith MJ, Silander Jr JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058–1069
- Milet-Pinheiro P, Schlindwein C (2009) Pollination in *Jacaranda rugosa* (Bignoniaceae): euglossine pollinators, nectar robbers and low fruit set. *Plant Biol* 11:131–141. <https://doi.org/10.1111/j.1438-8677.2008.00118.x>
- Miranda LS, Imperatriz-Fonseca VL, Giannini TC (2019) Climate change impact on ecosystem functions provided by birds in southeastern Amazonia. *PLoS One* 14:e0215229

- Mistry J (1998) Fire in the cerrado (savannas) of Brazil: an ecological review. *Progress in Physical Geography: Earth and Environment* 22:425–448.
<https://doi.org/10.1177/030913339802200401>
- Morais J, Consolaro H, Bergamini LL, Ferrero V (2020) Reproductive biology and pollinators in two enantiostylous *Qualea* species (Vochysiaceae) in the Brazilian Cerrado. *Plant Biol.* <https://doi.org/10.1111/plb.13091>
- Morales NS, Fernández IC, Baca-González V (2017) MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ* 5:e3093
- Morellato LPC, Alberti LF, Hudson I (2010) Applications of circular statistics in plant phenology: a case studies approach. In: *Phenological research*. Springer, pp 339–359
- Morin PJ (2011) *Community Ecology*, 2nd editio. Wiley-Brackwell, Oxford
- Moritz C, Patton JL, Conroy CJ, et al (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* (1979) 322:261–264
- Moss RH, Edmonds JA, Hibbard KA, et al (2010) The next generation of scenarios for climate change research and assessment. *Nature* 463:747–756
- Munin RL, Teixeira RC, Sigrist MR (2008) Esfingofilia e sistema de reprodução de *Bauhinia curvula* Benth.(Leguminosae: Caesalpinioideae) em cerrado no Centro-Oeste brasileiro. *Brazilian Journal of Botany* 31:15–25
- Munique LB, Calixto ES (2018) Spatial and temporal variation of plant fragment removal by two species of *Atta* leaf-cutting ants. *J Insect Behav* 31:255–263.
<https://doi.org/10.1007/s10905-018-9673-1>
- Muscarella R, Galante PJ, Soley-Guardia M, et al (2014) ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol Evol* 5:1198–1205
- Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
<https://doi.org/doi.org/10.1038/35002501>
- Nahas L, Gonzaga MO, Del-Claro K (2012) Emergent impacts of ant and spider interactions: Herbivory reduction in a tropical savanna tree. *Biotropica* 44:498–505. <https://doi.org/10.1111/j.1744-7429.2011.00850.x>
- Neff JL, Simpson BB (1981) Oil-collecting structures in the Anthophoridae (Hymenoptera): morphology, function, and use in systematics. *J Kans Entomol Soc* 54:95–123
- Negrelle RRB, Morokawa R, Ribas CP (2007) *Vochysia* Aubl. do Estado do Paraná, Brasil. *Acta Sci Biol Sci* 29:29–38

- Nettancourt D (1997) Incompatibility in angiosperms. *Sex Plant Reprod* 10:185–199
- Newstrom LE, Frankie GW, Baker HG, Colwell RK (1994) Diversity of long-term flowering patterns. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) *La selva: Ecology and natural history of a neotropical rain forest*. University Chicago, Chicago, pp 142–160
- Novaes LR, Calixto ES, Oliveira ML, et al (2020) Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: A new wind-based approach. *Science of The Total Environment* 730:139039
- Ohashi K, Yahara T (2001) Behavioral responses of pollinators to variation in floral display size and their influences on the evolution of floral traits. In: Chittka L, Tomson JD (eds) *Cognitive ecology of pollination: animal behaviour and floral evolution*. Cambridge University Press, Cambridge, p 334
- Oliveira G, Lima-Ribeiro MS, Terribile LC, et al (2015) Conservation biogeography of the Cerrado's wild edible plants under climate change: Linking biotic stability with agricultural expansion. *Am J Bot* 102:870–877. <https://doi.org/10.3732/ajb.1400352>
- Oliveira PEM (1998a) Sistemas de incompatibilidade: idéias a partir de plantas de Cerrado. *Boletim do Herbário Ezechias Paulo Heringer* 2:89–102
- Oliveira PEM (1998b) Reproductive biology, Evolution and taxonomy of Vochysiaceae in central Brazil. In: Owens SJ, Rudall PJ (eds) *Reproductive Biology*. Royal Botanic Gardens, pp 381–393
- Oliveira PEM, Gibbs PE (2000) Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora* 195:311–329. [https://doi.org/10.1016/S0367-2530\(17\)30990-8](https://doi.org/10.1016/S0367-2530(17)30990-8)
- Oliveira PEM, Gibbs PE (2002) Pollination and reproductive biology in cerrado plant communities. In: Oliveira PE, Marquis RJ (eds) *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, pp 329–347
- Oliveira PS, Marquis RJ (2002) *The cerrados of Brazil*. Columbia University Press New York
- Oliveira-Filho A, Ratter JA (2002) Vegetation physiognomies and woody flora of the Cerrado biome. In: Oliveira PS, Marquis RJ (eds) *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, pp 91–120
- Omondi SF, Odee DW, Ongamo GO, et al (2016) Synchrony in leafing, flowering, and fruiting phenology of *Senegalia senegal* within Lake Baringo Woodland, Kenya: implication for conservation and tree improvement. *International Journal of Forestry Research* 2016:

- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *The Annual Review of Ecology, Evolution and Systematics* 37:637–669
- Pepin NC, Arnone E, Gobiet A, et al (2022) Climate Changes and Their Elevational Patterns in the Mountains of the World. *Reviews of Geophysics* 60:. <https://doi.org/10.1029/2020RG000730>
- Peterson AT, Cobos ME, Jiménez-García D (2018) Major challenges for correlational ecological niche model projections to future climate conditions. *Ann N Y Acad Sci* 1429:66–77. <https://doi.org/10.1111/nyas.13873>
- Peterson AT, Soberón J, Pearson RG, et al (2011) *Ecological niches and geographic distributions (MPB-49)*. Princeton University Press
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259
- Pilon NAL, Udulutsch RG, Durigan G (2015) Padrões fenológicos de 111 espécies de Cerrado em condições de cultivo. *Hoehnea* 42:425–443
- Ponte G Da, Huth F, Wagner S (2020) Ensuring future regeneration success of *Qualea grandiflora* Mart. (Vochysiaceae) in neotropical savanna (cerrado) biomes by reviewing the available information and identifying research gaps. *IForest* 13:154–164. <https://doi.org/10.3832/ifor2684-013>
- Potascheff CM, Brito VLG, Galetto L, et al (2020) Nectar features, diurnal and nocturnal pollinators, and male fitness in *Qualea grandiflora* (Vochysiaceae). *Plant Systematics and Evolution* 306:1–12. <https://doi.org/10.1007/s00606-020-01646-y>
- Priti H, Aravind NA, Uma Shaanker R, Ravikanth G (2016) Modeling impacts of future climate on the distribution of Myristicaceae species in the Western Ghats, India. *Ecol Eng* 89:14–23
- Rather TA, Kumar S, Khan JA (2020) Multi-scale habitat modelling and predicting change in the distribution of tiger and leopard using random forest algorithm. *Sci Rep* 10:11473. <https://doi.org/10.1038/s41598-020-68167-z>
- Ratter J (1997) The Brazilian Cerrado Vegetation and Threats to its Biodiversity. *Ann Bot* 80:223–230. <https://doi.org/10.1006/anbo.1997.0469>
- Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the Floristic Composition of the Brazilian Cerrado Vegetation Iii: Comparison of the Woody Vegetation of 376 Areas. *Edinb J Bot* 60:57–109. <https://doi.org/10.1017/s0960428603000064>
- Raupp PP, Gonçalves RV, Calixto ES, Anjos DV (2020) Contrasting effects of herbivore damage type on extrafloral nectar production and ant attendance. *Acta Oecologica* 108:103638. <https://doi.org/10.1016/j.actao.2020.103638>
- Ribeiro JF, Castro LHR (1986) Método quantitativo para avaliar características fenológicas em árvores. *Revista Brasileira de Botânica* 9:7–11

- Rodrigues MI, Souza ÁN de, Joaquim MS, et al (2020) Concessão florestal na Amazônia brasileira. *Ciência Florestal* 30:1299–1308. <https://doi.org/10.5902/1980509821658>
- Rodrigues RR, Lima RAF, Gandolf S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biol Conserv* 142:1242–1251
- Rodríguez L, Satoja E (2008) Fenología, Biología floral y de Polinización de especies de la familia Vochysiaceae en la Guayana Venezolana. *Acta Bot Venez* 31:331–366
- Ruiz TZ, Arroyo MTK (1978) Plant reproductive ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica* 10:221–230
- Santamaria P, Elia A, Serio F (2002) Effect of solution nitrogen concentration on yield, leaf element content, and water and nitrogen use efficiency of three hydroponically-grown rocket salad genotypes. *J Plant Nutr* 25:245–258. <https://doi.org/10.1081/PLN-100108833>
- Santos ML, Afonso A de P, Oliveira PEM (1997a) Biologia floral de *Vochysia cinnamomea* Pohl (Vochysiaceae) em cerrados do Triângulo Mineiro, MG. *Revista Brasileira de Botânica* 20:127–132. <https://doi.org/10.1590/s0100-84041997000200003>
- Santos ML, Afonso A de P, Oliveira PEM (1997b) Biologia floral de *Vochysia cinnamomea* Pohl (Vochysiaceae) em cerrados do Triângulo Mineiro, MG. *Revista Brasileira de Botânica* 20:127–132. <https://doi.org/10.1590/s0100-84041997000200003>
- Séférian R, Nabat P, Michou M, et al (2019) Evaluation of CNRM Earth System Model, CNRM-ESM2-1: Role of Earth System Processes in Present-Day and Future Climate. *J Adv Model Earth Syst* 11:4182–4227
- Sen S, Gode A, Ramanujam S, et al (2016) Modeling the impact of climate change on wild *Piper nigrum* (Black Pepper) in Western Ghats, India using ecological niche models. *J Plant Res* 129:1033–1040
- Shcheglovitova M, Anderson RP (2013) Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecol Modell* 269:9–17
- Shimizu GH, Gonçalves DJP (2017) Flora das cangas da Serra dos Carajás, Pará, Brasil: Vochysiaceae. *Rodriguesia* 68:1159–1164. <https://doi.org/10.1590/2175-7860201768351>
- Shimizu GH, Yamamoto K (2012a) Vochysiaceae. In: Jacobi CM, Carmo FF (eds) *Diversidade florística nas Cangas do Quadrilátero Ferrífero*. Código Editora, Belo Horizonte, pp 209–210

- Shimizu GH, Yamamoto K (2012b) Flora da Serra do Cipó, Minas Gerais: Vochysiaceae. *Boletim de Botânica* 30:63–87. <https://doi.org/10.11606/issn.2316-9052.v30i1p57-61>
- Silva CI da, Araújo G, Oliveira PEAM de (2012) Distribuição vertical dos sistemas de polinização bióticos em áreas de cerrado sentido restrito no Triângulo Mineiro, MG, Brasil. *Acta Bot Brasilica* 26:748–760
- Silva PO da, Almeida SE da S, Oliveira TCS, et al (2020) Fenologia reprodutiva e vegetativa de *Qualea multiflora* Mart. em Cerradão. *Oecologia Australis* 24:127–140. <https://doi.org/10.21826/2446-82312019v74e2019013>
- Silva LMS, Dias AG, Nakajima JN (2022) As árvores do cerrado no Clube Caça e Pesca Itororó, Uberlândia, Estado de Minas Gerais, Brasil. *Hoehnea* 49:. <https://doi.org/10.1590/2236-8906-72-2021>
- Silvério DV, Lenza E (2010) Fenologia de espécies lenhosas em um cerrado típico no Parque Municipal do Bacaba, Nova Xavantina, Mato Grosso, Brasil. *Biota Neotrop* 10:205–216. <https://doi.org/10.1590/s1676-06032010000300024>
- Silvério D V, Brando PM, Macedo MN, et al (2015) Agricultural expansion dominates climate changes in southeastern Amazonia: the overlooked non-GHG forcing. *Environmental Research Letters* 10:104015. <https://doi.org/10.1088/1748-9326/10/10/104015>
- Simões S dos S, Zappi D, Costa GM da, et al (2020) Spatial niche modelling of five endemic cacti from the Brazilian Caatinga: Past, present and future. *Austral Ecol* 45:35–47
- Siqueira MF de, Peterson AT (2003) Consequences of global climate change for geographic distributions of cerrado tree species. *Biota Neotrop* 3:1–14. <https://doi.org/10.1590/S1676-06032003000200005>
- Somero GN (2011) Comparative physiology: a “crystal ball” for predicting consequences of global change. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 301:R1--R14
- Souza VC, Lorenzi H (2008) Botânica sistemática: guia ilustrado para identificação das famílias de fanerógamas nativas e exóticas no Brasil, baseado em APG II., 2ª edição. Instituto Plantarum, Nova Odessa
- Suinyuy TN, Johnson SD (2021) Evidence for pollination ecotypes in the African cycad *Encephalartos ghellinckii* (Zamiaceae). *Botanical Journal of the Linnean Society* 195:233–248
- Sutton WB, Barrett K, Moody AT, et al (2015) Predicted changes in climatic niche and climate refugia of conservation priority salamander species in the northeastern United States. *Forests* 6:1–26

