Universidade Federal de Minas Gerais

Departamento de Biologia Geral

Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre

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Disentangling the intensity and consequences of floral antagonists in a threatened mountaintop ecosystem

Belo Horizonte

2021

Irene Gélvez Zúñiga

Disentangling the intensity and consequences of floral antagonists in a threatened mountaintop ecosystem

Versão final

Tese apresentada ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial para obtenção do título de Doutora em Ecologia.

Orientador: Geraldo Wilson Fernandes

Belo Horizonte

2021

043 Zúñiga, Irene Gélvez.
Disentangling the intensity and consequences of floral antagonists in a threatened mountaintop ecosystem [manuscrito] / Irene Gélvez Zúñiga – 2021.

122 f. : il. ; 29,5 cm.

Orientador: Geraldo Wilson Fernandes.
Tese (doutorado) – Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas. Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre.

1. Ecologia. 2. Campo rupestre. 3. Relação inseto-planta. 4. Polinização por insetos. I. Fernandes, Geraldo Wilson. II. Universidade Federal de Minas Gerais. Instituto de Ciências Biológicas. III. Título.

CDU: 502.7

Ficha catalográfica elaborada pela bibliotecária Sônia M S Moraes – CRB 6 – 1357

UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

Ata da Defesa de Tese

Nº 203
Entrada: 2016/2

Irene Gélvez Zúñiga

No dia 30 de abril de 2021, às 09:00 horas, por vídeo conferência, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Irene Gélvez Zúñiga, orientando(a) do(a) Professor(a) Geraldo Wilson Fernandes, intitulada: **"Untangling the intensity and consequences of floral antagonists in a threatened mountaintop ecosystem"**. Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Geraldo Wilson Fernandes, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Lucas Neves Perillo (UFMG), Tatiana Garabini Cornelissen (UFMG), Pietro Kiyoshi Maruyama Mendonça (UFMG), Julia Astegiano (Universidad Nacional de Córboda) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

(X) Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;

( ) Reavaliação da tese com avaliação pelos membros da banca do documento revisado, sem nova defesa, no prazo máximo de 30 dias, sob possibilidade de reprovação;

( ) Reformulação da tese com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG a ao Regimento do PPG-ECMVS;

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A banca indica esta tese aos Prêmios CAPES e UFMG de teses? ( )SIM (X)NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 30 de abril de 2021.

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Documento assinado eletronicamente por **Julia Astegiano, Usuário Externo**, em 13/05/2021, às 10:43, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

Documento assinado eletronicamente por **Tatiana Garabini Cornelissen**, **Membro**, em 13/05/2021, às 10:48, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

Documento assinado eletronicamente por **Lucas Neves Perillo**, **Usuário Externo**, em 13/05/2021, às 21:20, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

Documento assinado eletronicamente por **Geraldo Wilson Afonso Fernandes**, **Professor do Magistério Superior**, em 14/05/2021, às 10:51, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

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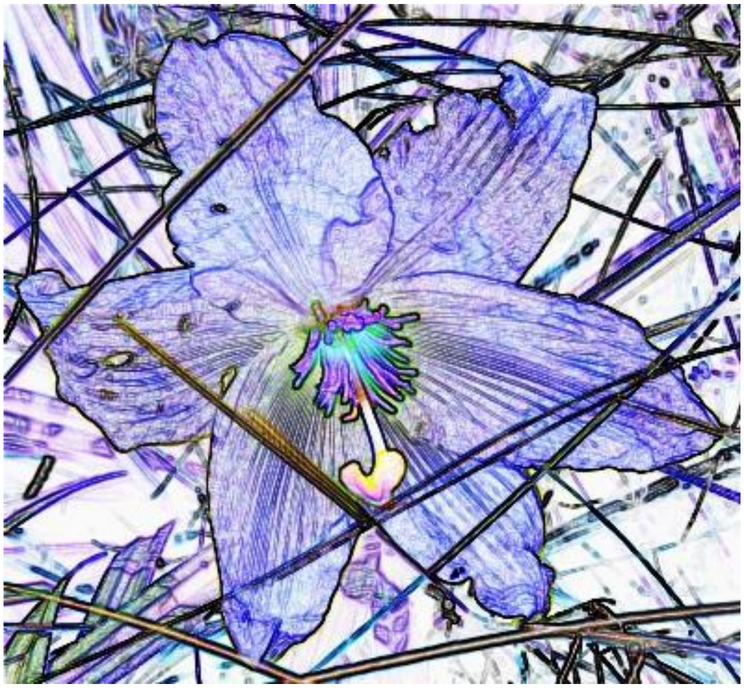

“This corner of the earth is like me in many ways
I can sit for hours here and watch the emerald feathers splay
I'm with this deep eternal universe from death until rebirth
I know this corner of the earth, it smiles at me”
Jason Kay (Jamiroquai) & Rob Harris

“De donde vengo yo, la cosa no es fácil pero siempre igual sobrevivimos
De tanto luchar siempre con la nuestra nos salimos
De aquí se habla mal, pero todo está mucho mejor
Tenemos la lluvia, el frio, el calor.
Subiendas de pescado, agua por todos lados
Selva espesa que ni el Discovery ha explotado
Minas llenas de oro y platino, reyes en la biodiversidad
De dónde vengo yo, de tanto luchar siempre con la nuestra nos salimos”
ChocQuibTown - Oro

Agradecimentos

Meu mais profundo agradecimento aos meus pais pela escolha de criar sua filha com liberdade, independência e valentia para forjar seus próprios caminhos. Por sempre me encorajar a desenvolver uma interação harmônica com a natureza e a abraçar as lutas que me fazem feliz. Esse apoio e incentivo possibilitaram que as minhas asas (e força) voassem pelo mundo com a certeza de ter sempre um lar me esperando para trocar aprendizados, compartilhar histórias, renovar as forças e continuar me encorajando para seguir com a caminhada. Obrigada a toda minha família pelo amor e apoio constante, por estarem sempre presentes, atentos e compreensivos mesmo na distância. Obrigada também à minha família adotiva no Brasil: Sonia, Vitoria e Samuel por todo o acolhimento, amor e por me mostrarem esse outro Brasil que não se vive na bolha da Universidade. Nossa conexão e carinho irão além do tempo!

Obrigada ao Professor Geraldo Wilson Fernandes pelos anos de ensinamentos no Laboratório de Ecologia Evolutiva e Biodiversidade, pela orientação e o apoio durante toda essa minha aventura em terras brasileiras. Sou muito grata por fazer parte de um laboratório composto por pessoas dispostas a ajudar, trabalhar em equipe, trocar idéias e fazer parcerias. Muito obrigada por sua imensa ajuda durante esses oito anos, Yumi Oki, você é uma mulher com um coração gigante! Obrigada aos meus amigos do LEEB para a vida Thaise, Marina, Wallace e Hernani. Obrigada também ao Julio Santiago pelo compromisso em várias etapas desse projeto, pela parceria, pela conexão e sintonia, pelo apoio e amor e por estarmos trilhando diversos caminhos juntos.

Como a maioria dos trabalhos de campo, os dados coletados para esse projeto são o resultado de um grande esforço conjunto. Obrigada a todas as pessoas que me ajudaram nas campanhas: Julio Cesar Santiago Lopes, Jhonatan de Assis Martins, Michel Jacoby Pereira, Dario Caminha Paiva, Bárbara Ferreira, Bárbara Dias, Milena Patrocínio, Keila Moreira, Luisa Fernanda Mejía Toro, Lucas Arantes Garcia, Jordan Reska, Joaquim Julio Lacerda e a todo mundo do LEEB que sempre esteve disposto a me ajudar. Obrigada a W. Kenedy Siqueira pela enorme ajuda com a parte gráfica e desenhos dos métodos e resultados. Agradeço profundamente a todas as pessoas envolvidas na identificação dos exemplares vegetais e animais coletados nesse projeto: Lica Hayasema, Frederico Dutra Kirst e Alessandre Pereira Colavite na identificação dos Diptera; Alessandro Lima, Lucas Neves Perillo, Rogério Botion Lopes, Marcos Magalhães de Souza e Ivan

Fernandes Golfetti pelo auxílio na identificação das vespas; José Eustáquio Santos-Junior pelo apoio na identificação das abelhas e por compartilhar um pouco do seu vasto conhecimento sobre elas comigo; ao Paulo Ricardo Siqueira pela grande ajuda decifrando fotos de beija-flores tiradas nas rápidas visitas as minhas plantas; ao Flávio Siqueira Castro pela ajuda identificando as formigas, e por me dar aquelas informações interessantes sobre o comportamento delas.

Desvendar as identidades dos besouros foi um grande desafio dentro do meu trabalho e não são poucas as pessoas envolvidas nesse processo. Quero agradecer em primeiro lugar ao professor Sergio Antonio Vanin porque ele me colocou em contato com um grande número de especialistas e me deu "aula" de como separar e montar gorgulhos, ele deve estar agora ensinando em outros planos astrais. Obrigada ao Samuel Novais pela ajuda na separação dos exemplares por família. Obrigada à Letizia Migliore quem me auxiliou na identificação dos Buprestidae, ao Gabriel Biffi pela ajuda com os Cantharidae, ao Luciano A. de Moura pela ajuda com os Crhrysomelidae e à Lúcia Massutti pelos Coccinellidae. Obrigada também à Adaiane CM Jacobina e ao Carlos Campaner pela ajuda com os Curculionidae.

Obrigada à Leonor Patrícia Morellato por disponibilizar os dados de identificação das plantas com flores das parcelas do PELD-Cipó, e de forma especial à sua aluna Beatriz Monteiro Lopes quem me ajudou muito na organização e identificação, e ainda se tornou uma amizade para a vida. Ao Júlio Joaquim Lacerda pela disposição e ajuda na identificação das plantas no campo, você me ensinou bastante sobre taxonomia de várias famílias de plantas nesse processo. Ao Carlos Alberto Ferreira Júnior por dividir seu conhecimento sobre as maravilhosas Velloziaceae (e várias outras famílias botânicas) com a gente e estar sempre disposto a ajudar. Agradeço à Bárbara Ferreira pelo auxílio na triagem das inúmeras exsicatas, pela ajuda com a organização dos exemplares e no herbário comparando exsicatas. Obrigada a Wallace Beiroz pela ajuda e aquelas dicas do R que me ajudaram nos momentos de "angustia" com a estatística, e a Marina Beirão pelos ensinamentos e paciência com os detalhes no R. Agradeço também ao Daniel Negreiros pela ajuda com as questões da filogenia. Graças aos esforços da Alexandra Elbakyan (Sci-Hub) e a equipe da organização Z-library de compartilhamento gratuito de livros, pois ambos foram fundamentais para a finalização desse trabalho, especialmente nas condições de trabalho remoto devido à pandemia da Covid-19.

Aos campos rupestres e ao pessoal da Serra do Cipó por continuarem me fazendo sentir em casa após todos esses anos. Agradeço às políticas e investimentos em aperfeiçoamento com estímulos para estrangeiros dos governos passados (especialmente aos governos Lula entre 2003-2011 e Dilma entre 2011-2016) porque foi graças a elas que eu comecei a sonhar em vir para o Brasil, que consegui de fato estudar aqui e conseqüentemente, me encontrar enquanto pesquisadora no mundo. Mesmo que a ciência no Brasil passe por um momento de escuridão e de trevas, confio na nossa resistência e resiliência para sermos agentes de mudança na busca de tempos melhores.

Agradeço muito a todas as pessoas da Casa da Caridade por me mostrarem outros mundos possíveis e me acolherem (a mim e a minha mãe) com tanta naturalidade e carinho. Esse apoio foi uma luz em tempos difíceis e sou muito grata em tê-los por perto. Finalmente, agradeço ao Conselho Nacional de Desenvolvimento Científico e Tecnológico pela concessão da bolsa. Aos professores e servidores administrativos do Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da UFMG. Obrigada à Reserva Vellozia, Parque Nacional da Serra do Cipó, Cedro Têxtil, ICMBio, Pousada Pedra do Elefante e Pousada Rancho Cipó pelo apoio logístico. Agradeço também as entidades que financiaram, direta e indiretamente, esse estudo: PELD-Cipó, FAPEMIG, ComCerrado, CAPES e CNPq.

Resumo

A dinâmica de interação entre plantas com flores e insetos pode abranger um contínuo que inclui mutualismos, antagonismos e as relações possíveis entre eles. Essas interações são consideradas um importante motor na história evolutiva de ambos os grupos, pois exercem pressões seletivas simultâneas em ações repetitivas durante o ciclo de vida do inseto e que podem, em última instância, afetar o sucesso reprodutivo da planta. As plantas com flores fazem investimentos em atração floral e recompensas para aumentar sua atratividade aos polinizadores. Porém, também desencadeiam visitas de agentes não polinizadores como florivoros, ladrões de néctar e/ou pólen ou pilhadores. Nesse sentido, este estudo teve como objetivo entender as tendências e a variação da florivoria natural exercida por insetos florívoros ao longo da elevação e sua relação com atributos florais e atração a polinizadores no *campo rupestre*, um hotspot de biodiversidade dentro do bioma Cerrado, Brasil. Verificamos que 26% das plantas com flores apresentaram sinais de florivoria e 7% das flores apresentaram remoção de pétalas por insetos na comunidade de plantas. Besouros, principalmente das famílias Chrysomelidae e Curculionidae, foram os insetos que mais se alimentam de flores, seguidos por formigas e abelhas. Em geral, as espécies de plantas com menor número de flores, flores grandes e tempo de floração mais longo são mais atacadas por insetos florívoros. Além disso, as flores com maior proporção de ataque por florívoros apresentam pólen como recompensa, estão organizadas em unidades solitárias de polinização, com corolas assimétricas e antese diurna. O ataque às flores aumenta com a elevação e é maior nos meses com menos flores disponíveis na comunidade. Finalmente, descobrimos que a florivoria exercida por insetos aumenta com a elevação em flores com morfologias menos restritivas, e é maior quando a recompensa é néctar, a simetria actinomórfica e quando a espécie é visitada por mais de dois grupos de visitantes florais. A florivoria exercida por insetos representa um fenômeno tão frequente e complexo quanto à herbivoria foliar, e a sincronia espaço-temporal entre as plantas com flores e seus insetos visitantes é crucial para garantir sua reprodução e permanência ao longo do tempo, especialmente em ambientes tropicais, biodiversos e sob severas pressões antrópicas.

Palavras Chave: *campo rupestre*, gradiente de elevação, atributos florais, insetos florívoros, atração floral, interação inseto-planta.