- Tatebe H, Ogura T, Nitta T, et al (2019) Description and basic evaluation of simulated mean state, internal variability, and climate sensitivity in MIROC6. *Geosci Model Dev* 12:2727–2765
- Thomas CD, Cameron A, Green RE, et al (2004) Extinction risk from climate change. *Nature* 427:145–148
- Torezan-Silingardi HM, Oliveira PEM (2004) Phenology and Reproductive Ecology of *Myrcia rostrata* and *M. tomentosa* (Myrtaceae) in Central Brazil. *Phyton (B Aires)* 44:23–43
- Trenberth K (2011) Changes in precipitation with climate change. *Clim Res* 47:123–138. <https://doi.org/10.3354/cr00953>
- Trigueiro WR, Nabout JC, Tessarolo G (2020) Uncovering the spatial variability of recent deforestation drivers in the Brazilian Cerrado. *J Environ Manage* 275:111243
- Urban MC (2015) Accelerating extinction risk from climate change. *Science* (1979) 348:571–573
- Van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu Rev Ecol Syst* 24:353–377
- Vaz ÚL, Nabout JC (2016) Using ecological niche models to predict the impact of global climate change on the geographical distribution and productivity of *Euterpe oleracea* Mart.(Arecaceae) in the Amazon. *Acta Bot Brasilica* 30:290–295
- Vilela AA, Del-Claro VTS, Torezan-Silingardi HM, Del-Claro K (2017) Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. *Arthropod Plant Interact* 12:215–227. <https://doi.org/10.1007/s11829-017-9572-y>
- Vitorino LC, Reis MNO, Bessa LA, et al (2020) Landscape and Climate Influence the Patterns of Genetic Diversity and Inbreeding in Cerrado Plant Species. *Diversity (Basel)* 12:421
- Wu Q, Hu Y, Ke H, et al (2005) Study pollen grains in rice by using multispectral imaging techniques. In: *Spectral Imaging: Instrumentation, Applications, and Analysis III*. pp 100–109
- Wu T, Lu Y, Fang Y, et al (2019) The Beijing Climate Center climate system model (BCC-CSM): The main progress from CMIP5 to CMIP6. *Geosci Model Dev* 12:1573–1600
- Yamamoto LF, Kinoshita LS, Martins FR, others (2007) Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. *Acta Bot Brasilica* 21:553–573

- You J, Qin X, Ranjitkar S, et al (2018) Response to climate change of montane herbaceous plants in the genus *Rhodiola* predicted by ecological niche modelling. *Sci Rep* 8:1–12
- Zwiener V, Lira-Noriega A, Grady CJ, et al (2018) Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. *Global Ecology and Biogeography* 27:298–309

Capítulo 3

Predicting the impact of global climate change in the geographic distribution of anemochoric species

Larissa Alves-de-Lima¹, Douglas Fernandes Rodrigues Alves¹, Diego Vinicius Anjos¹, Fernando Anco Valdivia^{2,3} and Helena Maura Torezan-Silingardi¹, 3*

¹ Universidade Federal de Uberlândia, Instituto de Biologia, Bloco 2D - Rua Ceará 1084, Campus Umuarama, Uberlândia – MG (38405-315)

² Museo de Historia Natural (MUSA), Universidad Nacional de San Augustin de Arequipa, Área de entomologia, Arequipa - Peru

3 Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Departamento de
Biologia, Universidade de São Paulo, Avenida Bandeirantes – 3900, Monte Alegre,
Ribeirão Preto – SP (14040-901)

*e-mail: hmtsilingardi@gmail.com; torezan.silingardi@ufu.br

Seguindo as normas de edição da revista Plants.

Abstract: Protected areas serve as crucial sanctuaries for biodiversity, strictly prohibiting the direct exploitation of natural resources. However, even species within these areas face challenges from climate changes. This study assesses potential species richness in 30 protected Brazilian parks. Our methodology involved overlaying binarized maps of five common woody species and extracting statistical metrics: mean potential, standard deviation, minimum, and maximum potential using the 'extract' function from the raster package. Results revealed the dynamic nature of species distribution, as all five species exhibited changes in their distribution areas in future projections. *Aspidosperma tomentosum* could lose between 26.271% to 100.000% of its current distribution area, while *Kielmeyera coriacea* may experience losses of 38.394% to 100%. *Peixotoa tomentosa*'s distribution could decrease by 40.461% to 96.661%. *Qualea multiflora* might face losses between 7.340% to 100%, with potential gains of up to 92.215%. *Senna velutina* may lose between 4.521% and 99.997% of its area, with the most significant gain been 22.079%. These findings are crucial for ongoing biodiversity conservation efforts,

offering insights into species habitat dynamics and emphasizing the need for informed, adaptive conservation strategies. This study reinforces the urgency of preserving natural ecosystems to ensure a sustainable future for their flora and fauna.

Keywords: *Aspidosperma tomentosum*, *Kielmeyera coriacea*, *Peixotoa tomentosa*, *Qualea multiflora*, *Senna velutina*, Ecological Niche Model, Global Warming, Savanna, Cerrado, Extinction.

Introduction

Climate change is increasingly recognized as a threat to global biodiversity, impacting the structure and functionality of ecosystems [1,2]. Climate projections based on greenhouse gas emissions indicate that by the end of the century, global temperature can increase by up to 3.1°C [3]. However, in the case of South America, the temperature rise is even more significant, potentially reaching up to 4°C [4]. Specially for the Brazilian Savanna, known as the Cerrado, estimates suggest temperature increases ranging from 2° to 6°C [5]. Additionally, precipitation is expected to decrease by up to 70% compared to current levels, along with changes in the distribution of rainfall throughout the year [5,6]. These changes will impact various species of animals [7–9], plants [10–12] and seaweeds [13,14] in diverse ways and different scales [15], potentially leading to the extinction of many species [9,16].

Climatic changes can have a significant impact on plants, affecting genetic diversity [17], biotic interactions[18], phenology [18–20], reproductive success[18] and the geographic distribution of the species [21–23]. Climatic forecasts indicate that global warming will likely result in a reduced geographic distribution for several terrestrial plant species due to physiological limitations[19,23,24]. However, some species also have the ability to migrate and expand their distribution, seeking out new areas with climate conditions that are better suited for their survival, maintenance and reproduction [25].

In the case of the Cerrado, multiple models suggest that climate change may potentially threat plant biodiversity, leading to a significant reduction in the abundance and diversity of species [5,9,23,26]. Changes in the ecosystem's structure can disrupt the balance within communities, affecting ecosystem services such as pollination, nutrient cycling, hydrological cycle regulation and carbon sequestration [5].

In addition to climate change, the processes of deforestation and the increasing frequency of wildfires elevate the risk of extinction for various plant populations [27–30]. The Brazilian Cerrado has already experienced deforestation in approximately 61% of its natural areas [31] and possesses legal protection covering only 2.2% of its native territories [28]. Due to its intense deforestation and high species richness, Cerrado is designated as a biodiversity hotspot [32], and conservation units play a pivotal role in mitigating the impacts of deforestation on these populations [33].

The ecological niche refers to the combination of conditions and resources that a species may exploit. It can be further divided into two principal components: the fundamental niche, which encompasses the environmental conditions that enable a species to survive, and the realized niche, which takes into account biological interactions, such as competition with other species [34]. Ecological niche model (ENM) has proven

to be a reliable tool for predicting future scenarios, but it is not a consensus [22,35]. The ENM is based on the fundamental niche, functioning with a duality of geographic and environmental space. It utilizes data from geographic occurrences and climatic variables' values while taking into account the species' current limitations, without addressing possible adaptations [36,37]. The ENM had been widely employed to assess the influence of climate change on the geographic distribution of species, guiding conservation planning efforts by identifying climatically suitable areas with potential extinction risks [38–42].

The objectives of this study were as follows: (i) to evaluate ecological niche models, (ii) to determine which bioclimatic variables best explains the geographic distribution of five woody plant species, (iii) to assess the current distribution of these species, (iv) predict changes under distinct future climatic scenarios, and (v) to analyze the potential species richness within Brazilian national parks.

Results

How to evaluate the model?

The distribution models were prepared to five species: *Aspidosperma tomentosum* Mart. (Apocynaceae), *Kielmeyera coriacea* Mart. & Zucc. (Calophyllaceae), *Peixotoa tomentosa* A.Juss. (Malpighiaceae), *Qualea multiflora* Mart. (Vochysiaceae) and *Senna velutina* (Vogel) H.S. Irwin & Barneby (Fabaceae/Caesalpinioideae), and considered the area under the curve (AUC). The model was considered excellent to *P. tomentosa* (AUC=0.906±0.004) and considered good to *A. tomentosum* (AUC=0.857±0.001), *K. coriacea* (AUC=0.864±0.002), *Q. multiflora* (AUC=0.883±0.001) and *S. velutina*

(AUC=0.805±0.006). The true skill statistic values (TSS) confirm that the models are acceptable (Table 1).

Table 1. Ecological Niche Models of five Cerrado plant species. Occurrence records (N) used to perform the model parameters (Feature: L: linear, Q: quadratic, H: hinge, Rm: regression models, AUC: area under the curve, TSS: true skill statistic, SD: standard deviation, P: product and their combinations; rm (0.5, 1, 1.5, 2, 2.5, 3, 3.5 and 4) and model performance with AUC train, AUC test average, AUC test variation, TSS and Logistic threshold (tenth percentile training presence -TPTP).

Species	N	Feature	R m	AUC		TSS		Logistic threshold	
				Mean	SD	Mean	SD	Mean	SD
<i>Aspidosperma tomentosum</i>	497	LQ	1	0.857	0.001	0.538	0.020	0.361	0.018
<i>Kielmeyera coriácea</i>	549	LQ	1	0.864	0.002	0.501	0.012	0.329	0.022
<i>Peixotoa tomentosa</i>	108	LQ	1	0.906	0.004	0.471	0.069	0.071	0.023
<i>Qualea multiflora</i>	606	LQH	1	0.883	0.001	0.568	0.009	0.295	0.021
<i>Senna velutina</i>	301	LQ	1	0.805	0.006	0.442	0.018	0.375	0.021

Which bioclimatic variables best explained the geographic distribution for each species?

The most important bioclimatic variables that explained the geographic distribution varied among species (Table 2). For example, 80.70% of *A. tomentosum*'s distribution was explained by the precipitation of coldest quarter (41.46%), precipitation of warmest quarter (16.16%), annual precipitation (11.85%) and temperature seasonality (11.23%). For *K. coriacea*, 75.01% of its distribution was explained by the precipitation of coldest quarter (26.87%), precipitation of warmest quarter (19.04%), annual precipitation (16.15%) and temperature seasonality (12.95%). Meanwhile 79.95% of *P. tomentosa*'s distribution was explained by the annual mean temperature (61.78%), precipitation of warmest quarter (10.23%) and precipitation seasonality (7.94%). Approximately 77.34% of *Q. multiflora*'s distribution was explained by the precipitation of warmest quarter (31.00%), annual precipitation (20.00%), annual mean temperature (17.78%) and temperature seasonality (8.56). In contrast, 78.06% of *S. velutina*'s distribution was explained by the precipitation of coldest quarter (47.90%), temperature seasonality (17.30%), and precipitation of the warmest quarter (12.86%).

Table 2. Contribution of bioclimatic variables to the distribution of each species.
Code refers to the Bioclimatic variables considered in the statistic analysis.

Species	Code	Bioclimatic variables	Contribution (%)	
			Mean	SD
<i>Aspidosperma tomentosum</i>	Bio19	Precipitation of coldest quarter	41.46	0.167
	Bio18	Precipitation of warmest quarter	16.16	0.140
	Bio12	Annual precipitation	11.85	0.290
	Bio4	Temperature seasonality	11.23	0.069
	Bio1	Annual mean temperature	7.23	0.117
	Bio2	Mean diurnal range	6.90	0.084
	Bio3	Isothermality	4.87	0.120
	Bio15	Precipitation seasonality	0.23	0.021
	Bio14	Precipitation of driest month	0.07	0.007
<i>Kielmeyera coriacea</i>	Bio19	Precipitation of coldest quarter	26.87	0.390
	Bio18	Precipitation of warmest quarter	19.04	0.127
	Bio12	Annual precipitation	16.15	0.254
	Bio4	Temperature seasonality	12.95	0.183
	Bio1	Annual mean temperature	9.56	0.267
	Bio3	Isothermality	6.45	0.135
	Bio2	Mean diurnal range	5.75	0.129
	Bio15	Precipitation seasonality	3.13	0.125
	Bio14	Precipitation of driest month	0.1	0.004
<i>Peixotoa tomentosa</i>	Bio1	Annual mean temperature	61.78	0.284
	Bio18	Precipitation of warmest quarter	10.23	0.267
	Bio15	Precipitation seasonality	7.94	0.428
	Bio14	Precipitation of driest month	6.78	0.230
	Bio19	Precipitation of coldest quarter	5.61	0.089
	Bio3	Isothermality	2.46	0.087
	Bio4	Temperature seasonality	2.78	0.112
	Bio12	Annual precipitation	1.88	0.091
	Bio2	Mean diurnal range	0.49	0.060
<i>Qualea multiflora</i>	Bio18	Precipitation of warmest quarter	31.00	5.880
	Bio12	Annual precipitation	20.00	0.248
	Bio1	Annual mean temperature	17.78	0.305
	Bio4	Temperature seasonality	8.56	0.224
	Bio3	Isothermality	7.12	0.339
	Bio19	Precipitation of coldest quarter	5.86	0.397
	Bio14	Precipitation of driest month	5.82	0.269
	Bio15	Precipitation seasonality	1.95	0.100
	Bio2	Mean diurnal range	1.91	0.059
<i>Senna velutina</i>	Bio19	Precipitation of coldest quarter	47.91	0.547
	Bio4	Temperature seasonality	17.30	0.205
	Bio18	Precipitation of warmest quarter	12.86	0.399
	Bio12	Annual precipitation	7.46	0.272
	Bio14	Precipitation of driest month	7.03	0.265
	Bio3	Isothermality	4.37	0.212
	Bio2	Mean diurnal range	1.93	0.264
	Bio15	Precipitation seasonality	1.01	0.064

Bio1	Annual mean temperature	0.12	0.032
------	-------------------------	------	-------

What is the current distribution of the species?

The five species were distributed across a total of 2061 location points, with 497 belonging to *A. tomentosum*, 549 to *K. coriacea*, 108 to *P. tomentosa*, 606 to *Q. multiflora* and 301 to *S. velutina* (Table 1). Our study identified areas considered climatically suitable for the survival of *A. tomentosum* (Figure 1a) and *K. coriacea* (Figure 1b). These areas were similar, spanning latitudes between -30° and -0° and longitudes between -70° and -35°, with a total extent of 3,288,314 hectares (ha) for *A. tomentosum* and 3,421,897 ha for *K. coriacea* (Table 3). *Peixotoa tomentosa* was located within the latitude range of -25° and -5°, and longitude range of -60° and -40°, covering an area of 1,621,865 ha (Figure 1c, Table 3). *Qualea multiflora* has its habitat spanned latitudes between -25° and -10° and longitudes between -75° and -40°, occupying 2,933,077 ha (Figure 1d, Table 3). Lastly, *S. velutina* was found within the latitude range of -25° to -0°, and longitude range of -65° to -25°, encompassing a total area of 3,281,471 ha (Figure 1e, Table 3).

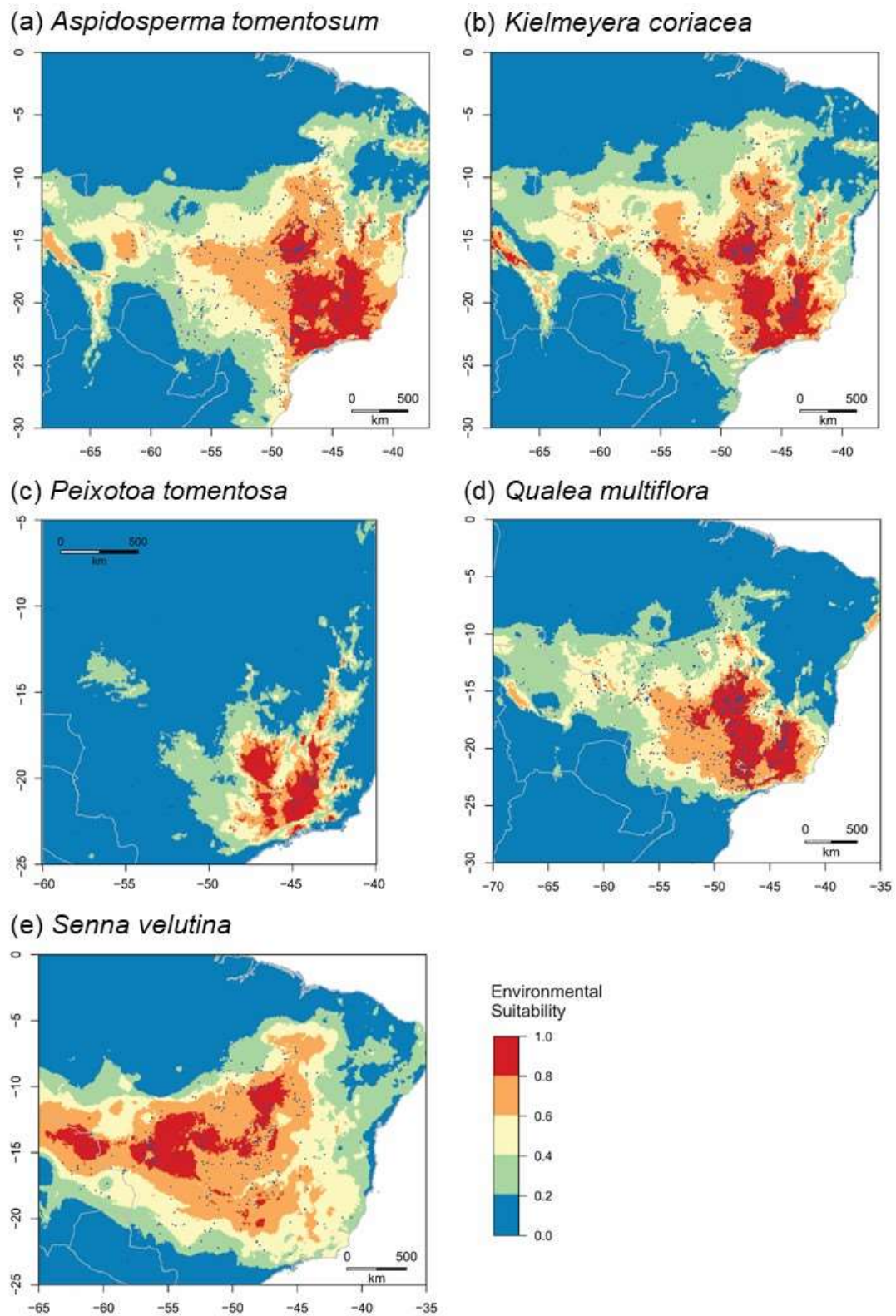


Figure 1. Environmental suitability map for *Aspidosperma tomentosum*, *Kielmeyera coriacea*, *Peixotoa tomentosa*, *Qualea multiflora*, and *Senna velutina* at present. Blue dots represent the selected points for each model.

Table 3. Predicted change in distribution of *Aspidosperma tomentosum*, *Kielmeyera coriacea*, *Peixotoa tomentosa*, *Qualea multiflora* and *Senna velutina*, considering the projections BCC-CSM2-MR (Beijing Climate Center Climate System Model), CNRM-ESM2-1 (Evaluation of CNRM Earth System Model) and MIROC6 (Model for Interdisciplinary Research on Climate and greenhouse gas release scenarios) considering RCP2.6, RCP4.5, RCP6.0, and RCP8.5 in 2080-2010.

Species	Projection	Area in the presente (ha)	Area in the future (ha)	Loss (ha)	Gain (ha)	Area maintained in the furute (ha)	Lost+kept (ha)	Maintained (%)	Loss (%)	Gain (%)
<i>Aspidosperma tomentosum</i>	BCC CSM2 MR RCP2.6	3288314	2506820	863865	82371	2424449	3288314	73.729	26.271	2.505
	BCC CSM2 MR RCP4.5	3288314	1742697	1583900	38283	1704414	3288314	51.832	48.168	1.164
	BCC CSM2 MR RCP6.0	3288314	1031593	2277418	20697	1010896	3288314	30.742	69.258	0.629
	BCC CSM2 MR RCP8.5	3288314	1116782	2188524	16992	1099790	3288314	33.445	66.555	0.517
	CNRM ESM2 1 RCP2.6	3288314	2112920	1183160	7766	2105154	3288314	64.019	35.981	0.236
	CNRM ESM2 1 RCP4.5	3288314	1846504	1451224	9413	1837090	3288314	55.867	44.133	0.286
	CNRM ESM2 1 RCP6.0	3288314	1027361	2277739	16786	1010575	3288314	30.732	69.268	0.510
	CNRM ESM2 1 RCP8.5	3288314	0	3288314	0	0	3288314	0.000	100.000	0.000
	MIROC6 RCP2.6	3288314	2101960	1204046	17692	2084268	3288314	63.384	36.616	0.538
	MIROC6 RCP4.5	3288314	1698958	1595593	6237	1692721	3288314	51.477	48.523	0.190
	MIROC6 RCP6.0	3288314	1333248	1962025	6959	1326289	3288314	40.333	59.667	0.212
	MIROC6 RCP8.5	3288314	939040	2364790	15516	923524	3288314	28.085	71.915	0.472
<i>Kielmeyera coriacea</i>	BCC CSM2 MR RCP2.6	3421897	2163349	1313797	55249	2108100	3421897	61.606	38.394	1.615
	BCC CSM2 MR RCP4.5	3421897	1223386	2251572	53061	1170325	3421897	34.201	65.799	1.551
	BCC CSM2 MR RCP6.0	3421897	621012	2839651	38766	582247	3421897	17.015	82.985	1.133
	BCC CSM2 MR RCP8.5	3421897	604809	2862591	45502	559307	3421897	16.345	83.655	1.330
	CNRM ESM2 1 RCP2.6	3421897	1642657	1797446	18206	1624451	3421897	47.472	52.528	0.532
	CNRM ESM2 1 RCP4.5	3421897	895851	2548427	22380	873470	3421897	25.526	74.474	0.654
	CNRM ESM2 1 RCP6.0	3421897	292278	3154460	24841	267437	3421897	7.815	92.185	0.726