Abstract

Insect-flower interactions may encompass a continuum of interactions including from mutualisms to antagonisms. These interactions between flowering plants and their visitors are considered an important driver in the evolutionary history of both groups, as they may exert simultaneous selective pressures in actions such as foraging for food or mating which are repeated several times during insect life cycle, and that can ultimately affect plant reproductive success. Flowering plants make investments in floral advertisement and rewards to increase their attractiveness to pollinators, thus triggering visits by non-pollinator agents such as florivores, nectar and/or pollen robbers and thieves. This study aimed to unveil the intensity, trends and variation of natural florivory by insects along an elevation gradient, and its relationship with floral attributes and flower advertisement in the *campo rupestre* hotspot, in southeastern Brazil. We recorded a total of 207 plant species and 25% (51 out of 207) of the species showed damages by floral antagonists. In the plant community, 26% of the total flowering individuals recorded had signs of damages by floral antagonists and 7% of the flowers had petals removed by insects. Beetles, especially Chrysomelidae and Curculionidae, were the most abundant insects consuming the flowers, followed by ants and bees. Overall plant species with lower floral display, large flower size, and longer flowering period are more attacked by floral antagonists. Furthermore, the greater proportion of attack was found in flowers with pollen as reward, distributed in solitary pollination units, with asymmetric corollas and diurnal anthesis. Damages exerted by insect florivores varied in space (elevation) and time (months) with flower attack increasing with elevation and in moths with less flowers available in the community. Finally, we found greater damages by antagonists, and that increased with elevation, in nectar-rewarded flowers, actinomorphic corollas and more than two groups of flower visitors. Floral damages exerted by insects represent a phenomenon as frequent and complex as leaf herbivory, and the space-time synchrony between flowering plants and their insect visitors is crucial to guarantee plant reproduction and permanence over time, especially in tropical, speciose environments and under severe anthropic pressures.

Key words: *campo rupestre*, elevation gradient, floral attributes, floral damages, florivore insects, flower advertisement, insect-plant interactions.

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General introduction

Interactions between plants and their floral visitors are crucial for the reproduction evolution and ecology angiosperms, since flowers are essential resources for the ultimate production of fruits and seeds. The evolution and radiation of insects and flowering plants is certainly intertwined and may encompass a continuum from mutualist to antagonist interactions (Thompson 2005, Ollerton et al. 2007). Pollinators are recognized as one of the main drivers of evolution, since they exert selective pressures, which have enabled flowering plants to maximize their attractiveness to pollination vectors (Stebbins 1970, Fenster et al. 2004, Rosas-Guerrero et al. 2014). However, floral advertisement does not always involve just interactions with mutualistic partners, since pollen and/or nectar thieves, robbers and florivores are frequently found visiting flowers (Shykoff et al. 1996, Bronstein 2007, McCall & Irwin 2006). Simultaneously, these non-mutualistic partners can also exert selection pressures on some plant attributes and, primarily on flower attributes (McCall & Irwin 2006).

Florivory is an important biotic interaction which is generally recognized as any damage caused by consumption of floral structures (including pre-anthesis floral buds and early-stage fruits) before fruit maturation and release of seeds (Burgess 1991). Specifically, florivory includes any consumption of floral tissues such as bracts, sepals, petals, stamens, pistils, as well as ovules and pollen grains (McCall & Irwin 2006). Florivory can be a phenomenon as extended and comprehensive as leaf herbivory, and its consumption rates can occur with equal or greater frequency than leaf or root herbivory in some plant communities (reviewed by Moreira et al. 2019). Flower-feeding organisms may include primates, bats, birds and, most frequently insects (Frame 2003, McCall & Irwin 2006). Florivore insects comprise several orders and exhibit different foraging strategies including generalist herbivores (e.g. consuming any plant tissue) to specialist pollen collectors and/or strictly nectarivores (Inouye 1980, Frame 2003, McCall & Irwin 2006).

Overall, pollinators and florivores forage by the same nutritional resources, such as pollen and nectar, while florivores may also feed on non-reproductive floral tissues without providing any pollination service (Strauss & Irwin 2004). As flowers demand high-energy investments for their production and maintenance (Roddy 2019), and because flowers are intrinsically related to reproduction, florivores can ultimate interfere with plant female and/or male reproductive success. The consequences of florivory for plant reproduction might be mediated by direct or indirect effects, in which direct effects are those originated by the direct consumption of flower structures, while indirect effects are mainly driven by a decrease in floral attractiveness for pollinators after florivore attacks (Bronstein et al. 2007, Jones & Agrawal 2017). The possible outcomes of florivory are mainly dependent upon the amount and intensity of floral damage, and overall negative to plant fitness components (Moreira et al. 2019, Irwin 2010, Navarro & Medel 2009, Irwin et al. 2001, Mothershead & Marquis 2000).

The floral attributes and investments in advertisement exhibited by a given plant species are the result of distinct selective forces between mutualistic pollinators, environmental conditions and floral antagonists (Strauss & Whittall 2006, Roddy et al. 2021). The relationship between floral advertisement and pollinator visits is relatively well documented. For instance, greater flower numbers have been related with increasing in pollinator visitation rates and, consequently greater fruit production (Brody & Mitchell 1997, Thompson 2001, Harder & Johnson 2005, Delmas et al. 2014). Likewise, larger flowers have also been associated with greater advertisements to pollinators, with a subsequent increase in cross-pollination and reproductive success gains (Galen 1996, Kudoh & Whigham 1998, Aigner 2005, Teixido & Valladares 2014). Long-lived flowers have shown to promote greater pollen transfer/reception resulting in increased pollinator visitation (Arista & Ortiz 2007). Concomitantly, greater flower numbers and floral size have also been reported to intensify the presence of florivores (Galen 1999, Teixido et al. 2011, Ruane et al. 2014), or favoring the incidence of nectar and pollen robbers (Irwin & Brody 1998, Wang et al. 2013, Lobo et al. 2016).

Despite of the importance of florivory in angiosperm reproduction and maintenance in different ecosystems, just until recently pollination ecologists and entomologists have increased efforts to understand florivory mechanisms, consequences and dynamics. From an evolutionary perspective, both florivores and robbers can exert negative selective pressures on the same floral attributes selected positively by pollinators (Irwin et al. 2001, 2010, Strauss & Whittall 2006, Castro et al. 2008, Wang et al. 2013). In this way, an integrative approach of environmental conditions and biotic -mutualists and antagonist- partners can significantly improve the understanding of selective pressures on floral advertisement and, ultimately flower evolution (Strauss & Irwin 2004, Strauss & Whittall, 2006). Notwithstanding, the combined effects of selection mediated by the environment, pollinators and florivores still remains unstudied and deserve more attention (Irwin 2006, Wang et al. 2013), especially in face of the threats imposed by global change, which is of particular importance in tropical communities.

Campo rupestre encompass an ancient biodiversity hotspot which provides important ecosystem services, especially regarding water and food security for about 25 million people (Neves et al. 2016). In spite of its importance *campo rupestre* is under high anthropic disturbances, inadequate conservation policies and exotic species invasion (Silveira et al. 2016, Fernandes et al. 2020). Particularly, *campo rupestre* landscapes face radical changes in land use due mainly to mining activities and urban expansion (Fernandes et al. 2016). Indeed, a predictive critical scenario estimates that 82% of *campo rupestre* areas may be lost in the near future (Fernandes et al. 2018). The aim of this study was to address the floral herbivory exerted by insect florivores in a *campo rupestre* plant community. By focusing on flower attributes and plant investments in floral advertisement, we expected to unveil insect florivores behavior, intensity, and subsequently, to quantify florivory in different plant phenology stages (pre-anthesis floral buds, open flowers and early-stage fruits) to detect the trends and mechanisms of floral herbivory in this speciose ecosystem. Furthermore, we tested the variation of florivory along an environmental gradient determined by changes in the elevation.

This project was started in January 2017 and the samplings were carried out betrween May 2018 and August 2019. Thirty fixed plots were set within the areas of the Long-Term Ecological Research of Serra do Cipó LTER-CRSC, CNPq/Fapemig (PELD in portuguese abbreviation) at Serra do Cipó, southeastern, Brazil. As the region is characterized by vegetation mosaics, all plots were set in rocky outrcops and avoiding Atlantic forest patches (capão de mata), gallery forests and/or Poaceae grasslands. This thesis is divided in two chapters; the first one reports the damages exerted by insect floral antagonists in the *campo rupestre* plant community, describing the nature of this plant-insect interaction and their relationship with some flower attributes (i.e. corolla shape, flower symmetry, floral rewards), and with plant advertisements to attract floral visitors (i. e. flower number, flower size and flowering period). In the second chapter we focused on the variation of damages by floral antagonists in space (elevation) and time (months of the year) during the 14-month samplings. Furthermore, the variation between damages by floral antagonists and plant investments in flower attraction were also addressed in this mountaintop ecosystem.

CHAPTER 1

Florivory in a biodiversity hotspot: trends, mechanisms and floral damages.

Gélvez-Zúñiga I, Novais S, Santiago JC, Quesada M, Fernandes GW.

Keywords: *campo rupestre*, floral attributes, floral damages, florivore insects, flower advertisement, insect-plant interactions.

Introduction:

Interactions between insects and plants are long-standing associations and the evolutionary history of both groups is intimately related in practically. Fossil insect-plant relationships include early herbivory records (c.a. 420-385Ma) and the effects of pollinators in angiosperm radiation (ca. 125-90Ma) (Labandeira 2013). Such relationships may encompass interactions ranging from mutualisms such as pollination, neutral such as commensalism, to antagonisms like herbivory (Labandeira 2002). Pollination is a widely documented interaction which may involve obligate mutualism specialists, where a single species pollinates one plant species only, to facultative generalists, in which a broad range of floral visitors offers pollination services to the same plant species (Ollerton et al. 2007). About 85% of angiosperms are pollinated by biotic vectors, and in the tropics this number can rise up to 94%, which matches with a higher frequency of specialized pollination systems in tropical plant communities (Ollerton et al. 2011). Therefore, biotic pollination is a major factor related with the diversification of plant and animal groups (Dodd et al. 1999, Ollerton et al. 2019). In addition, antagonist insect-plant interactions such as herbivory of vegetative tissues are also relatively well documented in most terrestrial habitats, reporting several impacts of herbivores in plant distribution, growth, defense strategies and fitness consequences (Kozlov et al. 2015, Mendes et al. 2021). However, an essential phenomenon such as floral herbivory and the consequences of flower consumption to plant are still poorly explored (McCall & Irwin 2006), but see meta-analysis by González-Browne et al. (2016).

There are evidences of insect feeding on plant reproductive spores in natural systems since the late Silurian (approx. 434-444Ma) (Frame 2003), which suggests that the phenomenon of florivory might be as extended as leaf herbivory (Strauss et al. 2004, McCall & Karban 2006). In addition, florivores are found in many insect orders and it may encompass several food preferences and strategies, including species from opportunistic consumers of floral tissues to obligatory feeding on flower structures (i.e. pollenivores) (Ehrlich & Raven 1964, McCall & Karban 2006). Also, it is plausible that florivore insects may equal or even exceed in number the pollinators as floral visitors, at least whe considering general pollination systems (Frame 2003, Ollerton et al. 2007). Ecologically, florivory can comprise consequences connected to both herbivory and pollination. Plant reproduction, pollination success, plant investments in floral advertisement, and ultimately, flower evolution might be, at least partially, mediated by florivores (McCall & Irwin 2006, Caruso et al. 2019). Hence, florivory may encompass different outcomes linked to the dynamics of plant communities, making essential the understanding of florivory patterns and mechanisms behind the insects who feed on flower tissues.

The consequences of florivory in plant reproduction may result in two overall outcomes: i) direct trophic effects on gamete production or maturation affecting male and female plant fitness (Krupnick & Weis 1999, Canela & Sazima 2003); and ii) indirect non-trophic effects which may decrease the quality and quantity of floral attributes, reducing plant attractiveness to pollinators (Krupnick et al. 1999, Mothershead & Marquis 2000). As any other biotic relationship, florivory is a highly context dependent interaction. Since florivore insects harm floral structures they can reduce flower resource quality, thus interfering in the competition for pollinators with co-flowered individuals (Canela & Sazima 2003). Also, florivory may affect pollen supply for cross-pollination which can be critical in limited-pollen communities, or for anemophylous species (Bertness & Shumway 1992). Besides the plant biomass removal naturally by floral antagonists, florivory can alter plant source–sink dynamics induced by physiological changes in the damaged flowers (Krupnick & Weis 1999, Hargreaves et al. 2009, Irwin et al. 2010). Despite its relevance for plant reproductive success, there are some limitations when quantifying florivory due to the ephemeral nature of flowers. Also, because florivores usually exploit simultaneously and/or sequentially floral advertisement structures (petals and sepals) and gamete-bearing organs (carpels, anthers) (Riba-Hernández & Stoner 2005). Finally, in response to insect herbivory, plants may overcompensate by increasing flower advertisement investments in new flowers or re-allocating resources to recent sired ovules, challenging to quantify the direct and indirect effects of florivory separately (Garcia & Eubanks 2019).

Plants which relay in pollination have developed strategies to attract floral visitors and enhance partners' attraction, and these strategies involve investments in floral attributes and reward advertising either between species and/or within individuals (Ashman & Morgan 2004). Pollinators are widely known for exerting positive selective pressures on floral advertisement attributes such as greater flower number, larger floral size, higher nectar concentration (Barrett & Harder 1996, Fenster et al. 2004). On the other hand, as florivore insects usually forage for the same floral resources than pollinators, florivory can neutralize pollinator positive selection by exerting negative impacts on attributes such flower number, size, and floral reward (Strauss et al. 1996, Lehtilä & Strauss 1997, Barber et al. 2011, Moreira et al. 2019). Therefore, those attraction attributes are predictable to undergo opposing selection pressures mediated by florivore effects (reviewed by Strauss & Whittall 2006), ultimately affecting negatively plant fitness (Bronstein et al. 2007, Jones & Agrawal 2017). Investments in larger flowers with open corollas, greater floral number production, and many-flowered pollination units have been linked to greater attraction of both pollinators and insect florivores (Cunningham 1995, Galen & Butchart 2003, Ashman et al. 2004, reviewed by Strauss & Whittall 2006). Conflicting selection on flower color has been reported since both pollinators and herbivores have shown preferences for flowers with lower anthocyanin content (Strauss et al. 2004) or different color morphs (McCall et al. 2013). Florivory may diminish plant attraction to pollinators due to lower flower production induced in individuals with greater florivory levels (Jones & Agrawal 2017).