	CNRM ESM2 1 RCP8.5	3421897	0	3421897	0	0	3421897	0.000	100.000	0.000
	MIROC6 RCP2.6	3421897	2108752	1327686	14540	2094212	3421897	61.200	38.800	0.425
	MIROC6 RCP4.5	3421897	1409019	2029363	16484	1392535	3421897	40.695	59.305	0.482
	MIROC6 RCP6.0	3421897	974481	2468157	20741	953740	3421897	27.872	72.128	0.606
	MIROC6 RCP8.5	3421897	648324	2806411	32837	615486	3421897	17.987	82.013	0.960
<i>Peixotoa tomentosa</i>	BCC CSM2 MR RCP2.6	1621865	807214	816244	1593	805622	1621865	49.673	50.327	0.098
	BCC CSM2 MR RCP4.5	1621865	526793	1097800	2728	524066	1621865	32.313	67.687	0.168
	BCC CSM2 MR RCP6.0	1621865	350516	1271349	0	350516	1621865	21.612	78.388	0.000
	BCC CSM2 MR RCP8.5	1621865	254036	1367915	85	253951	1621865	15.658	84.342	0.005
	CNRM ESM2 1 RCP2.6	1621865	604088	1017777	0	604088	1621865	37.246	62.754	0.000
	CNRM ESM2 1 RCP4.5	1621865	381130	1240735	0	381130	1621865	23.500	76.500	0.000
	CNRM ESM2 1 RCP6.0	1621865	166831	1455034	0	166831	1621865	10.286	89.714	0.000
	CNRM ESM2 1 RCP8.5	1621865	54152	1567713	0	54152	1621865	3.339	96.661	0.000
	MIROC6 RCP2.6	1621865	966140	656216	491	965649	1621865	59.539	40.461	0.030
	MIROC6 RCP4.5	1621865	590859	1031006	0	590859	1621865	36.431	63.569	0.000
	MIROC6 RCP6.0	1621865	357494	1264371	0	357494	1621865	22.042	77.958	0.000
	MIROC6 RCP8.5	1621865	287042	1334823	0	287042	1621865	17.698	82.302	0.000
<i>Qualea multiflora</i>	BCC CSM2 MR RCP2.6	2933077	3297260	739984	1104166	2193093	2933077	74.771	25.229	37.645
	BCC CSM2 MR RCP4.5	2933077	4093110	698692	1858725	2234385	2933077	76.179	23.821	63.371
	BCC CSM2 MR RCP6.0	2933077	4140277	400596	1607795	2532481	2933077	86.342	13.658	54.816
	BCC CSM2 MR RCP8.5	2933077	4580950	215300	1863173	2717777	2933077	92.660	7.340	63.523
	CNRM ESM2 1 RCP2.6	2933077	4108590	712233	1887746	2220844	2933077	75.717	24.283	64.361
	CNRM ESM2 1 RCP4.5	2933077	4968018	491779	2526720	2441298	2933077	83.233	16.767	86.146
	CNRM ESM2 1 RCP6.0	2933077	5276745	361075	2704743	2572002	2933077	87.690	12.310	92.215
	CNRM ESM2 1 RCP8.5	2933077	0	2933077	0	0	2933077	0.000	100.000	0.000
	MIROC6 RCP2.6	2933077	3336496	769348	1172767	2163729	2933077	73.770	26.230	39.984
	MIROC6 RCP4.5	2933077	4028839	729924	1825686	2203153	2933077	75.114	24.886	62.245
	MIROC6 RCP6.0	2933077	4695596	640547	2403066	2292531	2933077	78.161	21.839	81.930

<i>Senna velutina</i>	MIROC6 RCP8.5	2933077	4821525	531004	2419452	2402073	2933077	81.896	18.104	82.489
	BCC CSM2 MR RCP2.6	3281471	3355999	180081	254609	3101390	3281471	94.512	5.488	7.759
	BCC CSM2 MR RCP4.5	3281471	3351891	264772	335191	3016699	3281471	91.931	8.069	10.215
	BCC CSM2 MR RCP6.0	3281471	3378962	377371	474861	2904100	3281471	88.500	11.500	14.471
	BCC CSM2 MR RCP8.5	3281471	3688871	317028	724429	2964443	3281471	90.339	9.661	22.076
	CNRM ESM2 1 RCP2.6	3281471	3120622	249387	88538	3032085	3281471	92.400	7.600	2.698
	CNRM ESM2 1 RCP4.5	3281471	2981696	417034	117258	2864438	3281471	87.291	12.709	3.573
	CNRM ESM2 1 RCP6.0	3281471	2506217	892436	117181	2389036	3281471	72.804	27.196	3.571
	CNRM ESM2 1 RCP8.5	3281471	82	3281389	0	82	3281471	0.003	99.997	0.000
	MIROC6 RCP2.6	3281471	3321539	148366	188433	3133106	3281471	95.479	4.521	5.742
	MIROC6 RCP4.5	3281471	2809890	517827	46245	2763644	3281471	84.220	15.780	1.409
	MIROC6 RCP6.0	3281471	2702376	637161	58066	2644310	3281471	80.583	19.417	1.770
	MIROC6 RCP8.5	3281471	2329345	967572	15445	2313900	3281471	70.514	29.486	0.471

What changes will occur?

All five species exhibited changes in their distribution areas in the future projections (Table 3). *Aspidosperma tomentosum* had a loss ranging from 26.271% to 100.000% of its current distribution area, with a maximum gain of 2.505% (Figure S1). *Kielmeyera coriacea* experienced a lost ranging from 38.394% to 100% and a maximum gain of 1.615% (Figure S2). *Peixotoa tomentosa*'s distribution decreased by 40.461% to 96.661%, with the most significant gain being 0.168% (Figure 2). *Qualea multiflora* showed losses ranging from 7.340% to 100% and a substantial gain of up to 92.215% (Figure 3). *Senna velutina* exhibited a lost ranging from 4.521% to 99.997% of its area, with the most significant gain being 22.079% (Figure S3).

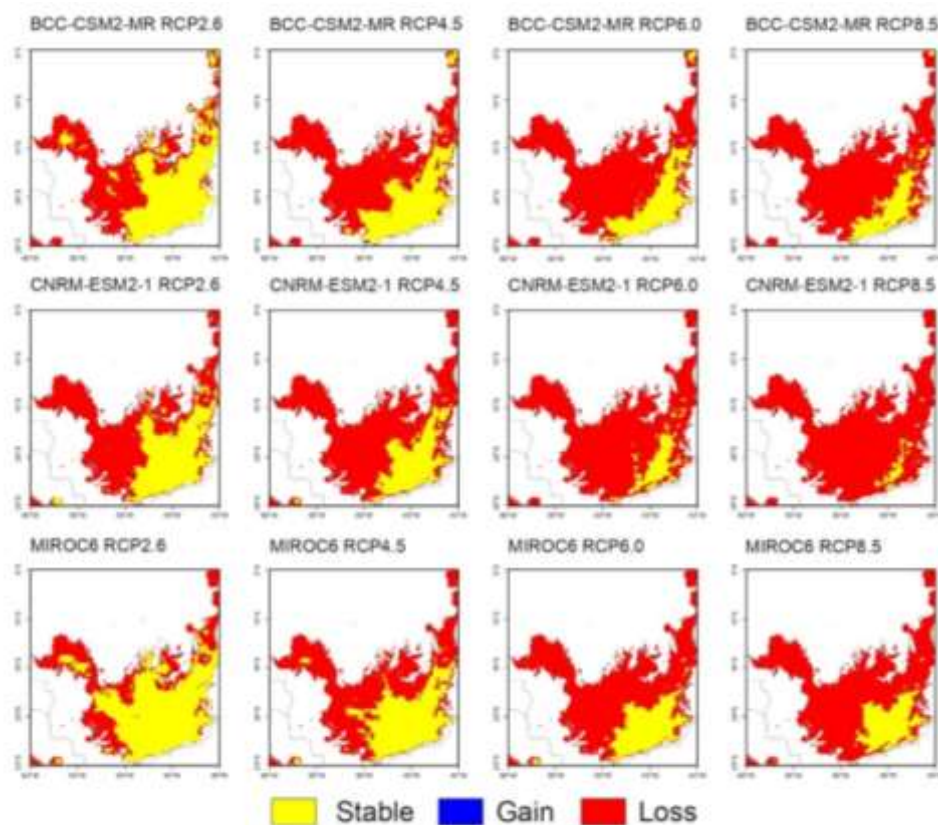


Figure 2. Predicted new distribution of *Peixotoa tomentosa* under future climate scenarios.

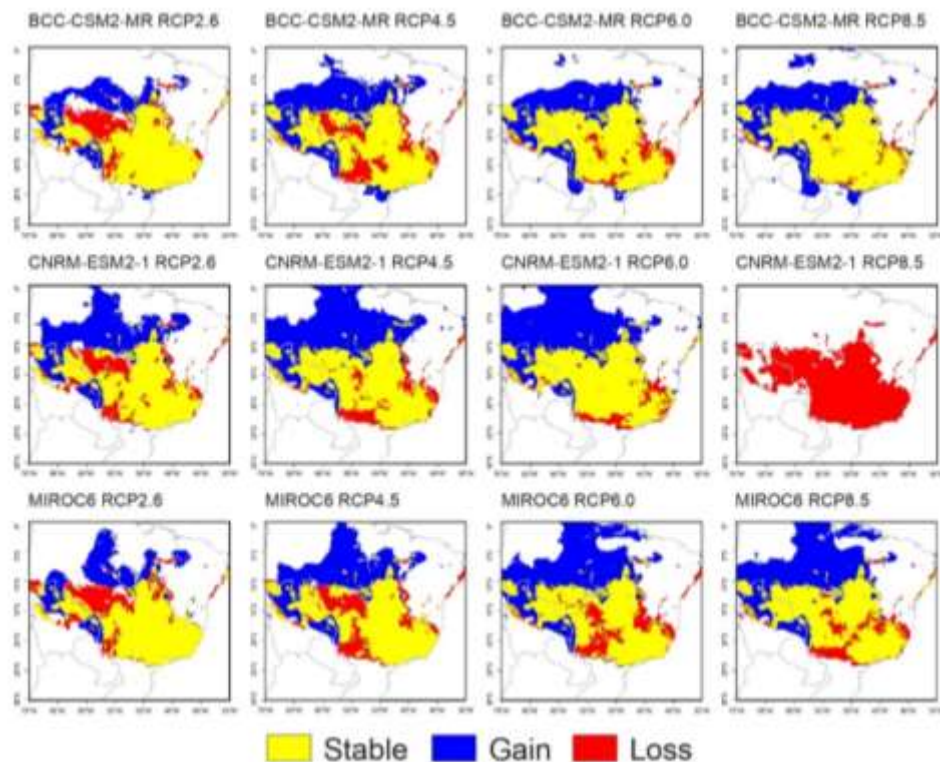


Figure 3. Predicted new distribution of *Qualea multiflora* under future climate scenarios.

Which conservation unit will have the greatest potential for species richness?

In the current scenario, and considering the spatial projection of ecological niche models, the parks with the greatest potential for conservation of the five species are Parque Nacional da Chapada dos Veadeiros, Parque Nacional da Serra da Canastra, Parque Nacional da Serra do Cipó, Parque Nacional do Gandarela, Parque Nacional das Emas, Parque Nacional das Sempre-Vivas, Parque Nacional de Brasília, Parque Nacional de Caparaó and Parque Nacional de Itatiaia (Table 4). When considering future projections, the five parks with the greatest potential for species richness are Parque Nacional do Gandarela and Parque Nacional da Serra do Cipó, both with a potential richness score of five in all projections except

CNRM-ESM2-1-585. They are followed by Parque Nacional da Serra da Canastra, Parque Nacional das Sempre-Vivas and Parque Nacional de Caparaó.

Table 4. Average species richness potential of conversation units. considering the present and 12 future projections

Conservation Units	Present	BCC- CSM2 RCP2.6	BCC- CSM2 RCP4.5	BCC- CSM2 RCP6.0	BCC- CSM2 RCP8.5	CNRM- ESM2-1 RCP2.6	CNRM- ESM2-1 RCP4.5	CNRM- ESM2-1 RCP6.0	CNRM- ESM2-1 RCP8.5	MIROC6 RCP2.6	MIROC6 RCP4.5	MIROC6 RCP6.0	MIROC6 RCP8.5
Parque Nacional Cavernas do Peruaçu	3.714	2.857	2.714	0.857	1.857	2.714	2.286	1.286	0.000	3.000	2.857	2.286	1.857
Parque Nacional da Chapada da Diamantina	4.421	3.895	3.316	1.526	1.316	3.526	2.368	0.842	0.000	4.842	3.789	2.105	2.474
Parque Nacional da Chapada das Mesas	1.190	0.000	0.857	0.238	0.190	0.762	1.143	1.000	0.000	0.571	1.048	0.810	0.952
Parque Nacional da Chapada dos Guimarães	4.800	4.000	2.600	2.000	2.000	4.000	3.400	2.400	0.000	4.400	3.400	1.600	2.000
Parque Nacional da Chapada dos Veadeiros	5.000	4.733	4.267	3.567	3.467	4.467	4.000	3.267	0.000	4.900	4.300	4.000	3.800
Parque Nacional da Serra da Bocaina	4.083	4.333	4.333	4.167	4.250	3.833	3.333	3.083	0.667	4.167	3.500	3.333	3.000
Parque Nacional da Serra da Bodoquena	2.889	2.667	0.889	1.222	2.000	0.111	0.000	0.444	0.000	1.000	0.000	0.000	0.111
Parque Nacional da Serra da Canastra	5.000	5.000	5.000	4.522	4.565	5.000	4.913	4.783	0.000	5.000	5.000	5.000	5.000
Parque Nacional da Serra da Capivara	0.583	0.500	0.250	0.000	0.000	0.917	0.917	0.250	0.000	1.000	0.500	0.167	0.000
Parque Nacional da Serra das Confusões	1.421	1.000	0.832	0.221	0.158	1.000	0.937	0.347	0.000	0.842	0.274	0.011	0.021
Parque Nacional da Serra do Cipó	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	0.667	5.000	5.000	5.000	5.000

Parque Nacional da Serra do Gandarela	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	1.000	5.000	5.000	5.000	5.000
Parque Nacional da Serra do Pardo	0.000	0.000	0.519	0.000	0.308	0.019	1.000	1.000	0.000	0.000	0.942	1.000	1.000
Parque Nacional da Serra dos Orgãos	4.000	5.000	5.000	5.000	5.000	4.000	4.000	3.500	0.500	4.000	4.000	4.000	4.000
Parque Nacional das Emas	5.000	4.000	4.000	1.000	1.313	4.000	4.000	2.000	0.000	5.000	4.000	3.938	1.000
Parque Nacional das Nascentes do Rio Parnaíba	3.211	2.622	1.244	1.233	1.189	2.678	1.667	1.133	0.000	2.522	1.700	1.556	1.689
Parque Nacional das Sempre-Vivas	5.000	5.000	5.000	4.824	4.824	5.000	5.000	4.353	0.000	5.000	5.000	4.647	4.824
Parque Nacional de Boa Nova	3.000	3.000	1.818	0.727	0.909	2.000	2.000	0.273	0.000	2.818	1.909	0.727	0.455
Parque Nacional de Brasília	5.000	5.000	4.400	4.000	4.000	4.800	4.000	4.000	0.000	5.000	4.600	4.000	4.000
Parque Nacional de Caparaó	5.000	5.000	5.000	5.000	5.000	5.000	5.000	4.333	1.000	5.000	5.000	4.000	4.000
Parque Nacional de Itatiaia	5.000	5.000	5.000	4.333	5.000	5.000	4.333	4.000	1.000	4.333	4.000	4.000	3.333
Parque Nacional do Acari	0.000	0.500	1.000	0.049	0.000	1.000	1.000	1.000	0.000	1.000	1.000	1.000	1.000
Parque Nacional do Araguaia	3.217	2.000	2.000	2.000	2.000	1.971	2.000	1.812	0.000	2.101	1.464	1.000	1.000
Parque Nacional do Boqueirão Da Onça	0.467	0.244	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000
Parque Nacional do Jamanxim	0.000	0.420	0.950	0.510	0.000	0.970	1.000	1.000	0.000	0.700	1.000	1.000	1.000
Parque Nacional do Juruena	0.196	1.000	1.000	2.000	2.000	1.000	1.000	1.061	0.000	0.987	1.000	1.000	1.000

Parque Nacional do Pantanal Mato-Grossense	2.063	2.875	2.000	2.000	2.000	2.000	3.000	1.000	0.000	2.000	2.000	2.250	1.375
Parque Nacional do Rio Novo	0.000	0.985	1.000	2.000	2.000	1.000	1.000	1.000	0.000	0.815	1.000	1.000	1.000
Parque Nacional dos Campos Ferruginosos	0.000	0.000	0.000	0.250	0.125	0.000	1.000	1.000	0.000	0.000	0.125	1.000	1.000
Parque Nacional Grande Sertão Veredas	5.000	5.000	4.000	1.586	2.207	4.552	3.655	3.000	0.000	4.724	3.931	2.862	1.862

Discussion

Our study indicates that the climatically suitable areas for maintaining populations of the five anemochoric species chosen in this study in the future (2080-2100) will be located in Brazil. These areas are primarily within the Cerrado regions, but they also extend into the Atlantic Forest, Amazon Forest, and the Caatinga, which is a unique vegetation type found in the Northeastern part of Brazil. The Caatinga is characterized by shallow and stony soils, low trees, crooked trunks, and thorny and deciduous leaves during the dry season. Preserving these areas is of extreme importance for maintaining populations of the observed species in the future. Notably, both the Cerrado and the Atlantic Forest, are considered Brazilian ecosystems recognized as biodiversity hotspots worldwide [32]. These ecosystems are known for their rich biological diversity, which is threatened by species extinction and extensive habitat destruction driven by human activities [32]. The Amazon Forest, in particular, has gained international attention due to the exponential increase in deforestation [43], primarily fueled by agricultural expansion[44] and timber exploitation [45]. Preserving these areas is not only vital for conserving these ecosystems but also for safeguarding other species, including many yet to be described [19,23,46]. By protecting species from different families that play a crucial role in the Cerrado, we are also conserving phylogenetic and functional diversity, along with essential ecosystem services. These services include provisioning services that provide resources used by humans, such as water, nutrient cycling, pollination and carbon sequestration [47].

Aspidosperma tomentosum, *K. coriacea* and *P. tomentosa* experienced significant losses in their distribution areas across all analyzed scenarios, losing up to 100%, 100% and 96.661%, respectively. *Senna velutina* also faced substantial losses, with up to 99.997% of its area being affected, but it could potentially gain up to 22.079% of its area.

Plants around the world will be affected by climate change in different regions [9]. Anthropogenic climate change is widely recognized as a major threat to biodiversity and has the potential to lead to the extinction of thousands of species over the next century [9]. Species extinction can be attributed to various factors, including physiological tolerance issues such as intolerance to high temperatures [48]. In the best-case scenario, it is estimated that 38-45% of woody plant species in the Brazilian Cerrado will cease to exist due to these climate changes. In the worst-case scenario, the estimate is as high as 56% of species [9].

Qualea multiflora generally expand its range, but when it experiences losses, it becomes vulnerable, potentially facing extinction with a 100% reduction in its current distribution area. Notably, *Q. multiflora* has expanded its range into the Amazon Forest, where there were previously no record of its occurrence [49]. The establishment of a species in a new environment depends on abiotic factors, such as the variables incorporated in the model, as well as biotic factors, including competition [50]. Furthermore, new factors need to be considered, such as anthropogenic activities in the Amazon region, which have resulted in significant deforestation [51]. However, it's worth noting that *Q. multiflora* previously existed in the Amazon region but later migrated to central Brazil, gaining areas further south in response to climatic fluctuations at the time [52]. We recommend further investigation into this expansion area of *Q. multiflora*.

The most relevant bioclimatic variable for *A. tomentosum*, *K. coriacea* and *S. velutina* distribution was the precipitation of coldest quarter (Bio 19). During the colder season, precipitation is lower, resulting in a negative relationship between fruiting and precipitation, as these three species exhibit fruit ripening between July and September [53,54]. For *P. tomentosa*, the most relevant bioclimatic variable was the annual mean temperature (Bio 1). Temperature is positively correlated with the flowering

and fruiting of *P. tomentosa* [53]. *Qualea multiflora* had precipitation of warmest quarter (Bio 18) as the most relevant variable. Precipitation during the warmest quarter corresponds to summer in the southern hemisphere, coinciding with the flowering period of *Q. multiflora*, which occurs between November and January [53]. The reproductive phenophase is crucial for maintaining species populations, as flowering marks the initial stage of seed generation, leading to successful seed dispersal and the establishment of new individuals[55]. Following fruiting, seed dispersal further supports population maintenance, especially during the dry season when wind intensities are higher [56].

The conservation units with the greatest potential for species in future were Parque Nacional do Gandarela and Parque Nacional da Serra do Cipó, followed by Parque Nacional da Serra da Canastra, Parque Nacional das Sempre-Vivas and Parque Nacional de Caparaó. Notably, the former two parks encompass a diverse and endangered Brazilian ecosystem[57]. It's worth noting that, in general, most Brazilian parks face some form of threat. When considering the best-case scenarios, the analyzed Brazilian parks have the climatic potential to support the studied populations. However, as these scenarios worsen, we observe a concerning decline in this capacity, which poses a probable high risk of extinction. Future studies on the effects of climate change are of great importance for the main plant families and their most abundant species, particularly for species that can sustain animals as pollinators or fruit dispersers.

Materials and Methods

Species data

The Cerrado biome is home to approximately 14,000 plant species [49], with about 30% of them exhibiting anemochory as their dispersal mechanism.

Anemochory is the second most common dispersion syndrome in the Cerrado [54,58]. For our study, we selected five common anemochoric species, each one from a representative Cerrado family (Table 5): *Aspidosperma tomentosum* Mart. & Zucc., *Kielmeyera coriacea* Mart. & Zucc., *Peixotoa tomentosa* A. Juss., *Qualea multiflora* Mart. and *Senna velutina* (Vogel) H.S. Irwin & Barneby. We compiled records of the geographic distribution of these species from two online sources: Species Link (CRIA 2014) and GBIF (Global Biodiversity Information Facility, <https://www.gbif.org/>) [23]. To enhance data quality, we conducted a complementary search for synonyms using Re flora – Flora do Brasil 2020 for all five species. This effort resulted in a total of 11,996 points, including 2,547 for *A. tomentosum*, 3,081 for *K. coriacea*, 911 for *P. tomentosa*, 4,086 for *Q. multiflora* and 1,371 for *S. velutina*. We filtered the species' location records by removing duplicate points, points lacking geographic coordinates, and points with improbable occurrence (examples: points in oceanic or Antarctic regions). Subsequently, the points were adjusted to a resolution of 5 minutes, which is approximately 81km². These occurrence points exclusively represent the realized niche and not account for the effective niche, as they only include locations where the species have been found.

Table 5. Characterization of the studied species lifestyle, fruit type and restriction area.

Species	Family	Lifestyle	Fruit type	Endemic to Brazil
<i>Aspidosperma tomentosum</i>	Apocynaceae Juss.	Tree	Dry follicle	No
<i>Kielmeyera coriacea</i>	Calophyllaceae J. Agardh	Shrub, Tree	Septicidal capsule	No
<i>Peixotoa tomentosa</i>	Malpighiaceae Juss.	Shrub	Samarid	Yes
<i>Qualea multiflora</i>	Vochysiaceae A. St.-Hil	Shrub, Tree	Loculicidal capsule	No
<i>Senna velutina</i>	Fabaceae Lindl.	Shrub	Samaroid	No

Environmental data

Bioclimatic variables were obtained from WorldClim version 2.0, with a 5 minutes resolution. To prevent excessive redundancy between these variables, Pearson's correlation was used and variables with a correlation equal to or greater than 75% were filtered out [59]. When two variables exhibited such a correlation, only the one deemed biologically significant for the species was retained [59]. After filtering the data, we identified nine variables that were applicable to all five species: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, temperature annual range, annual precipitation, precipitation of driest month, precipitation seasonality, precipitation of warmest quarter and precipitation of coldest quarter (Table 6).

Table 6. Nine bioclimatic variables included in the models.

Code	Bioclimatic variables
BIO1	Annual mean temperature
BIO2	Mean diurnal range [mean of monthly (max temp - min temp)]
BIO3	Isothermality (BIO2/BIO7) ($\times 100$)
BIO4	Temperature seasonality (standard deviation $\times 100$)
BIO12	Annual precipitation
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

How to evaluate the model?

To evaluate each model, we used the area under the curve (AUC) of the receiver operating characteristic (ROC), which compares the model's adequacy values with the observed data [19,60]. We further confirmed the results using the true skill statistic (TSS). AUC values range from 0 to 1, where values up to 0.6 indicate that the model has no predictive power, while a value of 1 indicates a perfect model for predicting species distribution [61]. To interpret the AUC values, we employed the following scale: $AUC > 0.9$ = excellent; $0.89 > AUC < 0.80$ = good; $0.79 > AUC < 0.70$ = fair; $0.69 > AUC < 0.60$ = poor; $AUC < 0.60$ = failure [64]. TSS values range from -1 to 1, where values below 0 indicate a random model, and values above 0 represent an acceptable model [62].

Which bioclimatic variables best explained the geographic distribution for each species?