The ancient *campo rupestre* (rupestrian grassland) ecosystem harbor a great biological diversity and endemism rates in South America (reviewed in Fernandes 2016, Silveira et al. 2019). Organisms that inhabit these remarkable environments are highly adapted to the harsh climate conditions, soil-nutrient deficits and dispersion limitation (Fernandes et al. 2018). Flowering plants of *campo rupestre* are predominantly wind or bee pollinated (Jacobi & Carmo 2011, Monteiro et al. 2021), however, the role and effects of antagonist flower visitors remains poorly explored (Guerra et al. 2016) but see Jacobi & Antonini (2008) and Gélvez-Zúñiga et al. (2018a). More than 6,000 plant species were recorded in this mountain ecosystem, perhaps regarded as the hottest biodiversity hotspot in South America, given the increasing threats (Fernandes et al. 2020). This study, for the first time, addressed the patterns and the intensity of floral antagonists and its relationship with flower morphology and advertisement attributes in a speciose mountaintop plant community. We hypothesized that less restrictive floral attributes and plant investments in flower advertisement will prompt damages by florivore insects by favoring flower visitors to access floral rewards. We predicted that type of antagonist damage, number of floral buds, flowers and early-stage fruits with signs of florivore attack, and levels of petal removal would be greater in: i) flowers with open corolla shapes; ii) nectar producing flowers; iii) radial symmetry flowers; iv) solitary pollination units; and, v) species with diurnal anthesis. Additionally, we tested whether the greater plant investments in flower advertisement increases damage by insects on the flowers. We expected to find a greater presence of florivory, number of flowers with signs of florivore attack, and levels of petal removal in; i) individuals with lower number of open flowers; ii) species with larger flowers; and iii) species with longer flowering periods.

Material and Methods:

Study area

This study was conducted in Serra do Cipó located in the southern part of the Espinhaço mountain range, Minas Gerais, Brazil. Sampling events were carried out montly May 2018 and August 2019, totalizing 14 campains (**Fig. 1A**). This mountain range harbor vegetation mosaics including quartzitic and ferruginous rocky outcrops, rocky and sandy grasslands, Atlantic Forest patches, gallery forests, while at lower elevations (~800 m. a.s.l.) the vegetation is dominated by Cerrado (savanna) (Fernandes et al. 2016). *Campo rupestre* is a fire-prone vegetation, with seasonal water deficit, and shallow, sandy, and nutrient impoverished soils (Fernandes 2016). The climate is humid subtropical, with wet warm summers (November-January) and dry cold winters (May to September). From February to April there is a post-rain period, while post-dry period occurs in October (Madeira & Fernandes 1999). In general, flowers and fruits are produced along the year in this plant community, with a slightly flowering peak between February-May, and the fruiting season occurring mainly from June to September (Madeira & Fernandes 1999, Belo et al. 2013, Rocha et al. 2016). The Angiosperm families Asteraceae, Melastomataceae, and Fabaceae are the most species-rich families, while at the genus level Velloziaceae and Xyridaceae are particularly well represented (Mota et al. 2018). In this megadiverse ancient ecosystem, where species face distribution constraints and several are threatened (Fernandes et al. 2020), many genera are endemic and/or reach their highest diversity (Rapini et al. 2008, Silveira et al. 2016). Despite the remarkable biodiversity, *campo rupestre* faces high disturbances caused by mining, fire encouraged by the cattle industry, biological invasion, harvesting of endemic ornamental plants, uncontrolled tourism and urban expansion, and eucalypt plantations (Kolbek & Alves 2008, Fernandes et al. 2018). Although its recognition as a conservation priority area in Brazil, strict protection conservation units are poorly consolidated and, together with permissive policy for natural resources exploitation, these areas are at imminent disappearance risk in the near future (e.g., Barbosa & Fernandes 2016, Pena et al. 2017, Fernandes et al. 2020, Hoffman et al. 2020).

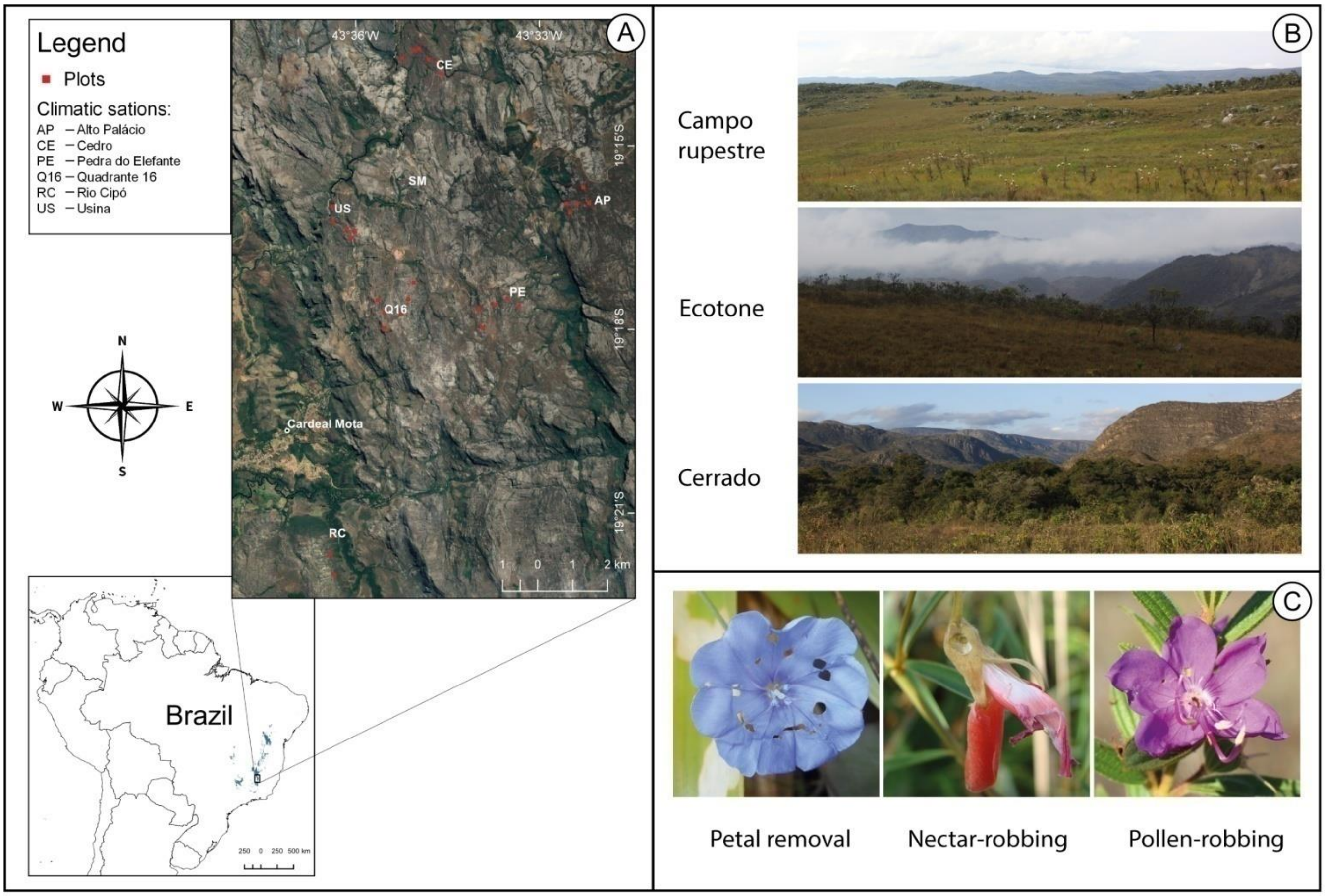


Figure 1. Study area location in the Espinhaço mountain range within the long-term ecological research site Serra do Cipó (LTER-CRSC), southeastern Brazil. Samplings occurred monthly between May 2018 and August 2019 in thirty plots. a) Area map and details of the plot location sampled to record floral damages exerted by insects; b) the three dominant vegetation types where the plots were set along the LTER-CRSC landscape; c) types of damages exerted by floral antagonists recorded to quantify the proportion of attack flowers.

Sampling

Antagonist damage type and presence of florivory

To address the intensity and damages exerted by florivore insects we sampled all the flowering plants in thirty fixed plots (15 × 15m), approximately 500 m apart from each other, distributed along the Serra do Cipó, ranging from 823 to 1411 m.a.s.l., during 14 months (**Fig. 1a,**

b). In each plot, all the flowering individuals were recorded and the number of open flowers, pre-anthesis floral buds, and early stage fruits with damages by antagonists was quantified. Up to ten individuals from the same plant species were registered in every plot, and the following response variables were recorded to account for insect florivory: i) the antagonist damage type (florivory, robbery or none); ii) the presence of florivory; iii) the proportion of damages present on open flowers (hereafter attacked flower), pre-anthesis floral buds (hereafter attacked bud), and early stage fruits (hereafter attacked fruit) per plant individual; and iv) the level of petal removal (hereafter removal level) of each attacked flower. Damages were considered florivory if flowers exhibited any harm to its structures as a result of insect foraging on tissues, nectar and/or pollen according to McCall & Irwin (2006). For the antagonist damage type variable, we divided robbing and florivory damages to estimate the frequency of each behavior in the plant community. Nectar-robbing was considered as any perianth holes present on flowers resulting from illegitimate nectar foraging, while pollen-robbing was considered as any anther removal according to Inouye (1980) and McCall & Irwin (2006) (**Fig. 1c**). Petal removal levels were visually estimated for every damaged flower in plant individuals and it represents the proportion (0 to 1) of the total area removed from the corolla by florivores on every attacked flower.

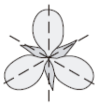
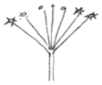
Proportion of florivory, floral attributes and floral advertisement

To test if less restrictive flowers favor florivory damages and levels, the reward offered by flowers and five morphological attributes related to flower visitation (corolla shape, symmetry, pollination unit, corolla color, and time of anthesis) related to flower visitation were recorded for each plant species sampled (**Table 1**). The type of reward (nectar, pollen, or oil) of each plant species was categorized based on field observations and/or literature searching. The corolla shapes were grouped into three categories according to reproductive structures exposure and/or openly disposed to collect rewards; Close, Intermediate, and Open (modified from Faegri & Pijl 1979, and Simpson 2019). The flower symmetry was categorized as actinomorphic, asymmetric or zygomorphic to assess if radial symmetry flowers are more attacked by florivores. The pollination units were categorized as solitary flowers or inflorescences. The anthesis period for each plant species was recorded to test if diurnal species are more attacked by florivores than crepuscular and/or nocturnal ones. Finally, to test if the prevailing corolla color to human vision (hereafter corolla color) influences florivory, colors were classified as greenish, orange, red, rose, violet (including blue), white, and yellow (Kearns & Inouye 1993, adapted from Machado & Lopes 2004).

To address if greater floral attractivity investments influence the presence of florivore insects and signs of petal removal, the total number of open flowers (hereafter flower number) per individual, the species flower size (hereafter flower size), and the amount of months each plant species flowered during the sampling period (hereafter flowering period) for every species found in plots were recorded. The flower number was quantified by the total number of open flowers (counting both attacked or not by florivores) on each plant individual per plot (N=30) on each sampling event (N=14). Flower size was categorized as small (less than 10 mm), medium (between 10-20 mm), large (between 20-30 mm), and very large (more than 30 mm) (adapted from Machado & Lopes 2004) (**Table 1**). Finally, the total number of months in which each sampled plant species showed open flowers during the sampling (hereafter flowering period) was recorded.

Table 1. Flower morphology and plant advertisement attributes registered for each plant species to assess the presence of insect floral antagonists in a *campo rupestre* plant community, southeastern, Brazil. Samplings between May 2018 and August 2019.

Floral attributes

Floral reward	Nectar			Oil		Pollen		
Corolla shape	Open	Brush Campanulate Coronate Cruciate Disk Infundibular Ligulate Rotate	Intermediate	Bilabiate Salverform Tubular Unguiculate	Close	Cuculate Gullet Papilionaceus Spurred Urceolate		
Flower symmetry	Actinomorphic		Asymmetric		Zygomorphic			
Pollination unit	Solitary		Inflorescence					
Time of anthesis	Diurnal	Crepuscular	Nocturnal					
Corolla color	Yellow	Orange	Red	Violet	Rose	White	Greenish	
Flower size (mm)	Small	<10	Medium	10-20	Large	20-30	Very large	>30

All insects found on flowers during the sampling on plots were observed to categorize their behavior, and then collected and preserved for later identification. Each insect was classified according to its functionality as potential pollinator (Fenster et al. 2004), florivore (McCall & Irwin 2006), robber, or thieve (Inouye 1980); for species that exhibit more than one behavior, all were recorded. When contacting both female and male reproductive structures while visiting flowers, the insect was considered as a potential pollinator. Florivores were considered insects that harm flowers and/or floral buds when chewing floral structures (i.e. bracts, sepals, petals, stamens or stigmas) as described in McCall & Irwin (2006). Robbers are visitors which produce holes in floral structures when removing nectar without providing pollination services (Inouye 1980, Irwin et al. 2001), while thieves forage for pollen or nectar without causing any morphological harm to flowers (sensu Inouye 1980; adapted from Irwin et al. 2010), but again without contributing to plant reproduction. Insects and plant material were collected, preserved and processed following standard techniques, and are provisionally in the Laboratório de Ecologia Evolutiva e Biodiversidade from the Federal University of Minas Gerais waiting for cataloging process in the Federal University of Minas Gerais Herbarium (BHCB) and the Taxonomic Collections Center (CCT-UFMG). Some insect specimens were donated to specialist taxonomists as counterparts for taxonomic identifications (see Acknowledgments).

Data analyses

To test if less restrictive floral attributes and flower advertisement investments influence the antagonist damage type variable we performed chi-square tests, in which corolla shape, reward, symmetry, pollination unit, color, and anthesis time, size, flower number, size, and flowering period were used as explanatory variables, and antagonist damage type as response variable. To test the hypothesis that less restrictive floral attributes and greater floral advertisement increase damages by florivore insects, Generalized Linear Mixed Models (GLMMs) were constructed using flower and advertisement attributes (corolla shape, reward, symmetry, pollination unit, color, and anthesis time, size, flower number, size, and flowering period) as explanatory variables and the proportion of floral buds and flowers attacked by florivores as response variables. As plot and sampling events (1 to 14) were repeatedly measured, we considered them as random effects. To test if less restrictive floral attributes and floral advertisement will increase levels of florivory, GLMMs were constructed using level of petal removal as response variable, and flower attributes as explanatory variables. Plot, sampling events and plant individuals we considered as random effects. All GLMMs were fitted using the *'lme4'* package considering a *'Binomial'* error distribution, and for posteriori comparisons the *'lsmeans'* package was used. Analyses were performed using the R software v.4.0.2 (R Development Core Team, 2021).