To elucidate the geographic distribution, we used the percentage contribution of the variables, as provided by MaxEnt. We considered the set of variables with higher importance values, collectively accounting for at least 70% of the model's influence.

What is the current distribution of the species?

The Ecological Niche Models (ENMS) were constructed using the Maximum Entropy Model (MaxEnt) incorporated within R 4.0. MaxEnt employs maximum entropy techniques, relying solely on presence points [63,64]. We used the ENMeval package to assess the model's fit parameters [65]. We designed 10

replicates of the model and calculated the average of these models. To optimize modeling process, we incorporated two parameters into the model to enhance its predictive power: feature class (fc) and a regularization multiplier (rm). Feature class represents a mathematical transformation of the various covariates used in model construction, allowing for the modeling of complex relationships [66,67]. The regularization multiplier is a parameter that introduces new constraints, primarily aimed at preventing excessive complexity and overfitting, thereby controlling the intensity of the chosen feature classes for the model [66,68]. The available resource classes included linear (L), product (P), quadratic (Q) and hinge (H), as well as their combinations LQ, LQH, LQHP and LQHPT. The multiplier values ranged from 0.5 to 4 (0.5, 1, 1.5, 2, 2.5, 3, 3.5 and 4). For each model, we generated 10,000 background points. The best models were selected based on the lowest Akaike Information Criterion (AIC). We employed the geographical block method to assess the performance of each model [59,65]. For future predictions (2080-2100), we tested three climate projections: BCC-CSM2-MR - Beijing Climate Center Climate System Model [69], CNRM-ESM2-1 - Evaluation of CNRM Earth System Model [70] and MIROC6 - Model for Interdisciplinary Research on Climate [71]. These were evaluated along with four greenhouse gas emission scenarios: RCP2.6 (490ppmv), RCP4.5 (650 ppmv), RCP6.0 (850 ppmv), and RCP8.5 (1370 ppmv) [3]. MIROC6 represents a milder model in terms of greenhouse gas emissions, whereas BCC-CSM2-MR is moderate, and CNRM-ESM2-1 is more extreme [72].

What changes will occur?

To analyze the area held, gained and lost, we performed the calculations using the area function of the ‘raster’ package [73]. For each species, we conducted 12 analyzes, working with the tree tested models for future predictions and considering the four greenhouse gas emission scenarios. The matrix data was transformed into binary values: 0 for absence, and 1 for presence [74]. The raster clogging limit was determined based on the tenth percentile of training presence (TPTP). TPTP excludes all regions with habitat suitability values lower than the 10% threshold based on current occurrence records. TPTP has been extensively used [75–77] and demonstrated superior results when compared to other thresholds, such as minimum training presence (MTP) [81]. TPTP is considered a conservative method [78,79].

Which conservation unit will have the greatest potential for species richness?

To assess the potential richness of species, we selected the park category as a basis since they are strictly protected areas, as the Brazilian law does not allow the direct use of natural resources [80]. For the analysis, we overlaid the binarized maps of the five species and extract the mean potential, standard deviation, minimum and maximum potential using the extract function from the raster package [73]. We focused on 30 parks located within the smallest polygon area, and we conducted 13 analyses: present, BCC-CSM2 RCP2.6, BCC-CSM2 RCP4.5, BCC-CSM2 RCP6.0, BCC-CSM2 RCP8.5, CNRM-ESM2-1 RCP2.6, CNRM-ESM2-1 RCP4.5, CNRM-ESM2-1 RCP6.0, CNRM-ESM2-1 RCP8.5, MIROC6 RCP2.6, MIROC6 RCP4.5, MIROC6-370 and MIROC6 RCP8.5 (Table 6).

Table 3. Conservation units used, Brazilian states of localization, biome and area (hectares).

Conservation Units	States	Biome	Size (ha)
Parque Nacional Cavernas do Peruaçu	MG	Cerrado	56449.004
Parque Nacional da Chapada da Diamantina	BA	Caatinga	152143.914
Parque Nacional da Chapada das Mesas	MA	Cerrado	159953.781
Parque Nacional da Chapada dos Guimarães	MT	Cerrado	32646.832
Parque Nacional da Chapada dos Veadeiros	GO	Cerrado	240586.563
Parque Nacional da Serra da Bocaina	RJ/SP	Atlantic Forest	106566.425
Parque Nacional da Serra da Bodoquena	MS	Cerrado	76973.530
Parque Nacional da Serra da Canastra	MG	Cerrado	197971.961
Parque Nacional da Serra da Capivara	PI	Caatinga	100764.194
Parque Nacional da Serra das Confusões	PI	Cerrado	823854.539
Parque Nacional da Serra do Cipó	MG	Cerrado	31639.535
Parque Nacional da Serra do Gandarela	MG	Atlantic Forest	31270.826
Parque Nacional da Serra do Pardo	PA	Amazonic Forest	445413.447
Parque Nacional da Serra dos Orgãos	RJ	Atlantic Forest	20020.746
Parque Nacional das Emas	MS/GO	Cerrado	132787.860
Parque Nacional das Nascentes do Rio Parnaíba	MA/PI/BA	Cerrado	749774.175
Parque Nacional das Sempre-Vivas	MG	Cerrado	124155.899
Parque Nacional de Boa Nova	BA	Atlantic Forest	12065.470
Parque Nacional de Brasília	DF	Cerrado	42355.542
Parque Nacional de Caparaó	ES/MG	Atlantic Forest	31763.291
Parque Nacional de Itatiaia	MG/RJ	Atlantic Forest	28086.350
Parque Nacional do Acari	AM	Amazônia	896410.954
Parque Nacional do Araguaia	TO	Cerrado	555524.438
Parque Nacional do Boqueirão Da Onça	BA	Caatinga	346908.103
Parque Nacional do Jamanxim	PA	Amazonic Forest	862895.273
Parque Nacional do Juruena	AM/MT	Amazonic Forest	1958014.417
Parque Nacional do Pantanal Mato-Grossense	MS/MT	Pantanal	135922.646
Parque Nacional do Rio Novo	PA	Amazonic Forest	538157.147
Parque Nacional dos Campos Ferruginosos	PA	Amazonic Forest	79086.038
Parque Nacional Grande Sertão Veredas	BA/MG	Cerrado	230856.143

Supplementary Materials:

Figure S1: Predicted change in *Aspidosperma tomentosum* Mart. & Zucc. distribution under future climate scenarios;

Figure S2: Predicted change in *Kilmeyera coriaceae* Mart. & Zucc. distribution under future climate scenarios;

Figure S3. Predicted change in *Senna velutina* (Vogel) H. S. Irwin & Barneby distribution under future climate scenarios.

Author Contributions: Conceptualization, L.A-d-L and F.A.V.; methodology, L.A-d-L, D.F.R.A. and F.A.V; formal analysis, L.A-d-L. and D.F.R.A.; investigation, L.A-d-L, D.F.R.A and F.A.V; data curation, L.A-d-L and D.F.R.A.; writing—original draft preparation, L.A-d-L and H.M.T.S.; writing—review and editing, L.A-d-L, D.F.R.A, D.V.A. and H.M.T-S.; supervision, D.F.R.A, D.V.A. and H.M.T-S.. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded in part by the Fundação de Amparo à Pesquisa do Estado de Minas Gerais – FAPEMIG - Finance code 001 (LAL), and Conselho Nacional de Desenvolvimento Científico e Tecnológico—Brazil (CNPQ)—Finance code 403647/2021-5 (HMTS).

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: Special thanks to introductory niche modeling course and Universidade Federal de Uberlândia for demonstrating the basic concepts and methodology needed to support a niche modeling project.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Parmesan C. Ecological and evolutionary responses to recent climate change. *The Annual Review of Ecology, Evolution and Systematics*. 2006;37: 637–669.
2. Zwiener V, Lira-Noriega A, Grady CJ, Padial AA, Vitule JRS. Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. *Global Ecology and Biogeography*. 2018;27: 298–309.
3. Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, Van Vuuren DP, et al. The next generation of scenarios for climate change research and assessment. *Nature*. 2010;463: 747–756.
4. Marengo JA. Mudanças climáticas globais e seus efeitos sobre a biodiversidade; caracterização do clima atual e definição das alterações climáticas para o território brasileiro ao longo do século 21. Ministério. Brasília, Distrito Federal, Brasil: Ministério do Meio Ambiente; 2006.
5. Bustamante M, Nardoto G, Pinto A, Resende J, Takahashi F, Vieira L. Potential impacts of climate change on biogeochemical functioning of Cerrado ecosystems. *Brazilian Journal of Biology*. 2012;72: 655–671. doi:10.1590/S1519-69842012000400005
6. Marengo JA, Ambrizzi T, da Rocha RP, Alves LM, Cuadra S V., Valverde MC, et al. Future change of climate in South America in the late twenty-first century: intercomparison of scenarios from three regional climate models. *Clim Dyn*. 2010;35: 1073–1097. doi:10.1007/s00382-009-0721-6
7. Miranda LS, Imperatriz-Fonseca VL, Giannini TC. Climate change impact on ecosystem functions provided by birds in southeastern Amazonia. *PLoS One*. 2019;14: e0215229.
8. Hidasi-Neto J, Joner DC, Resende F, de Macedo Monteiro L, Faleiro FV, Loyola RD, et al. Climate change will drive mammal species loss and biotic homogenization in the Cerrado Biodiversity Hotspot. *Perspect Ecol Conserv*. 2019;17: 57–63.
9. Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, et al. Extinction risk from climate change. *Nature*. 2004;427: 145–148.
10. Simões S dos S, Zappi D, Costa GM da, de Oliveira G, Aona LYS. Spatial niche modelling of five endemic cacti from the Brazilian Caatinga: Past, present and future. *Austral Ecol*. 2020;45: 35–47.
11. Atwater DZ, Barney JN. Climatic niche shifts in 815 introduced plant species affect their predicted distributions. *Global Ecology and Biogeography*, geb. 2021;13342.
12. Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* (1979). 2008;322: 261–264.
13. Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, et al. Effects of climate change on global seaweed communities. *J Phycol*. 2012;48: 1064–1078.

14. Evans SE, Wallenstein MD. Climate change alters ecological strategies of soil bacteria. *Ecol Lett.* 2014;17: 155–164.
15. Hughes L. Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol.* 2000;15: 56–61.
16. Urban MC. Accelerating extinction risk from climate change. *Science* (1979). 2015;348: 571–573.
17. Vitorino LC, Reis MNO, Bessa LA, Souza UJB de, Silva FG. Landscape and Climate Influence the Patterns of Genetic Diversity and Inbreeding in Cerrado Plant Species. *Diversity (Basel).* 2020;12: 421.
18. Vilela AA, Del-Claro VTS, Torezan-Silingardi HM, Del-Claro K. Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. *Arthropod Plant Interact.* 2017;12: 215–227. doi:10.1007/s11829-017-9572-y
19. Correa-Lima APA, Varassin IG, Barve N, Zwiener VP. Spatio-temporal effects of climate change on the geographical distribution and flowering phenology of hummingbird-pollinated plants. *Ann Bot.* 2019;124: 389–398. doi:10.1093/aob/mcz079
20. Frei ER, Ghazoul J, Matter P, Heggli M, Pluess AR. Plant population differentiation and climate change: responses of grassland species along an elevational gradient. *Glob Chang Biol.* 2014;20: 441–455.
21. Hoffmann AA, Sgro CM. Climate change and evolutionary adaptation. *Nature.* 2011;470: 479–485.
22. Priti H, Aravind NA, Uma Shaanker R, Ravikanth G. Modeling impacts of future climate on the distribution of Myristicaceae species in the Western Ghats, India. *Ecol Eng.* 2016;89: 14–23.
23. Oliveira G, Lima-Ribeiro MS, Terribile LC, Dobrovolski R, Telles MP d. C, Diniz-Filho JAF. Conservation biogeography of the Cerrado's wild edible plants under climate change: Linking biotic stability with agricultural expansion. *Am J Bot.* 2015;102: 870–877. doi:10.3732/ajb.1400352
24. Atwater DZ, Ervine C, Barney JN. Climatic niche shifts are common in introduced plants. *Nat Ecol Evol.* 2018;2: 34–43.
25. Jump AS, Penuelas J. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol Lett.* 2005;8: 1010–1020.
26. Siqueira MF de, Peterson AT. Consequences of global climate change for geographic distributions of cerrado tree species. *Biota Neotrop.* 2003;3: 1–14. doi:10.1590/S1676-06032003000200005
27. Costa MH, Pires GF. Effects of Amazon and Central Brazil deforestation scenarios on the duration of the dry season in the arc of deforestation. *International Journal of Climatology.* 2010;30: 1970–1979.