Results:

We recorded 207 angiosperm species grouped into 46 plant families (**Table S1**). Asteraceae was the most species-rich family with 36 out of the 207 species, followed by Melastomataceae with 25 species, Fabaceae with 22 species, Velloziaceae with 12 species, and Rubiaceae with 11 species. Altogether, these five families were represented by 106 species or 51% of the sampled community. Melastomataceae was the plant family with most abundant number of individuals, exhibiting 21% (2,587 out of 12,430) of total individuals sampled. The following most abundant families in terms of individuals were Asteraceae (15%), Xyridaceae (9.8%), and Malpighiaceae and Lythraceae with 8% each (**Table 2**). Altogether, these five families were represented by 7,727 individuals or 62% of all sampled individuals. Floral attributes are differentially distributed among plant families, and variations in corolla shape (χ^2= 203.33, p<0.001), floral reward (χ^2= 227.28, p<0.001), flower symmetry (χ^2= 177.25, p<0.001), pollination unit (χ^2= 954.19, p<0.001), time of anthesis (χ^2= 106.26, p<0.001), prevailing corolla color (χ^2= 384.23, p<0.001) and flower size (χ^2= 625.77, p<0.001) were detected when comparing the 46 plant families sampled (**Table S2**). Among the most abundant plant families, intermediate corolla shape is the most common and only Xyridaceae family showed solely open corolla flowers. Pollen flowers are present in Melastomataceae, Lythraceae and Fabaceae families, while Asteraceae and Lythraceae showed nectar flowers, and Malpighiaceae showed only oil flowers. These families include species with both actinomorphic and zygomorphic symmetry, but Malpighiaceae family shown only zygomorphic flowers. Asteraceae and Xyridaceae families are the only ones that have only solitary flowers, while the rest of the most abundant plant families show both, solitary flowers and inflorescences. Lastly, the five most abundant plant families have species with diurnal anthesis, with Xyridaceae and Lythraceae having only diurnal anthesis species, while Asteraceae and Malpighiaceae also have some nocturnal and crepuscular species, and Melastomataceae having species with the three types of anthesis.

The floral damages exerted by insects (both florivores and robbers) in the *campo rupestre* plant community comprised 26% (3,232 out of 12,340) of all recorded plant individuals. In terms of flowers, 7% (7548 out of 98386) showed signs of petal removal by florivore insects. The type of damages exerted by florivores more frequently found in the *campo rupestre* plant community are detailed in the **Figure 2**. Melastomataceae family showed 35% of all florivory damages with 1133 out of 3,232 individuals, followed by Lythraceae with 301 (9%), Velloziaceae with 297 (9%), Fabaceae with 294 (9%) and Malpighiaceae with 265 (8%) (**Table 2**). Altogether, these five families represented 70% of all individuals with florivory. Individuals from Bromeliaceae, Erythroxilaceae, Malvaceae, Rhamnaceae, Salicaceae and Solanaceae families did not show any floral damages exerted by insects, and altogether represented 0.3% of the total plant community with just 34 out 12,340 individuals.

Table 2. Proportion of damages exerted by florivores on plants in a *campo rupestre* plant community, southeastern, Brazil. The plant family species richness and abundance, proportion (mean ± SD) of pre-anthesis floral buds, open flowers, early stage fruits, and petal removal.

Family	Richness	Abundance	Floral buds	Open flowers	Early fruits	Petal removal
Acanthaceae	1	177	0.027 ± 0.10	0.108 ± 0.25	0.004 ± 0.039	0.37 ± 0.23
Amaranthaceae	1	140	0	0.040 ± 0.15	0.014 ± 0.119	0.19 ± 0.15
Apocynaceae	3	106	0.057 ± 0.22	0.060 ± 0.22	0	0.38 ± 0.28
Aquifoliace	1	18	0.007 ± 0.03	0.031 ± 0.12	0	0.50 ± 0.33
Asteraceae	36	1858	0.012 ± 0.09	0.049 ± 0.19	0.003 ± 0.049	0.27 ± 0.21
Bignoneaceae	2	19	0.020 ± 0.08	0.403 ± 0.40	0.038 ± 0.162	0.39 ± 0.28
Bromeliaceae	2	19	0.039 ± 0.12	0	0	0
Calophyllaceae	1	54	0.050 ± 0.20	0.352 ± 0.43	0	0.20 ± 0.12
Convolvulaceae	5	233	0.020 ± 0.10	0.162 ± 0.34	0.004 ± 0.037	0.25 ± 0.18
Droseraceae	2	31	0	0.048 ± 0.19	0	0.20 ± 0.10
Ericaceae	4	118	0.038 ± 0.17	0.077 ± 0.18	0.019 ± 0.130	0.29 ± 0.20

Eriocaulaceae	1	10	0	0.100 ± 0.32	0	0.15 ± 0.05
Erythroxilaceae	1	1	0	0	0	0
Euphorbiaceae	1	20	0	0.025 ± 0.11	0.017 ± 0.073	0.50 ± 0.00
Fabaceae	22	828	0.065 ± 0.21	0.207 ± 0.34	0.003 ± 0.048	0.30 ± 0.20
Gentianaceae	3	88	0.019 ± 0.09	0.165 ± 0.34	0.011 ± 0.106	0.32 ± 0.25
Iridaceae	5	80	0.038 ± 0.17	0.144 ± 0.35	0	0.21 ± 0.16
Lamiaceae	4	374	0.017 ± 0.09	0.090 ± 0.23	0	0.24 ± 0.18
Lentibulariaceae	1	17	0	0.235 ± 0.44	0	0.10 ± 0.00
Loganiaceae	2	159	0.035 ± 0.17	0.113 ± 0.28	0	0.29 ± 0.20
Loranthaceae	1	2	0	0 ± 0.00	0	0
Lythraceae	6	996	0.027 ± 0.13	0.148 ± 0.28	0.003 ± 0.055	0.38 ± 0.25
Malpighiaceae	9	1077	0.014 ± 0.09	0.119 ± 0.26	0.007 ± 0.076	0.30 ± 0.22
Malvaceae	1	2	0.048 ± 0.05	0 ± 0.00	0	0
Melastomataceae	25	2587	0.076 ± 0.21	0.275 ± 0.38	0.003 ± 0.052	0.31 ± 0.22
Myrtaceae	3	44	0.023 ± 0.15	0.185 ± 0.36	0	0.32 ± 0.19
Ochnaceae	5	192	0.070 ± 0.20	0.217 ± 0.34	0.001 ± 0.009	0.31 ± 0.23
Onagraceae	1	6	0	0 ± 0.00	0	0
Orchidaceae	7	64	0.031 ± 0.17	0.060 ± 0.23	0	0.29 ± 0.21
Orobanchaceae	5	108	0.042 ± 0.16	0.082 ± 0.23	0.009 ± 0.096	0.30 ± 0.18
Oxalidaceae	1	8	0.258 ± 0.37	0.063 ± 0.18	0	0.10 ± 0.00
Phyllanthaceae	1	80	0.018 ± 0.12	0.042 ± 0.14	0.026 ± 0.119	0.22 ± 0.14
Polygalaceae	2	116	0.007 ± 0.05	0.015 ± 0.11	0	0.13 ± 0.05
Polygonaceae	2	177	0.032 ± 0.12	0.040 ± 0.13	0.022 ± 0.133	0.32 ± 0.20
Rapateaceae	1	5	0	0	0	0
Rhamnaceae	1	10	0	0	0	0

Rubiaceae	11	204	0.016 ± 0.11	0.082 ± 0.21	0.003 ± 0.026	0.29 ± 0.19
Salicaceae	1	1	0	0	0	0
Sapindaceae	2	18	0.056 ± 0.23	0.116 ± 0.21	0	0.20 ± 0.18
Solanaceae	1	1	0	0	0	0
Turneraceae	1	101	0.057 ± 0.18	0.110 ± 0.26	0.030 ± 0.170	0.26 ± 0.15
Velloziaceae	12	479	0.114 ± 0.29	0.560 ± 0.47	0	0.36 ± 0.24
Verbenaceae	3	171	0.008 ± 0.08	0.046 ± 0.17	0	0.30 ± 0.22
Vochysiaceae	2	317	0.080 ± 0.23	0.210 ± 0.36	0.005 ± 0.041	0.48 ± 0.27
Winteraceae	1	15	0.040 ± 0.15	0.033 ± 0.13	0	0.38 ± 0.19
Xyridaceae	4	1209	0.004 ± 0.06	0.063 ± 0.23	0	0.31 ± 0.22
Total	207	12,340	1.463 ± 0.15	4.873 ± 0.22	0.226 ± 0.081	10.69 ± 0.18

Figure 2. Type of damages exerted by florivore insects on plant species in *campo rupestre* between May 2018 and August 2019 at Serra do Cipó, southeastern, Brazil. a) Petal removal in *Pleroma villosissimum* (Melastomataceae), b) petal removal in *Diplusodon lanceolatus* (Lythraceae), c) petal removal and pollen robbing in *Vellozia variabilis* (Velloziaceae), d) petal removal and pollen robbing in *Vellozia epidendroides* (Velloziaceae), e) petal removal in *Vellozia* sp. (Velloziaceae), f) pollen robbing in *Barbacenia blackii* (Velloziaceae), g) petal removal in *Lavoisiera mucorifera* (Melastomataceae), h) ligule removal in *Aspilia foliosa* (Asteraceae), i) petal removal in *Vellozia caruncularis* (Velloziaceae), j) pollen robbing in *Chamaecrista ochnacea* (Fabaceae), k) petal removal in *Banisteriopsis campestris (*Malpighiaceae), and l) petal removal in *Ipomoea procurrens* (Convolvulaceae)**.**

We collected 353 insects on flowers grouped into 10 orders, 31 families and 120 insect morphospecies (**Table 3**). Greater insect abundance and richness were found in the Hymenoptera and Coleoptera orders, with 172 and 152 individuals, and 54 and 51 morphospecies, respectively. Both Coleoptera and Hymenoptera orders represented 92% (324 out of 353) of all insects collected. Florivory was the most common behavior exerted by insect species, representing 43% (145 out of 353), followed by thieving 24% (86), robbery 17% (61), and potential pollinators 12% (43), whereas just 5% of all insect species showed more than one behavior when accessing flowers. As for the most abundant orders, beetles behaved as florivores in 90% of their visits (137 out of 152) (**Fig. 3a**, **b, i, l**), while robbing represented 6%, and thieving (4%) (**Fig. 3f**, **l**). Within hymenopterans, ants behaved more frequently as thieves with 83% of their visits (73 out 88 records) (**Fig. h**), followed by robbery with 14%. Hymenopteran species that showed more than one behavior when visiting flowers were the ant *Camponotus rufipes* Fabricius, 1775 (**Fig. 3g**) which acted as florivore and robber, the bee *Ceratina* sp. that behaved as potential pollinator and thieve, and the bees *Apis mellifera* Linnaeus, 1758, *Augochlora* sp., *Tetrapedia* sp. and *Trigona spinipes* Fabricius, 1793 which performed robbing and potential pollinator visits. Interestingly, bees were the only group that performed all behaviors when visiting flowers with a total of 78 records. Bees acted as potential pollinators in 55% of their visits (43 out of 78), followed by robbing with 22% (17), species with more than one behavior with 20%, while thieving represented 3%. Lastly, the four wasp species collected behaved as robbers. Altogether, Hemiptera (**Fig 3c**), Lepidoptera, Diptera, Orthoptera (**Fig. 3e**, **d**, **k**), Mantodea, Blatodea, Phasmida and Araneae represented 8% (29 out of 353) from all the insects recorded (see details of all insect species in **Table 3)**.

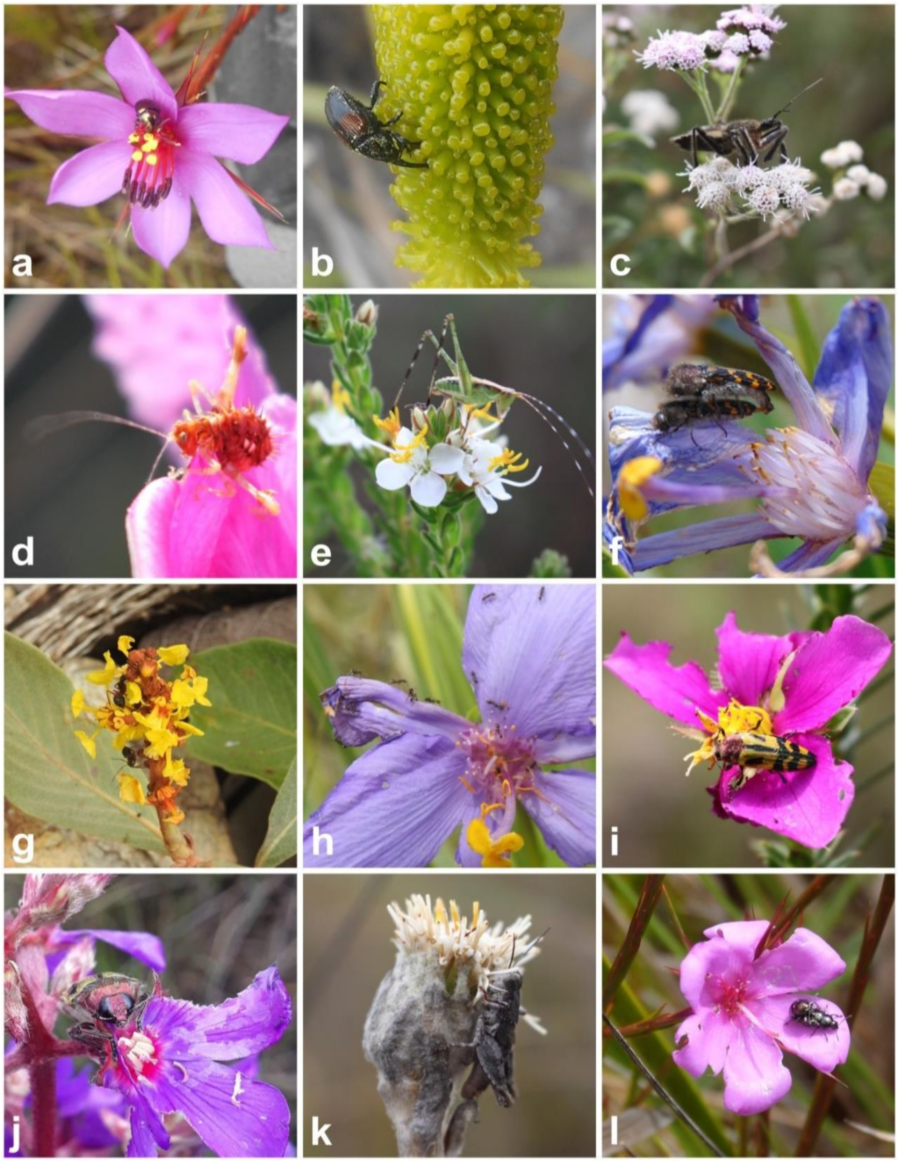


Figure 3. Floral damages exerted by insects when visiting plant species from *campo rupestre* at Serra do Cipó, southern Espinhaço range (Brazil) between May 2018 and August 2019. a) Chrysomelidae beetle behaving as florivore in *Microlicia* sp. (Melastomataceae); b) Curculionidae beetle behaving as florivore in *Barbacenia flava* (Velloziaceae); c) Hemipteran behaving as florivore in *Chromolaena squalida* (Asteraceae); Orthopteran immature behaving as florivore in d) *Kielmeyera regalis* (Calophyllaceae) and e) *Marcetia taxifolia* (Melastomataceae); f) *Lasionata* sp. beetle behaving as thieve in *Vellozia* sp. (Velloziaceae); g) *Camponotus rufipes* behaving as robber in *Heteropterys pteropetala* (Malpighiaceae); h) ant *Linepithema micans* behaving as thieve in *Vellozia variabilis* (Velloziaceae); i) *Conognatha compta* beetle behaving as florivore in *Lavoisiera* sp. (Melastomataceae); j) *Hyperantha* sp. beetle behaving as florivore in *Pleroma heteromallum* (Melastomataceae); k) Orthopteran behaving as florivore in *Richterago* sp. (Asteraceae); l) Chrysomelidae beetle behaving as thieve in *Microlicia* sp. (Melastomataceae).

Table 3. Insects behaving as floral antagonists and/or potential pollinators when visiting plant species from *campo rupestre* at Serra do Cipó, southern Espinhaço range (Brazil) between May 2018 and August 2019. Behavior (Flo: florivore, Pol: potential pollinator, Rob: nectar-robber, Thi: flower thieve), Plants: number of sampled plant species visited, floral Reward (N: nectar, O: oil, P: pollen, T: floral tissue).

Group	**Behaviour**	**Species**	**Abund.**	**Plants**	**Reward**
Ant	Flo-Rob-Thi	*Camponotus rufipes* Fabricius, 1775	19	10	N-P-T
Ant	Rob-Thi	*Camponotus crassus* Mayr, 1862	6	5	P-T
Ant	Rob-Thi	*Cephalotes pusillus* Klug, 1824	12	7	P-T
Ant	Rob-Thi	*Dorymeyrmex* sp1	1	1	P-T
Ant	Thi	*Acromyrmex subterraneus* Forel, 1893	1	1	P
Ant	Thi	*Brachymirmex cordemoyi* Forel, 1895	1	1	P
Ant	Thi	*Camponotus melanoticus* Emery, 1894	1	1	N
Ant	Thi	*Camponotus novogranadensis* Mayr, 1870	1	1	N
Ant	Thi	*Camponotus westermanni* Mayr, 1862	1	1	N
Ant	Thi	*Cephalotes minutus* Fabricius, 1804	1	1	P
Ant	Thi	*Crematogaster* sp1	2	2	P
Ant	Thi	*Crematogaster* sp2	1	1	P
Ant	Thi	*Ectatomma brunneum* Smith, F., 1858	4	3	P
Ant	Thi	*Ectatomma tuberculatum* Olivier, 1792	3	3	P
Ant	Thi	*Linepithema micans* Forel, 1908	34	14	N
Bee	Pol	Halictidae sp1	1	1	N
Bee	Pol	*Paratetrapedia* sp.	1	1	N
Bee	Pol	*Trigonopedia* sp.	1	1	N
Bee	Pol	*Anthrenoides* sp.	1	1	N
Bee	Pol	*Augochloropsis multiplex* Vachal, 1903	3	1	N
Bee	Pol	*Augochlora* sp2	1	1	N

Bee	Pol	*Augochlora* sp3	2	2	N
Bee	Pol	*Augochlora* sp4	1	1	N
Bee	Pol	*Augochlora* sp5	1	1	N
Bee	Pol	*Augochloropsis* sp.	2	1	N
Bee	Pol	*Bombus morio* Swederus, 1787	5	3	N
Bee	Pol	*Bombus pauloensis* Friese, 1913	5	3	N
Bee	Pol	*Centris trigonoides* Lepeletier,1841	1	1	N
Bee	Pol	*Ceratina (Crewela)* sp1	2	2	N
Bee	Pol	*Ceratina (Crewela)* sp3	2	2	N
Bee	Pol	*Coelioxys* sp.	1	1	N
Bee	Pol	*Dicranthidium arenarium* Ducke, A. 1907	1	1	N
Bee	Pol	*Lasioglossum* sp1	2	2	N
Bee	Pol	*Monoeca* sp.	1	1	N
Bee	Pol	*Pseudaugochlora graminea* Fabricius, 1804	2	1	N
Bee	Pol	*Xylocopa hirsutissima* Maidl, 1912	1	1	N
Bee	Pol-Rob	*Augochlora* sp1	1	1	N-P
Bee	Pol-Rob	*Trigona spinipes* Fabricius, 1793	9	4	N-P
Bee	Pol-Rob	*Xanthopedia* sp1	2	2	N-P
Bee	Pol-Rob	*Apis mellifera* Linnaeus, 1758	7	14	N-P
Bee	Pol-Rob	*Tetrapedia* sp.	9	5	O-N-P
Bee	Pol-Thi	*Ceratalictus* sp.	6	5	N-P
Bee	Pol-Thi	*Ceratina (Crewela)* sp2	1	1	N-P
Bee	Pol-Thi	*Megachile* sp.	3	1	N-P
Bee	Rob	*Xylocopa nogueirai* Hurd & Moure, 1960	1	1	P
Bee	Rob	*Xylocopa* sp.	1	1	P

Bee	Rob	*Exomalopsis auropilosa* Spinola, M. 1853	1	1	O-P
Bee	Rob	*Lasioglossum* (Dialictus) sp	2	2	P
Beetle	Flo	*Hoplopyga albiventris* Gory & Percheron, 1833	1	1	T
Beetle	Flo	Coccinelidae sp18	5	1	T
Beetle	Flo	Coccinelidae Sp23	1	1	T
Beetle	Flo	Tenebrionidae sp24	1	1	T
Beetle	Flo	*Astylus* sp35	2	1	T
Beetle	Flo	Chrysomelidae sp1	7	6	T
Beetle	Flo	Chrysomelidae sp10	1	1	T
Beetle	Flo	Chrysomelidae sp11	1	1	T
Beetle	Flo	Chrysomelidae sp12	2	1	T
Beetle	Flo	Chrysomelidae sp13	1	1	T
Beetle	Flo	Chrysomelidae sp14	6	5	T
Beetle	Flo	Chrysomelidae sp15	1	1	T
Beetle	Flo	Chrysomelidae sp16	11	9	T
Beetle	Flo	Chrysomelidae sp17	17	10	T
Beetle	Flo	Chrysomelidae sp19	1	1	T
Beetle	Flo	Chrysomelidae sp20	2	2	T
Beetle	Flo	Chrysomelidae sp21	1	1	T
Beetle	Flo	Chrysomelidae sp22	4	3	T
Beetle	Flo	Chrysomelidae sp3	4	3	T
Beetle	Flo	Chrysomelidae Sp4	1	1	T
Beetle	Flo	Bruchinae sp51	1	1	T
Beetle	Flo	Chrysomelidae sp6	2	2	T
Beetle	Flo	Chrysomelidae sp7	1	1	T

Beetle	Flo	Chrysomelidae sp8	3	3	T
Beetle	Flo	Chrysomelidae sp9	4	4	T
Beetle	Flo	*Agrilus* sp	7	3	T
Beetle	Flo	*Agrilus* sp2	1	1	T
Beetle	Flo-Thi	*Conognatha compta* Pery, 1830	7	6	N-T
Beetle	Thi	*Conognatha macleayi* Donovan, 1825	1	1	P
Beetle	Thi	*Hyperantha* sp27	1	1	P
Beetle	Thi	*Lampetis rudicollis* Gory, 1840	1	1	P
Beetle	Thi	*Lasionata* sp26	1	1	P
Beetle	Flo	*Chauliognathus tixieri* Pic, 1948	1	1	T
Beetle	Flo-Thi	*Chauliognathus steinbachi* Pic, 1930	11	8	N-T
Blattodea	Flo	Blattidae sp71	1	1	T
Crab spider	Thi	*Xysticus* sp.	1	1	P
Cricket	Flo	Tettigoniidae nymph	1	3	T
Cricket	Flo	Acrididae nymph	1	1	T
Fly	Thi-Rob	*Euxesta* sp.	3	3	N
Fly	Thi	*Pseudodorus clavatus* Fabricius, 1794	1	1	N
Fly	Thi	*Simulium* sp.	1	1	N
Hemipteran	Rob	*Chariesterus* sp.	1	1	N
Hemipteran	Rob	Coreidae sp54	2	2	N
Hemipteran	Rob	Coreidae sp55	1	1	N
Hemipteran	Rob	Coreidae sp56	1	1	N
Hemipteran	Rob	Alydidae sp57	1	1	N
Hemipteran	Rob	Hemiptera nymph	1	1	N
Hemipteran	Rob	Alydidae sp60	1	1	N

Hemipteran	Thi	*Aphis* sp.	1	1	N
Lepidoptera	Flo	*Leucanella* sp.	4	4	T
Lepidoptera	Thi	*Danaus gilippus* Cramer, 1776	1	1	N
Lepidoptera	Thi	*Parides bunichus* Boisduval, 1836	1	1	N
Mantid	Rob	Acontistidae sp.	2	2	T
Phasmid	Rob	*Ceroys* sp.	1	1	T
Wasp	Rob	*Ammophila* sp.	1	1	N-P
Wasp	Rob	*Campsomeris ianthina* Bradley, 1945	1	1	N-P
Wasp	Rob	*Polybia ignobilis* Haliday, 1836	1	1	P-T
Wasp	Rob	*Zeta argillaceum* Linnaeus, 1758	1	1	P-T
Wasp	Thi	*Polybia occidentalis* Olivier, 1792	1	1	N-P
Wasp	Thi	*Polybia sericea* Olivier, 1792	1	1	N-P
Weevil	Flo	Baridinae sp41	1	1	T
Weevil	Flo	Baridinae sp43	2	2	T
Weevil	Flo	Baridinae sp44	2	2	T
Weevil	Flo	Baridinae sp45	2	2	T
Weevil	Flo	Baridinae sp46	2	2	T
Weevil	Flo	Entiminae sp39	3	3	T
Weevil	Flo	Curculionidae sp42	1	1	T
Weevil	Flo	Curculionidae sp47	3	2	T
Weevil	Flo	Baridinae sp48	5	5	T
Weevil	Flo	Baridinae sp49	4	3	T
Weevil	Flo	Entiminae sp52	1	1	T
Weevil	Flo	Baridinae sp53	14	10	T

Antagonist damage type and presence of florivory

Florivory represented 94.5% of damages exerted by insects (3,164 out of 3,348), robbery 5.2% (176), and thieving 0.3% (8). As expected in our hypothesis, less restrictive floral attributes such as open corollas, actinomorphic symmetry, solitary pollination units and diurnal anthesis flowers showed greater types of floral damages exerted by insects. In open corolla flowers, florivory accounted for 58% of damages and it was twice as much as intermediate, and 4.2 times greater than in close corollas. Robbery represented 51% of damages in open corolla flowers and was 1.5 times bigger than in intermediate and 2.8 times bigger than in close corollas (χ^2=16.189, N= 12,340, p=0.0033) (**Fig. 4a**). In flowers with actinomorphic symmetry, florivory represented 66% of damages and it was 2.5 times greater than in zygomorphic and 8.2 times greater than in asymmetric flowers (χ^2=99.192, N= 12,340, p <0.001). Robbery accounted for 78% of damages in actinomorphic flowers and it was 4.7 times larger than in zygomorphic and 15.88 times larger than in asymmetric (**Fig. 4b**). In flowers arranged in solitary pollination units, 1,608 out of 3,164 damages were made by florivores, representing 51%. Robbery in solitary flowers was 2.2 times greater than in flowers grouped in inflorescences (χ^2=696.39, N= 12,340, p <0.001) and represented 58% of damages. In flowers with diurnal anthesis florivory damages represented 93% (3,066 out of 3,164) and robbery damages 94% (173 out of 184) when compared to flowers with crepuscular and nocturnal anthesis (χ^2=33.924, N= 12,340, p <0.001). Remarkably, pollen reward flowers showed more types of damages than nectariferous flowers, contrary to expected in the less restrictive flowers hypothesis. Pollen reward flowers showed 58% of damages by florivores and it was 1.8 times greater than in nectariferous flowers, and 6.8 times greater than in oil flowers. Robbery in pollen flowers was 1.3 larger than in nectariferous flowers and 10 times larger than in oil flowers (χ^2=281.48, N= 12,340, p <0.001) (**Fig. 4c**). Lastly, plants with greater investments in floral advertisement showed more types of damages by florivores, as expected. We found that 43% of damages on large and very large flowers were exerted by florivores and it was 1.2 times greater than in medium flowers and 1.9 times greater than in small flowers. Large and very large flowers had 1.2 more robbery damages than medium flowers and 2.8 times more robbery than small flowers (χ^2=394.62, N= 12,340, p <0.001) (**Fig. 4d**). Greater flowering periods favored florivory damages since species that flowered during up to 10 to 14 months showed 71% (2,240 out of 3,164) of florivory damages and 70% (129 out of 184) of robbery damages (χ^2=466.57, N= 12,340, p <0.001).