28. Klink CA, Machado RB. Conservation of the Brazilian cerrado. *Conservation biology*. 2005;19: 707–713.
29. Trigueiro WR, Nabout JC, Tessarolo G. Uncovering the spatial variability of recent deforestation drivers in the Brazilian Cerrado. *J Environ Manage*. 2020;275: 111243.
30. Mistry J. Fire in the cerrado (savannas) of Brazil: an ecological review. *Progress in Physical Geography: Earth and Environment*. 1998;22: 425–448.
doi:10.1177/030913339802200401
31. Filho IAM, Neves AJ das, Silva GE, Vieira A dos S. Áreas de proteção ambiental e a preservação do bioma cerrado. *Revista Brasileira de Estudos de Segurança Pública*. 2019;12: 10–19.
32. Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB da, Kent J. Biodiversity hotspots for conservation priorities. *Nature*. 2000;403: 853–858.
doi:doi.org/10.1038/35002501
33. Fonseca M, Lamas I, Kasecker T. O papel das unidades de conservação. *Scientific American Brasil*. 2010;39: 18–23.
34. Hutchinson GE. Concluding Remarks: animal ecology and demography. . *Cold Spring Harb Symp Quant Biol*. 1957;22: 415–427. doi:10.1101/SQB.1957.022.01.039
35. Peterson AT, Cobos ME, Jiménez-García D. Major challenges for correlational ecological niche model projections to future climate conditions. *Ann N Y Acad Sci*. 2018;1429: 66–77. doi:10.1111/nyas.13873
36. Colwell RK, Rangel TF. Hutchinson’s duality: the once and future niche. *Proceedings of the National Academy of Sciences*. 2009;106: 19651–19658. doi:https://doi.org/10.1073/pnas.0901650106
37. Guisan A, Mod HK, Scherrer D, Münkemüller T, Pottier J, Alexander JM, et al. Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities. *Global Ecology and Biogeography*. 2019;28: 1384–1392. doi:10.1111/geb.12967
38. Broennimann O, Thuiller W, Hughes G, Midgley GF, Alkemade JMR, Guisan A. Do geographic distribution, niche property and life form explain plants’ vulnerability to global change? *Glob Chang Biol*. 2006;12: 1079–1093.
39. Mendoza-González G, Martínez ML, Rojas-Soto OR, Vázquez G, Gallego-Fernández JB. Ecological niche modeling of coastal dune plants and future potential distribution in response to climate change and sea level rise. *Glob Chang Biol*. 2013;19: 2524–2535.
40. You J, Qin X, Ranjitkar S, Loughheed SC, Wang M, Zhou W, et al. Response to climate change of montane herbaceous plants in the genus *Rhodiola* predicted by ecological niche modelling. *Sci Rep*. 2018;8: 1–12.
41. Lopes TM, Bailly D, Almeida BA, Santos NCL, Gimenez BCG, Landgraf GO, et al. Two sides of a coin: Effects of climate change on the native and non-native distribution of *Colossoma macropomum* in South America. *PLoS One*. 2017;12: e0179684.

42. Sen S, Gode A, Ramanujam S, Ravikanth G, Aravind NA. Modeling the impact of climate change on wild *Piper nigrum* (Black Pepper) in Western Ghats, India using ecological niche models. *J Plant Res.* 2016;129: 1033–1040.
43. Matricardi EAT, Skole DL, Costa OB, Pedlowski MA, Samek JH, Miguel EP. Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science* (1979). 2020;369: 1378–1382.
44. Silvério D V, Brando PM, Macedo MN, Beck PSA, Bustamante M, Coe MT. Agricultural expansion dominates climate changes in southeastern Amazonia: the overlooked non-GHG forcing. *Environmental Research Letters.* 2015;10: 104015. doi:10.1088/1748-9326/10/10/104015
45. Rodrigues MI, Souza ÁN de, Joaquim MS, Lustosa Junior IM, Pereira RS. Concessão florestal na Amazônia brasileira. *Ciência Florestal.* 2020;30: 1299–1308. doi:10.5902/1980509821658
46. Carvalho RL, Resende AF, Barlow J, França FM, Moura MR, Maciel R, et al. Pervasive gaps in Amazonian ecological research. *Current Biology.* 2023;33: 3495-3504.e4. doi:10.1016/j.cub.2023.06.077
47. Ferreira RB, Parreira MR, Nabout JC. The impact of global climate change on the number and replacement of provisioning ecosystem services of Brazilian Cerrado plants. *Environ Monit Assess.* 2021;193. doi:10.1007/s10661-021-09529-6
48. Somero GN. Comparative physiology: a “crystal ball” for predicting consequences of global change. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology.* 2011;301: R1--R14.
49. Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Availale at: < <http://floradobrasil.jbrj.gov.br/> >. Aceessed on: February 10, 2024.
50. Morin PJ. *Community Ecology*. 2nd editio. Morin PJ, editor. Oxford: Wiley-Brackwell; 2011.
51. Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA. Climate change, deforestation, and the fate of the Amazon. *Science* (1979). 2008;319: 169–172.
52. Buzatti RS de O, Lemos-Filho JP, Bueno ML, Lovato MB. Multiple Pleistocene refugia in the Brazilian cerrado: evidence from phylogeography and climatic nichemodelling of two *Qualea* species (Vochysiaceae). *Botanical Journal of the Linnean Society.* 2017;185: 307–320.
53. Novaes LR, Calixto ES, Oliveira ML, Alves-de-Lima L, Almeida O, Torezan-Silingardi HM. Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: A new wind-based approach. *Science of The Total Environment.* 2020;730: 139039.
54. Pilon NAL, Udulutsch RG, Durigan G. Padrões fenológicos de 111 espécies de Cerrado em condições de cultivo. *Hoehnea.* 2015;42: 425–443.

55. Del-Claro K, Torezan-Silingardi HM. Ecologia das interações plantas-animais: Uma abordagem ecológico-evolutiva. Technical Books Editora; 2012.
56. Johansson V, Lönnell N, Rannik Ü, Sundberg S, Hylander K. Air humidity thresholds trigger active moss spore release to extend dispersal in space and time. *Funct Ecol*. 2016;30: 1196–1204.
57. Jacobi CM, do Carmo FF, Vincent RC, Stehmann JR. Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodivers Conserv*. 2007;16: 2185–2200. doi:10.1007/s10531-007-9156-8
58. Gottsberger G, Silberbauer-Gottsberger I. Dispersal and distribution in the cerrado vegetation of Brazil. *Sonderbd Naturwiss Ver Hamburg*. 1983;7: 315–352.
59. Lira FDA, Amado TF, Moura TA, Riul P. Vulnerable areas to accidents with scorpions in Brazil. *Tropical Medicine and International Health*. 2021;00. doi:10.1111/tmi.13561
60. Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, et al. Ecological niches and geographic distributions (MPB-49). Princeton University Press; 2011.
61. Araújo MB, Pearson RG, Thuiller W, Erhard M. Validation of species–climate impact models under climate change. *Glob Chang Biol*. 2005;11: 1504–1513.
62. Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology*. 2006;43: 1223–1232.
63. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. *Divers Distrib*. 2011;17: 43–57.
64. Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. *Ecol Modell*. 2006;190: 231–259.
65. Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, et al. ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol Evol*. 2014;5: 1198–1205.
66. Morales NS, Fernández IC, Baca-González V. MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ*. 2017;5: e3093.
67. Merow C, Smith MJ, Silander Jr JA. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*. 2013;36: 1058–1069.
68. Shcheglovitova M, Anderson RP. Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecol Modell*. 2013;269: 9–17.

69. Wu T, Lu Y, Fang Y, Xin X, Li L, Li W, et al. The Beijing Climate Center climate system model (BCC-CSM): The main progress from CMIP5 to CMIP6. *Geosci Model Dev*. 2019;12: 1573–1600.
70. Séférian R, Nabat P, Michou M, Saint-Martin D, Voldoire A, Colin J, et al. Evaluation of CNRM Earth System Model, CNRM-ESM2-1: Role of Earth System Processes in Present-Day and Future Climate. *J Adv Model Earth Syst*. 2019;11: 4182–4227.
71. Tatebe H, Ogura T, Nitta T, Komuro Y, Ogochi K, Takemura T, et al. Description and basic evaluation of simulated mean state, internal variability, and climate sensitivity in MIROC6. *Geosci Model Dev*. 2019;12: 2727–2765.
72. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*. 2005;25: 1965–1978. doi:10.1002/joc.1276
73. Rather TA, Kumar S, Khan JA. Multi-scale habitat modelling and predicting change in the distribution of tiger and leopard using random forest algorithm. *Sci Rep*. 2020;10: 11473. doi:10.1038/s41598-020-68167-z
74. Freeman EA, Moisen GG. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecol Modell*. 2008;217: 48–58.
75. Jacobsen CD, Brown DJ, Flint WD, Pauley TK, Buhlmann KA, Mitchell JC. Vulnerability of high-elevation endemic salamanders to climate change: A case study with the Cow Knob Salamander (*Plethodon punctatus*). *Glob Ecol Conserv*. 2020;21: e00883.
76. Brambilla M, Ficetola GF. Species distribution models as a tool to estimate reproductive parameters: a case study with a passerine bird species. *Journal of Animal Ecology*. 2012;81: 781–787.
77. Hernández-Lambrano RE, González-Moreno P, Sánchez-Agudo JÁ. Towards the top: niche expansion of *Taraxacum officinale* and *Ulex europaeus* in mountain regions of South America. *Austral Ecol*. 2017;42: 577–589.
78. Sutton WB, Barrett K, Moody AT, Loftin CS, DeMaynadier PG, Nanjappa P. Predicted changes in climatic niche and climate refugia of conservation priority salamander species in the northeastern United States. *Forests*. 2015;6: 1–26.
79. Bosso L, Rebelo H, Garonna AP, Russo D. Modelling geographic distribution and detecting conservation gaps in Italy for the threatened beetle *Rosalia alpina*. *J Nat Conserv*. 2013;21: 72–80.

Supplementary

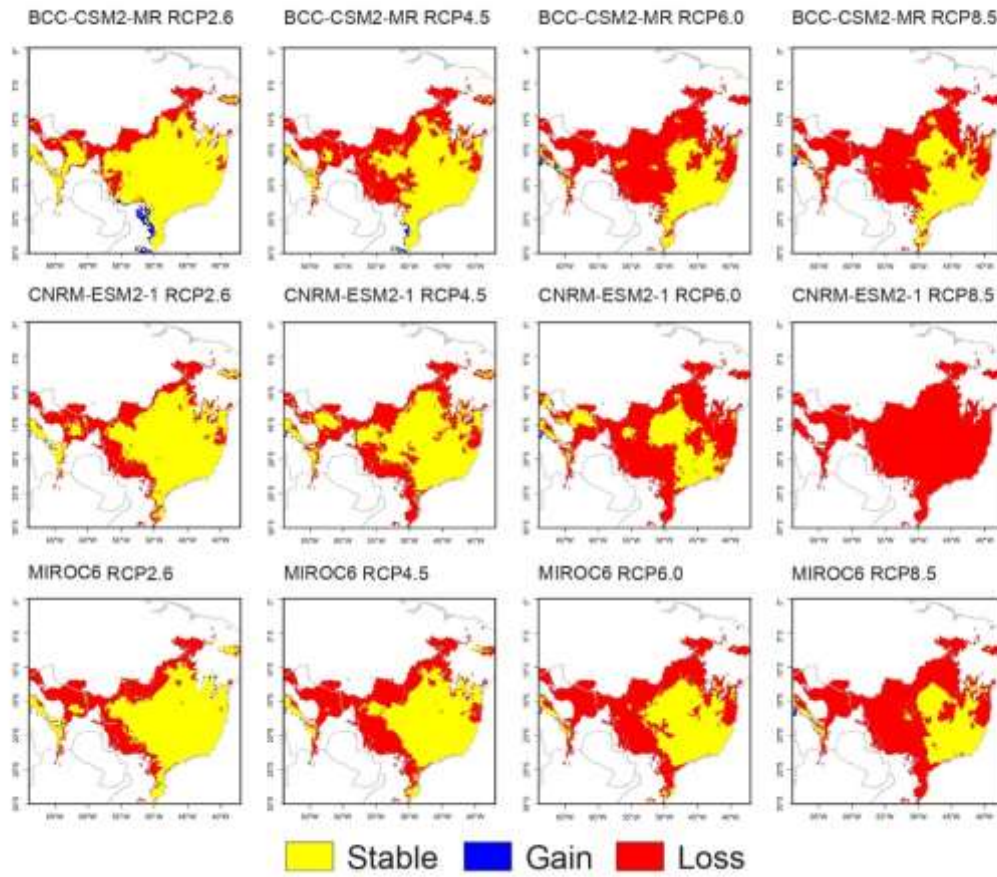


Figure S1. Predicted change in *Aspidosperma tomentosum* Mart. & Zucc. distribution under future climate scenarios.