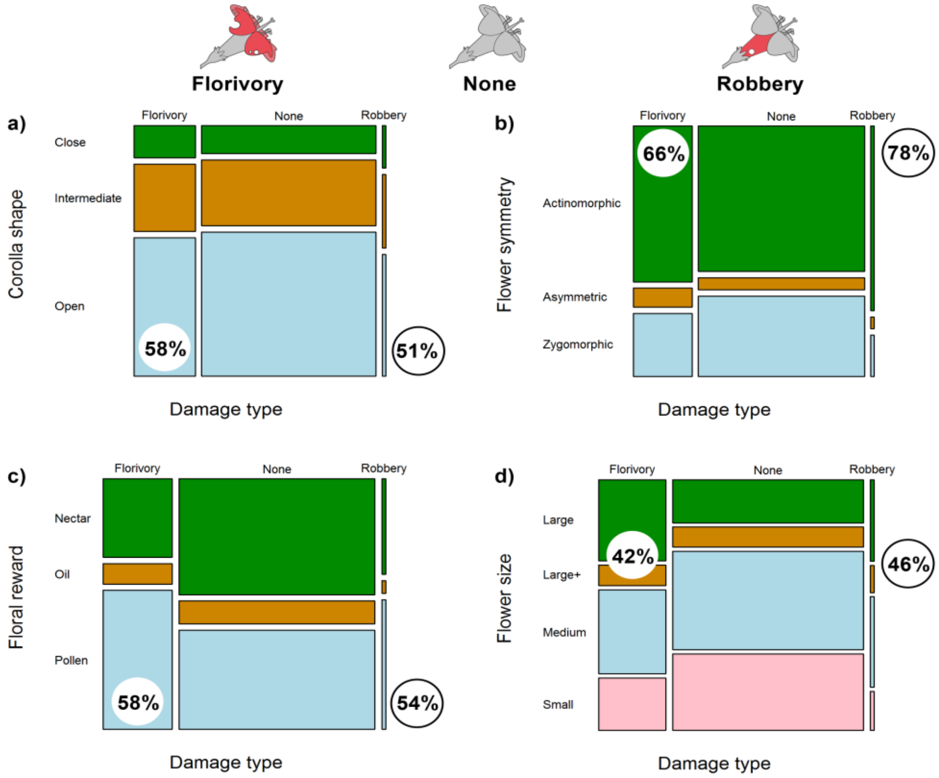


Figure 4. Incidences and types of floral damages exerted by insects recorded between May/18 and August/19 in thirty *campo rupestre* vegetation plots at Serra do Cipó, Minas Gerais, Brazil. a) Corolla shape (modified from Faegri & Pijl 1979); b) type of flower symmetry; c) type of floral reward; d) overall flower size, small (<10 mm), medium (10-20 mm), large (20-30 mm), very large (>30 mm)).

Proportion of florivory, floral attributes and floral advertisement

The proportion of flowers attacked was greater in solitary pollination units than inflorescences (χ^2=462.75, p <0.001, **Fig.5a)**. Species with diurnal anthesis also showed greater flower attack when compared to nocturnal anthesis, but there was no difference of flower attack between crepuscular and diurnal species (χ^2=28.763, p <0.001, **Table 3**). Contrary to the expected in the less restrictive floral attributes hypothesis, the proportion of attacked flowers showed no differences between open and close corollas and there were both higher than in intermediate corolla flowers (**Fig. 5d, Table 3**). Nectariferous flowers were less attacked than pollen flowers and the roportion of flower attack was no different between nectarifeorus and oil-producing flowers (**Table 3**). Also, the actinomorphic flower symmetry showing greater flower attack prediction was not confirmed since the greater proportion of attack was on asymmetric flowers.

However, actinomorphic flowers suffered greater flower attack when compared only to zygomorphic symmetry (χ^2=109.63, p<0.001). The greater flower attack on plants with higher investments in floral advertisement hypothesis was partially corroborate for flower size since large flowers showed greater flower attack than medium and small flowers, but very large flowers showed smaller attack than large flowers (χ^2=469.74, p<0.001) (**Table 4**). Plant species with longer flowering period showed slightly greater flower attack proportion as expected in the flower investment hypothesis (**Fig. 5b**). Finally, the proportion of flowers attacked by florivores slightly diminished in individuals with greater floral numbers (**Fig. 5c**, **Table 4**).

Flowers arranged in solitary pollination units showed greater proportion of buds attacked by florivores when compared to flowers grouped in inflorescences (χ^2=84.541, p<0.001). Also, differences in the proportion of floral bud attack was not detected for species with actinomorphic and asymmetric; however, both showed higher attack than zygomorphic flowers (χ^2=38.272, p<0.001, **Fig. 6a)**. Contrary to expected in the less restrictive flowers hypothesis, a greater proportion of floral bud attack was found in pollen flowers when compared to nectarifeorus and oil-producing flowers (χ^2=66.002, p<0.001, **Fig. 6b**). Moreover, plant species with crepuscular anthesis showed greater proportion of floral bud attack (**Fig. 6c**), and species with diurnal and nocturnal show no differences in floral bud attack (see comparisons in **Table 3**). The greater floral bud attack in plants with higher floral advertisement prediction was confirmed only for flower size. Small flowers had a lower proportion of floral bud attack (**Fig. 6d**). Medium and very large flowers showed no differences in terms of attacked floral buds, and large flowers were the most targeted by insect florivores (χ^2=79.549, p< 0.001, see comparisons in **Table 4**). Contrary to expected for floral advertisement, greater flower numbers resulted in a slightly decrease of floral buds attacked (χ^2=61.392, p< 0.001). Plant species flowering period was not statistically different in terms of floral buds attacked by insect florivores (p=0.07952, **Table 4**). Interestingly, proportion of early stage fruits attacked by florivores showed no differences for morphological attributes (pollination unit p=0.3367), nor floral advertisement (flowering period p=0.8126, flower number p=0.1491).

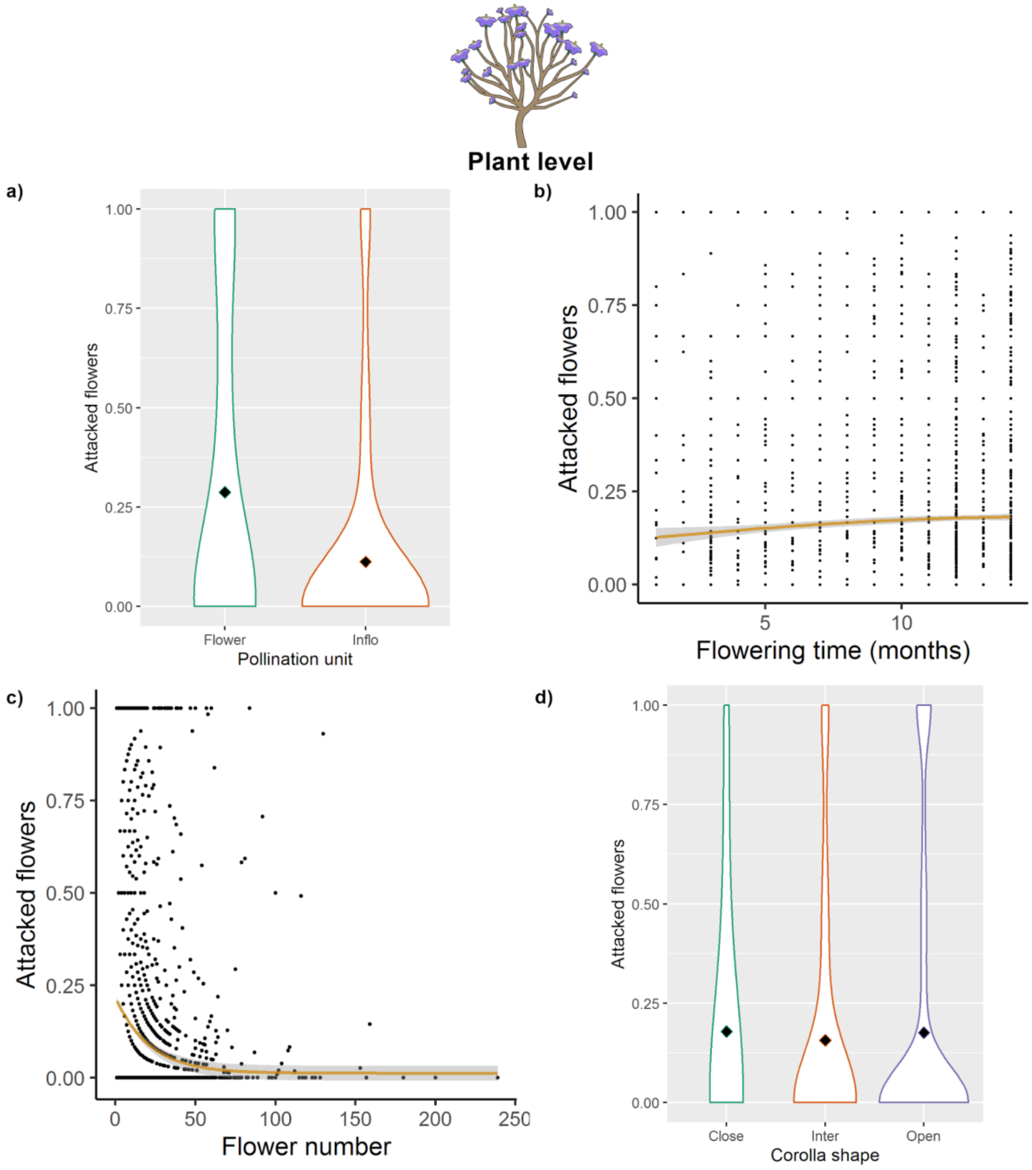


Figure 5. Proportion of open flowers attacked by florivore insects in *campo rupestre* vegetation, southeastern Brazil. a) Flowers arragned in solitary flowers (Flower) or inflorescences (Inflo); b) number of months each species flowered during sampling events; c) total number of open flowers per plant individual; d) Corollas with Close, intermediate (Inter) or Open shapes (modified from Faegri & Pijl 1979). The diamonds represent the mean value of each sample.

Table 4. Results of Generalized Linear Mixed Models showing the effect of flower morphological attributes and reward on the proportion of flowers attacked, proportion of pre-anthesis floral buds attacked and petal removal levels exerted by florivore insects in Serra do Cipó, between May 2018 and August 2019.

Response variable	**Explanatory variable**	**Random factors**	**Error distribution**	**χ2**	**AIC**	**p-value**	**Comparison**
Attacked flowers	Corolla shape	Plot & sampling event	Binomial	16.541	9033.9	0.000256	Close = Open > Int
	Floral reward			175.04	8875.4	< 0.001	Pollen > Nectar = Oil
	Flower symmetry			109.63	8940.8	< 0.001	Assy > Acti > Zigo
	Pollination unit			462.75	8585.7	< 0.001	Flor > Inflo
	Color			247.66	8810.8	< 0.001	(Ro = Vio = Ora = Red = Ye) > Whi = Gre
	Anthesis			28.763	9021.7	< 0.001	Crep = Diur > Noct
	Plant family			1156.7	7979.8	< 0.001	NA
Attacked floral buds	Floral reward	Plot & sampling event	Binomial	66.002	2601.3	< 0.001	P > N > O
	Flower symmetry			38.272	2629	< 0.001	(Assy = Acti) > Zigo
	Pollination unit			84.541	2580.7	< 0.001	Flor > Inflo
	Anthesis			16.974	2650.3	< 0.001	Crep > (Diur = Noct)
	Plant family			287.01	2879	< 0.001	NA
Attacked early fruits	Pollination unit	Plot & sampling event				0.3367	
	Plant family					0.268	
Petal removal level	Corolla shape	Plot, sampling event & individual	Binomial	24.45	6825.2	< 0.001	Close > Open = Int
	Floral reward			14.707	6835	< 0.001	N > P , O = P
	Flower symmetry			30.994	6818.7	< 0.001	Zigo > Acti, Acti = Assy
	Pollination unit					0.545	
	Color			51.37	6806.3	< 0.001	Y > Ro > Vio > Whi / Red = Gre = Ora = Whi
	Anthesis			15.046	6834.6	< 0.001	Diur > Crep = Noct
	Plant family			227.98	6689.7	< 0.001	NA

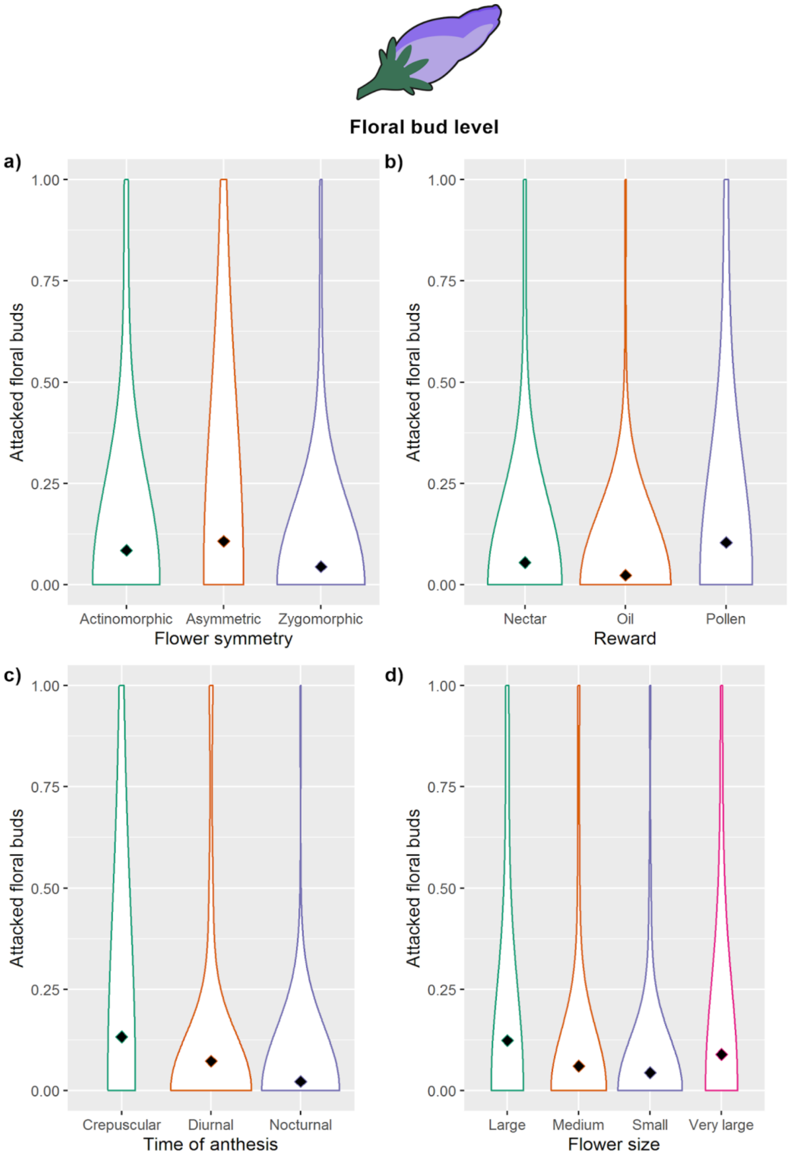


Figure 6. Proportion of pre-anthesis floral buds attacked by florivore insects in *campo rupestre* vegetation, at Serra do Cipó, Brazil. a) type of flower symmetry; b) type of floral reward; c) time of anthesis; d) overall flower size, small (<10 mm), medium (10-20 mm), large (20-30 mm), very large (>30 mm). The diamond represents the mean value of each sample.

Petal removal by florivores

The prediction for greater proportion of petal removal by insects on attacked flowers in less restrictive flowers was confirmed for floral rewards and time of anthesis. Nectariferous flowers showed greatest removal levels than pollen and oil flowers ($\chi^2=14.707$, $p<0.001$, **Table 4**). Species with diurnal anthesis exhibited greater removal levels than crepuscular and nocturnal species ($\chi^2=15.046$, $p<0.001$). The removal levels were not influenced by the pollination unit ($p=0.545$).

Greater removal levels were found in some flower restrictive morphological attributes such as corolla shape and flower symmetry. Flowers with close corollas showed greater removal levels than open and intermediate (χ^2=24.45, p<0.001, **Table 4**). Flowers with zygomorphic symmetry had greater levels of florivory than actinomorphic and asymmetric flowers (χ^2=30.994, p<0.001, see comparisons in **Table 4**). Greater removal levels were found in species with higher investments in flowering period, since a slightly increase of removal levels was detected in species producing flowers for longer periods of time (**Fig. 7a**). The removal levels were not influenced by investments in flower size (p=0.484) and flower number (p=0.1641).

Interestingly, greater petal removal levels were found in yellow corollas, followed by rose and violet (**Fig. 7b**). However, removal level was not different in the rest of corolla colors (see comparisons in **Table 4).** In general, the proportion of attack by florivores and the petal removal level showed no clear pattern for the prevailing corolla color. In open flowers and floral buds, higher attack proportion was found in rose and violet corollas, while greenish and white corollas showed lower attack proportion (χ^2=51.37, p<0.001).

Table 5. Results of Generalized Linear Mixed Models showing the effect of plant investments in floral advertisement on the proportion of attacked flowers, pre-anthesis floral buds, and petal removal exerted by florivore insects in a *campo rupestre* plant community at Serra do Cipó (Brazil), between May 2018 and August 2019.

Response variable	**Explanatory variable**	**Random factors**	**Error distribution**	**Chisq**	**AIC**	**p-value**	**Comparison**
Attacked flowers	Size	Plot & sampling event	Binomial	469.74	8582.7	< 0.001	L > L+ > M > S
	Flowering period		Binomial	49.426	9043.5	0.0262	
	Flower number		Binomial	190.97	8857.5	< 0.001	
Attacked floral buds	Size	Plot & sampling event	Binomial	79.549	2589.7	< 0.001	L > (L+ = M) > S
	Flowering period					0.07952	
	Flower number		Binomial			< 0.001	
Petal removal level	Size	Plot, sampling event & individual				0.484	
	Flowering period		Binomial	39.315	6843.8	0.04739	
	Flower number					0.1641	

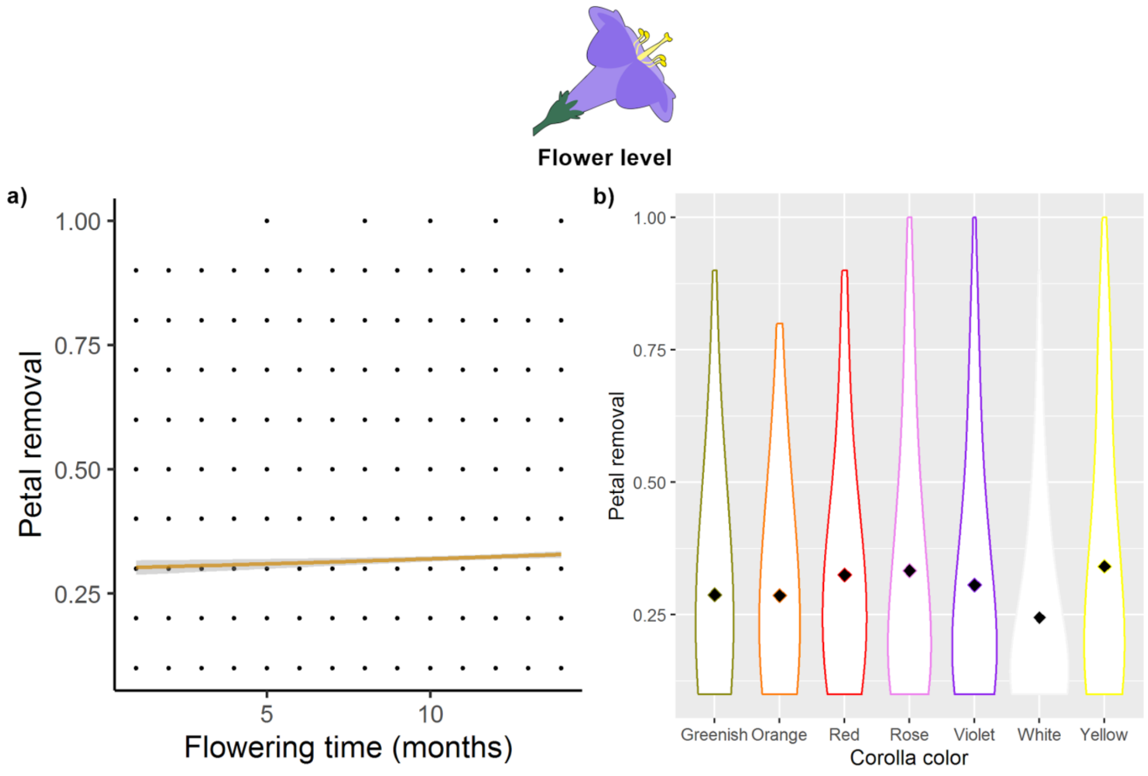


Figure 7. Proportion of petal removal exerted by florivore insects at single flowers in a *campo rupestre* plant community, southeastern, Brazil. a) Number of months each plant species developed flowers; b) prevailing corolla color of each plant species (adapted from Machado & Lopes 2004). The diamond represents the mean value of each sample.

Discussion:

This study provides the first record of damages exerted by florivore insect species in the *campo rupestre* plant community, and their relationship with floral attributes and flower advertisement to visitors. Floral damages comprise 26% of the total plant community recorded, and Melastomataceae, Lythraceae, Velloziaceae, Fabaceae, and Malpighiaceae plant families are the most attacked by insect florivores. The 92% of insects feeding on flower structures in *campo rupestre* plants are Coleopterans and Hymenopterans, and 43% of their visits they behave as florivores. We demonstrated that less restrictive floral attributes like diurnal time of anthesis and solitary flowers are indeed more likely to have pre-anthesis floral buds, open flowers and early stage fruits attacked by florivores. We detected that insect florivores are more likely to attack pollen flowers in this plant community, but once a flower is attacked, nectar-rewarded flowers have greater levels of petal removal. In addition, we detected that asymmetric flowers are more likely to be attacked by florivores, but again once a flower is attacked, the greater levels of petal removal are found in zygomorphic flowers. Also, we demonstrated that individuals with fewer numbers of open flowers, species with large flowers, and species which greater flowering period are more prone to be attacked by florivores. Our results strengthen the assumption that the combination of floral attributes exhibited by flowering plants is the result of simultaneous mutualistic and antagonistic plant-insect interactions, and that to disentangle the preferences and effects of antagonist floral visitors is essential to fully understand plant reproductive ecology in speciose ecosystems.

In our study, three out of the five plant families attacked the most by insect florivores, Melastomataceae, Velloziaceae and Fabaceae, are also commonly listed among the most species-rich families in *campo rupestre* plant communities (Silveira et al. 2016, Mota et al. 2018). Although their high abundance and species richness Asteraceae, Rubiaceae and Xyridaceae families showed little proportion of florivory in attacked flowers, pre-anthesis buds, early fruits or petal removal levels in *campo rupestre* plant communities. The overall greater number of flowers produced by these abundant plant families suggests that massive flower production is not entirely related with greater proportions of flower attack and petal removal levels. Simultaneously, floral resources associated with greater attacked by florivores showed to be commonly distributed among the most attacked and abundant plant families. Hence, our results suggest that greater flower quantity may not be the mechanism driving the florivores preferences in the *campo rupestre* plant community.

Moreover, the results also indicate that insect florivore incidence and petal removal levels are not, at least entirely, related with resource concentration of flower resources (Root 1973).

Our results are, to our knowledge, the first broad report of insect florivore frequency, behavior and proportion of petal area removal in speciose plant communities. Synthesis on leaf herbivory reported a global frequency of herbivory signs in 56% of the individuals, and 7% of area removed of background herbivory (Kozlov et al. 2015). However, Turcotte et al. (2014) reported a 5.2% of plant leaf tissue removal by herbivores across vascular, and more recently, Mendes et al. (2021) published a data set including several species from the tropics where the leaf area consumption averaged 5.3%. This numbers suggests that leaf herbivory may play a smaller role in energy and nutrient dynamics than currently thought, at least for several plant species (Turcotte et al 2014, Kozlov et al. 2015, but see Price 1997). Although our results are not as comprehensive or refined as the synthesis available for leaf herbivory, our findings represent a starting point in the path to unraveling how many flowers and floral tissue are insect florivores consuming in speciose neotropical environments. The findings reported here opens an avenue of opportunities to record the effects of these high rates of flower consumption in life time fitness of plants and resulting effects in community assembly and evolution.

From the herbivory perspective, all the insects collected on flowers are categorized as polyphagous herbivores, since they exploited floral rewards and tissues from plant species belonging to different, even phylogenetically distant, families. In fact, our findings support the idea that the same herbivore species rarely feed on plants from more than four botanical families (Bernays & Graham, 1988, Rasmann et al. 2014), since just 9% of the florivore insects species interacted with several plant families. Flower beetles (Chrysomelidae) and weevils (Curculionidae) are very common floral visitors (Frame 2003) and were the most florivore species-rich families found in our study. Flower beetles preferred mostly pollen flowers, while weevils interacted with pollen, nectar and oil rewards. Overall, these beetles consume mainly pollen grains, stamens and corolla structures, and are rarely reported as pollinators (Gottsberger 1990, Corllet 2004). Flower-feeding Chrysomelidae may feed on dipterocarpic leaves between flowering periods, which suggests that they are not entirely dependent on flower resources (Corllet 2004). Despite beetle opportunistic use of flowers resources, plant species visited by these insects showed no relationship with frequently beetle-pollinated flower attributes (i.e. thermogenic inflorescences or stigmatic secretions) (Gottsberger 1990).

Ants from the genus *Camponotus* and *Cephalotes* were the most frequent hymenopterans in nectar and oil flowers, acting mainly as nectar thieves in *campo rupestre* plants. Yet, *Camponotus* ants have been proven to contribute to pollination of *Euphorbia heterophylla* (Euphorbiaceae) and wind-pollinated species in the Himalayan region (Corllet 2004). Also, pollination of *Paepalanthus lundii* by *Camponotus crassus* was recently reported in a Brazilian savanna (Del-Claro et al. 2019). Hence, as *campo rupestre* harbors several wind-pollinated species, especially at higher elevations (Monteiro et al. 2021), and since *Camponotus* ants play crucial roles in ant-plant interactions in these plant communities (Costa et al. 2016), the role of ants visiting flowers, as robbers and pollinators, deserve more attention. Wasp records on flowers are scare but adults often forage for nectar, and some species may even chew the stigma surface when foraging for nectar, leading to a fitness reduction in some Verbenaceae species (Reddy et al. 1992). In *campo rupestre*, Vespidae species have also been recorded as nectar-robbers in the *Collaea cipoensis* endemic legume (Gélvez-Zúñiga et al. 2018b). Lastly, our records are likely to have underestimated small florivore insects such as thrips (Thripidae) because of the non-destructive sampling performed when sampling flowers. However, we are aware that thrips are commonly feeding on sap from flower tissues and pollen, and since they synchronize population growth periods to match floral resource availability along flowering periods (Corllet 2004), more attention to these small florivore insects should be addressed in future studies.

The flowers from Malpighiaceae family species accounted for the 8% of the total damages exerted by insects and exhibited attributes associated with more restrictive morphologies such as oil-rewarded flowers and zygomorphic symmetry. Oil was the least frequent floral reward in the *campo rupestre* plant community, and the proportion of floral buds and open flowers attacked by florivores was significantly lower in zygomorphic species (except in proportion of petal removal) than asymmetric and actinomorphic flowers. In addition, our results show that solitary bees from *Tetrapedia* genus are the main robbers of Malpighiaceae flowers, which often behave as robbers when foraging for oil in Malpighiaceae systems (Cappellari et al. 2010). For instance, *Tetrapedia* species have been reported to behave as both robbers and pollinators in *Peixotoa tomentosa* flowers switching between positive and negative its impact on plant reproduction depending on its behavior (Barônio et al. 2020). This represent an intriguing system to disclosure the effects of simultaneous mutualistic and antagonist interactions in the continuum from mutualistic to antagonistic interactions. Furthermore, as specialized biotic interactions are expected to occur in *campo rupestre* environments (Fernandes & Price 1991, Hopper 2009), and in flower-florivore interactions, the florivory in the Malpighiaceae family might be an example of specialized, or at least more specific, interaction within the florivory spectrum.

Although we expected to find greater damages by insect florivores in open corollas no clear pattern was detected in proportion of attacked flowers and floral buds. However, close corolla shapes (cuculate, gullet, papilionaceus, spurred, and urceolate) showed a slight increase in the petal removal by insect florivores than open or intermediate corollas. Cuculate and papilionaceus are exclusive from the Fabaceae family, gullet from the Orchidaceae family, spurred are exclusively from the Vochysiaceae family, and urceolate grouped species from the Ericaceae, Phyllanthaceae and Polygonaceae plant families. This petal removal increase in the *campo rupestre* plant community might be related to the fact Cuculate flowers show only pollen rewards. Although, florivore and pollinator preferences for open corollas have shown to diminish plant reproduction success, due to florivore neutralization of the advantages associated to open corolla preferences by mutualists counterparts (Galen & Cuba 2001, Gómez 2003). Since cuculate flowers are pollinated by bees foraging for pollen, a conflicting selection scenario it is likely to occur in these systems.

Remarkably, our findings showed that insect florivores attacked the most pollen rewarded flowers as reported here for presence of florivory, pre-anthesis floral buds and open flowers. This might be related to three main reasons. First, the insect species more frequently found on flowers are known for foraging mostly for pollen resources, such as Chrysomelidae, Buprestidae, Cantharidae, and some Curculionidae beetles (Frame 2003, Corllet 2004). Second, plant species that succeeded in the harsh environmental *campo rupestre* environments, exhibit specialized pollen-flower pollination systems like poricidal anthers (Buchmann & Hurley 1978, Vallejo-Marín et al. 2010) and stamen dimorphism (Buchmann 1983, Luo et al. 2008), and these species are largely represented in the Fabaceae and Melastomataceae families. Third, pollen grains are rich in fatty acids and proteins, representing high nutritional food resources for insects (Edlund et al. 2004). Furthermore, the detrimental consequences of pollen robbing for pollen-flowers species reproduction may be much more severe than nectar consumption since pollen cannot be restocked (Lau & Galloway 2004, Solís-Montero et al. 2015). In *campo rupestre* environments the trade-off between nectar production cost and increasing attractivity to pollinators may not be as advantageous for plant reproduction (Gélvez-Zúñiga et al. 2018a) and since in these environments plant species have developed strategies to assure pollen flow between populations (Silveira et al. 2016), pollen-rewarded flowers seems to be a smart choice to survive in *campo rupestre* conditions.