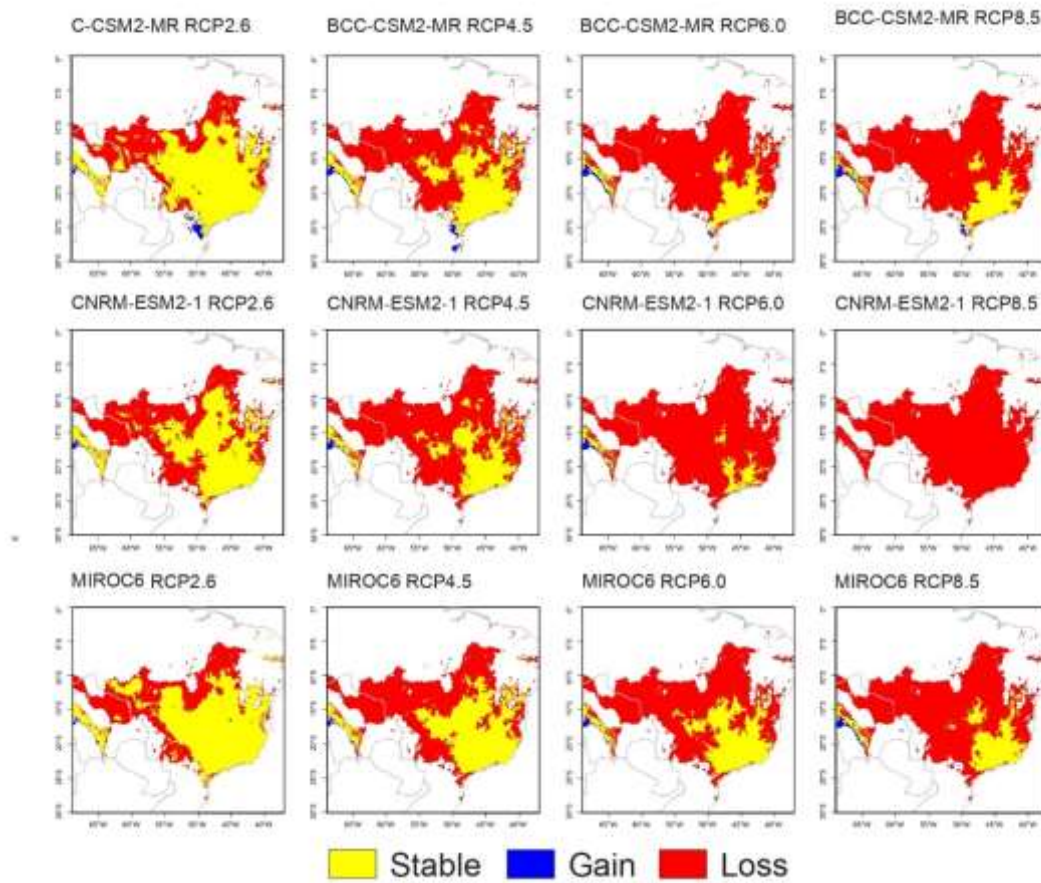


Figure S2. Predicted change in *Kilmeyera coriaceae* Mart. & Zucc. distribution under future climate scenarios.

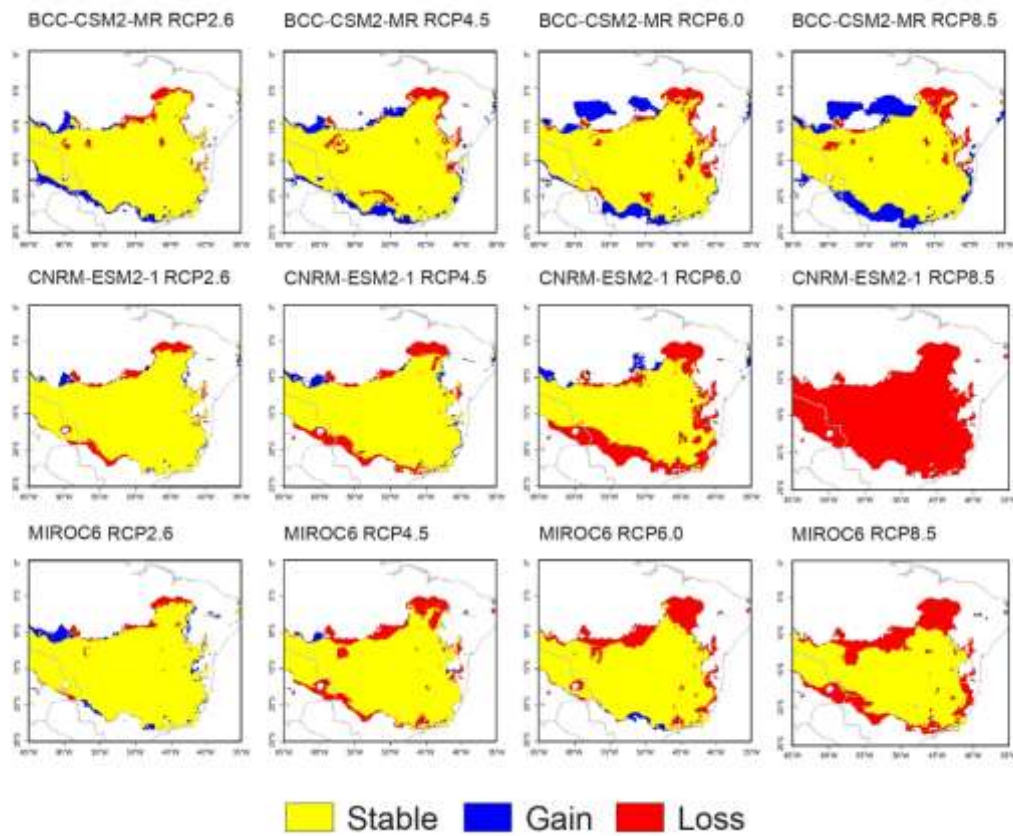


Figure S3. Predicted change in *Senna velutina* (Vogel) H. S. Irwin & Barneby distribution under future climate scenarios.

Table S1. Average species richness potential of conversation units. considering the present and 12 future projections

Conservation Units	Present	BCC- CSM2 RCP2.6	BCC- CSM2 RCP4.5	BCC- CSM2 RCP6.0	BCC- CSM2 RCP8.5	CNRM- ESM2-1 RCP2.6	CNRM- ESM2-1 RCP4.5	CNRM- ESM2-1 RCP6.0	CNRM- ESM2-1 RCP8.5	MIROC6 RCP2.6	MIROC6 RCP4.5	MIROC6 RCP6.0	MIROC6 RCP8.5
Parque Nacional Cavernas do Peruaçu	3.714	2.857	2.714	0.857	1.857	2.714	2.286	1.286	0.000	3.000	2.857	2.286	1.857
Parque Nacional da Chapada da Diamantina	4.421	3.895	3.316	1.526	1.316	3.526	2.368	0.842	0.000	4.842	3.789	2.105	2.474
Parque Nacional da Chapada das Mesas	1.190	0.000	0.857	0.238	0.190	0.762	1.143	1.000	0.000	0.571	1.048	0.810	0.952
Parque Nacional da Chapada dos Guimarães	4.800	4.000	2.600	2.000	2.000	4.000	3.400	2.400	0.000	4.400	3.400	1.600	2.000
Parque Nacional da Chapada dos Veadeiros	5.000	4.733	4.267	3.567	3.467	4.467	4.000	3.267	0.000	4.900	4.300	4.000	3.800
Parque Nacional da Serra da Bocaina	4.083	4.333	4.333	4.167	4.250	3.833	3.333	3.083	0.667	4.167	3.500	3.333	3.000
Parque Nacional da Serra da Bodoquena	2.889	2.667	0.889	1.222	2.000	0.111	0.000	0.444	0.000	1.000	0.000	0.000	0.111
Parque Nacional da Serra da Canastra	5.000	5.000	5.000	4.522	4.565	5.000	4.913	4.783	0.000	5.000	5.000	5.000	5.000
Parque Nacional da Serra da Capivara	0.583	0.500	0.250	0.000	0.000	0.917	0.917	0.250	0.000	1.000	0.500	0.167	0.000
Parque Nacional da Serra das Confusões	1.421	1.000	0.832	0.221	0.158	1.000	0.937	0.347	0.000	0.842	0.274	0.011	0.021
Parque Nacional da Serra do Cipó	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	0.667	5.000	5.000	5.000	5.000
Parque Nacional da Serra do Gandarela	5.000	5.000	5.000	5.000	5.000	5.000	5.000	5.000	1.000	5.000	5.000	5.000	5.000
Parque Nacional da Serra do Pardo	0.000	0.000	0.519	0.000	0.308	0.019	1.000	1.000	0.000	0.000	0.942	1.000	1.000
Parque Nacional da Serra dos Orgãos	4.000	5.000	5.000	5.000	5.000	4.000	4.000	3.500	0.500	4.000	4.000	4.000	4.000
Parque Nacional das Emas	5.000	4.000	4.000	1.000	1.313	4.000	4.000	2.000	0.000	5.000	4.000	3.938	1.000
Parque Nacional das Nascentes do Rio Parnaíba	3.211	2.622	1.244	1.233	1.189	2.678	1.667	1.133	0.000	2.522	1.700	1.556	1.689
Parque Nacional das Sempre-Vivas	5.000	5.000	5.000	4.824	4.824	5.000	5.000	4.353	0.000	5.000	5.000	4.647	4.824
Parque Nacional de Boa Nova	3.000	3.000	1.818	0.727	0.909	2.000	2.000	0.273	0.000	2.818	1.909	0.727	0.455
Parque Nacional de Brasília	5.000	5.000	4.400	4.000	4.000	4.800	4.000	4.000	0.000	5.000	4.600	4.000	4.000
Parque Nacional de Caparaó	5.000	5.000	5.000	5.000	5.000	5.000	5.000	4.333	1.000	5.000	5.000	4.000	4.000
Parque Nacional de Itatiaia	5.000	5.000	5.000	4.333	5.000	5.000	4.333	4.000	1.000	4.333	4.000	4.000	3.333
Parque Nacional do Acari	0.000	0.500	1.000	0.049	0.000	1.000	1.000	1.000	0.000	1.000	1.000	1.000	1.000

Parque Nacional do Araguaia	3.217	2.000	2.000	2.000	2.000	1.971	2.000	1.812	0.000	2.101	1.464	1.000	1.000
Parque Nacional do Boqueirão Da Onça	0.467	0.244	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000
Parque Nacional do Jamanxim	0.000	0.420	0.950	0.510	0.000	0.970	1.000	1.000	0.000	0.700	1.000	1.000	1.000
Parque Nacional do Juruena	0.196	1.000	1.000	2.000	2.000	1.000	1.000	1.061	0.000	0.987	1.000	1.000	1.000
Parque Nacional do Pantanal Mato-Grossense	2.063	2.875	2.000	2.000	2.000	2.000	3.000	1.000	0.000	2.000	2.000	2.250	1.375
Parque Nacional do Rio Novo	0.000	0.985	1.000	2.000	2.000	1.000	1.000	1.000	0.000	0.815	1.000	1.000	1.000
Parque Nacional dos Campos Ferruginosos	0.000	0.000	0.000	0.250	0.125	0.000	1.000	1.000	0.000	0.000	0.125	1.000	1.000
Parque Nacional Grande Sertão Veredas	5.000	5.000	4.000	1.586	2.207	4.552	3.655	3.000	0.000	4.724	3.931	2.862	1.862