Flowers with actinomorphic symmetry were the most frequent in *campo rupestre* (62%) and this pattern match the worldwide trend (Neal et al. 1998). This means that a zygomorphic symmetry is less likely to suffer florivore attack, but once it is attacked, removal levels are greater than in other types of symmetry. Zygomorphic symmetry evolution, which restricts the approach and movement of floral visitors, prompts specific pollen deposition on the pollinator's body, thus, increasing a potential isolation in incipient species (Sargent 2004). Also, zygomorphic lineages tend to be more species-rich (due to higher speciation rates) than sister actinomorphic lineages (Sargent 2004). As the *campo rupestre* environments represent areas of recent speciation (Silveira et al. 2016), zygomorphic flowers may represent an increasing resource opportunity for florivore insects. On the other hand, species with diurnal anthesis were the most frequent in *campo rupestre* (95%) and this pattern matches the findings of Souza et al. (2016) in a Brazilian palm swamp community. Crepuscular species were more attacked by florivores than species with diurnal and nocturnal anthesis. Yet, differences in florivore attack between diurnal and nocturnal flowers were not clearly detected. Having a crepuscular anthesis in *campo rupestre* may represent a disadvantage for the plants since high temperature and solar radiation (Silva et al. 2017, see also Fernandes & Price 1991) may reduce insect foraging activities during light-day hours, thus prompting an activity peak at dusk, when crepuscular species just offered their rewards.

The pattern of insect florivores attacking more solitary flowers than inflorescences is consistent across florivory presence, attack, and levels of petal removal. This might be due to florivore avoiding potential competitors in dense pollination units, or inflorescences (Hassell & Southwood 1978). In addition, plant defense resources allocated to inflorescences may be greater than into solitary flowers, since inflorescences are energetically more expensive to produce and maintain (Galen 1999, Irwin et al. 2004). Finally, inflorescences might be more related to attract pollinators at long-distances than to represent visual attractivity to flower-feeding insects (Brody & Mitchell 1997). Our findings show that corollas with prevailing rose and violet color are most attacked by insect florivores in *campo rupestre*; however, as no clear pattern was detected among the florivore variables our results are not conclusive. This lack of clear pattern might be related with the difficulty to detect color preferences in a broad system (of plants and insects) within a sensitive spectrum such as wavelengths perceived by insects. Hence, future studies shall address these trends in the future.

The consequences of florivory for plant reproduction and its relationship with florivores and pollinators preferences for large-sized flowers and great number of open flowers have been broadly reported (Karban & Strauss 1993, Gómez 2000, Strauss & Whittall 2006, Parachnowitsch & Kessler 2010, Teixido et al. 2016). Yet, changes in petal size from bud to flower involve hydraulic cell expansion (Galen 1999) and may interfere with photosynthetic rates under drought conditions (Galen 2000). Hence, greater flower size involves a compromise between environmental conditions and pollinator preference for large-flowered individuals (Strauss & Whittall 2006). For instance, Ashman et al. (2004) found that larger flowers have been correlated with more pollinator visits and weevil florivore destruction in *Fragaria virginica* (Rosaceae) flowers. Also, greater number of flowers in the bat pollinated *Calyptrogyne ghiesbreghtiana* (Arecaeae) has shown a simultaneous increase in pollinator visits and damages by Tettigoniidae grasshoppers (Cunningham 1995). Interestingly, Souza et al. (2016) reported that individuals with greater number of open flowers, but small-sized, are more likely to receive antagonist visits in a Brazilian palm swap plant community. Furthermore, these florivore-pollinator-plant dynamics may indicate several multi-scale outcomes. For instance, in the obligate pollination mutualism between *Yucca filamentosa* (Agavaceae) and its moth pollinator *Tegeticula cassandra*, a hemipteran generalist and a specialist beetle florivores, have shown discrepant selective pressures overall diminishing seed production due to floral abscission, and simultaneously, increasing of pollinator larva mortality (Althoff et al. 2013). These trade-offs are yet to be fully evaluated in this speciose and year-round flowering mountaintop ecosystem.

Half of the species recorded here (50.5%) produced flowers during 12-14 months and we detected a trend of increasing florivore insect attack in species with greater flowering periods. This matches the results of Madeira & Fernandes (1999), Belo et al. (2013) and Rocha et al. (2016) where they found species flowering throughout the year in *campo rupestre* plant communities. The flowering period is mainly triggered by environmental cues (Amasino 2005), and pollinators and florivores usually synchronize their life cycles to match floral resources availability using environmental signs (Strauss & Whittall 2006). Again, our findings contradict the predictability of antagonist visitation in plants with short flowering periods (less than 10 months) reported by Souza et al. (2016) in a palm swamp community. However, insect abundance is clearly related to rainfall dynamics, to assure synchrony between plant flowering and insect abundance it is important to consider that birds, mostly hummingbirds, and wind-pollination also represent important pollination vectors in *campo rupestre* (Monteiro et al. 2021), and this may explain flowering patterns besides insect-plant synchrony.

The lack of differences for the most floral attributes and advertisements on the proportion of early-stage fruits attacked by florivores is probably related to plant overcompensation to florivory. It is relatively well documented that when florivores consume flower structures a plant fitness reduction occurs through direct consumption effects or indirect interference on pollination quality (Mothershead & Marquis 2000, McCall & Irwin 2006, Moreira et al. 2019). Hence, herbivore-damaged plants may eventually allocate more resources to reproductive structures to mitigate the energy losses resulting from florivores activity (Irwin et al. 2008), and since flowers are costly structures directly related to plant fitness than leaves (McCall & Fordyce 2010, Garcia & Eubanks 2019), plant compensation to florivory is very likely to occur and might be more common than leaf herbivory compensation. For instance, partial compensation, by increasing secondary inflorescences ramification development, to beetle florivory in *Paepalanthus speciosus* (Eriocaulaceae) was reported in *campo rupestre* by Fernandes & Ribeiro (1990). Lastly, but not the least, we want to highlight the opposite patterns detected in the petal removal levels when compared with the other evaluated florivory responses. Since, 6 out of 9 floral attributes and flower advertisements tested did show opposite trends when assessing petal removal levels. We believe that this trend divergence is related to the nature of the foraging behavior of petal chewing florivore insects, in which for the majority of variables less restrictive pollen-flowers represent a more interesting floral resource to forage for in *campo rupestre* environments. Nevertheless, when the target is specifically the petal tissue other aspects such as palatability, water content, petal biomass, and floral volatiles (Roddy et al. 2021) might play a significant role in flower choice by florivores. Therefore, other approaches, such as those proposed by Roddy et al. (2021), might engage other floral attributes variation to allow the detection of trade-offs in the construction and function of flowers at the community level mediated by florivory. Hence, future studies shall address attributes like flower mass area, floral longevity and/or floral water content and its relationship with biotic pressures such as florivory incidence.

Overall, our results represent a pioneer first formal quantification of incidence and levels of florivory damages exerted by insect species, and its relationship with floral advertisements in perhaps the most diverse, endemic, and ancient vegetation in the Neotropics, the *campo rupestre*. Florivore influence ought to be relevant on the fate of fruit production and life time fitness, and hence community organization and assembly. However, florivory patterns remain far less unknown that leaf herbivory patterns. Our findings in florivore insect frequencies indicate that the set of floral attributes are a result of multi-scale biotic interaction combinations (Adler 2008, Parachnowitsch & Kessler 2010, Ruane et al. 2014, Caruso et al. 2019), and environmental conditions (Galen 2000, Zhao & Wang 2015). Our results also indicate that plant–antagonist interactions are highly context-dependent, and that insect florivore preferences are mainly related to plant investments to attract pollinators. The florivory dynamics and effects require detailed and more attention in future approaches in pollination ecology and herbivory pattern studies, since they do not seem to act separately one from another, and its understanding may contribute to a more complete perspective on both insect-flower evolution. Finally, insect florivory dynamics in the speciose *campo rupestre* ecosystem represent fertile land to test long standing hypotheses on flower–antagonist interactions.

Acknowledgements:

The authors also thank JE Santos-Junior, L Migliore, G Biffi, LR Vasconcellos, SA Vanin, FS Castro, L Perillo, LA de Moura, L Massutti, ACM Jacobina, A Lima, GC Pereira, Beirão M, CA Ferreira Júnior, Júlio JL, LPC Morellato and B Monteiro for assistance with insect and plant species identification. IGZ thanks A. Elbakyan for her contribution to research papers public access. This study was funded by PELD/CNPq and Fapemig, ComCerrado, and CAPES. IGZ received a scholarship from CNPq. We thank Reserva Vellozia, Parque Nacional da Serra do Cipó, Cedro Textil, ICMBio, Pousada Pedra do Elefante, and Pousada Rancho Cipó for logistical support.

Supplementary material

Table S1. Plant species, attractivity and morphological attributes in *campo rupestre* vegetation during 14-month sampling at Serra do Cipó, Minas Gerais, Brazil, between May 2018 and August 2019. Mean number of open flowers (Display), flower size (S= <10 mm, M= 10-20 mm, L= 20-30 mm, VL= >30 mm), flowering period (Flowering), floral symmetry (Act= actinomorphic, Asy= asymmetric, Zyg= zygomorphic), Anthesis (D= diurnal, C= crepuscular, N= nocturnal), corolla shape, pollination unit (Flo= flower, Inf = inflorescence), floral reward (N= nectar, O= oil, P= pollen), prevailing corolla color (Color) and IUCN threat status (Status).

	Attractivity traits			**Morphological traits**							
	Display	Size	flowering	Symmetry	Anthesis	Corolla	Unit		Reward	Color	Status
Acanthaceae											
Ruellia villosa	3.0	VL	6	Zyg	D	Bilabiate	Flo		N	Red	NE
Amaranthaceae											
Gomphrena incana	26.6	S	14	Act	D	Ligulate	Inf	Head	N	White	NE
Apocynaceae											
Mandevilla tenuifolia	1.0	M	2	Act	D	Rotate	Flo		N	Violet	NE
Minaria decussata	19.3	S	10	Act	D	Campanulate	Inf	Cymes	P	Yellow	NE
Odontadenia lutea	6.9	VL	5	Asy	N	Infundibular	Inf	Raceme	N	White	NE
Aquifoliace											
Ilex nummularia	25.4	S	5	Act	D	Cruciate	Inf	Cymes	N	White	NE
Asteraceae											
Acritopappus longifolius	26.6	S	4	Zyg	D	Brush	Inf	Panicle	N	Violet	NE
Ageratum conyzoides	14.3	S	2	Act	D	Brush	Inf	Corymb	N	Violet	NE
Aspilia foliosa	10.7	M	6	Zyg	D	Ligulate	Inf	Head	N	Yellow	NE
Aspilia jolyana	10.3	M	14	Zyg	D	Ligulate	Inf	Head	N	Yellow	NE
Aspilia fruticosa	18.3	M	3	Zyg	D	Ligulate	Inf	Head	N	Yellow	NE

Baccharis platypoda	50.0	S	3	Act	D	Disk	Inf	Corymb	N	Greenish	NE
Calea graminifolia	2.0	M	1	Zyg	D	Ligulate	Inf	Head	N	Yellow	NE
Chromolaena squalida	15.2	S	12	Act	D	Brush	Inf	Corymb	N	Violet	NE
Chrysolaena sp	20.0	S	1	Act	D	Brush	Inf	Head	N	Violet	NA
Cyrtocymura scorpioides	34.8	S	3	Act	D	Brush	Inf	Head	N	Violet	NE
Dasyphyllum reticulatum	26.3	S	7	Zyg	N	Ligulate	Inf	Head	N	Greenish	NT
Eremanthus erythropappus	58.2	S	3	Zyg	D	Disk	Inf	Glomerule	N	Violet	NE
Eremanthus incanus	100.0	S	1	Act	D	Disk	Inf	Head	N	Violet	NE
Lepidaploa lilacina	17.2	S	3	Act	D	Brush	Inf	Head	N	Violet	NE
Lepidaploa rufogrisea	32.7	S	4	Act	D	Brush	Inf	Head	N	Violet	NE
Lessingianthus graminifolius	8.1	S	7	Act	D	Brush	Inf	Head	N	Violet	NE
Lessingianthus linearifolius	23.6	S	1	Asy	D	Brush	Inf	Head	N	Violet	NE
Lychnophora passerina	20.6	S	11	Act	D	Disk	Inf	Head	N	Violet	NT
Lychnophora salicifolia	40.3	S	7	Zyg	D	Disk	Inf	Head	N	Violet	NE
Lychnophora sellowii	24.2	S	4	Act	D	Disk	Inf	Head	N	Violet	EN
Mikania purpurascens	22.8	S	8	Act	D	Brush	Inf	Panicle	N	White	NE
Mikania reticulata	11.9	S	1	Act	D	Brush	Inf	Panicle	N	Greenish	NE
Mikania sessilifolia	26.3	S	7	Act	D	Brush	Inf	Panicle	N	Greenish	NE
Minasia pereirae	18.4	S	7	Act	D	Disk	Inf	Glomerule	N	Violet	EN
Paralychnophora bicolor	2.0	S	2	Act	D	Disk	Inf	Head	N	Greenish	EN
Piptolepis ericoides	11.9	S	2	Act	D	Disk	Inf	Head	N	Violet	NT
Porophyllum obscurum	11.9	S	7	Act	D	Disk	Inf	Head	N	Violet	NE
Praxelis basifolia	9.0	S	1	Zyg	D	Brush	Inf	Glomerule	N	White	NE
Pseudobrickellia angustissima	36.0	M	2	Act	D	Brush	Inf	Panicle	N	Greenish	NE
Richterago lanata	24.3	S	11	Zyg	N	Ligulate	Inf	Head	N	White	EN
Richterago stenophylla	19.5	S	11	Zyg	D	Ligulate	Inf	Head	N	White	EN
Stenophalium chionaeum	24.8	S	4	Act	D	Brush	Inf	Head	N	Violet	NE

Trichogonia hirtiflora	21.3	S	7	Act	D	Brush	Inf	Corymb	N	Violet	NT
Trichogonia villosa	42.0	S	8	Act	D	Brush	Inf	Corymb	N	Violet	NE
Trixis vauthieri	39.0	M	1	Zyg	D	Bilabiate	Inf	Corymb	N	Yellow	NE
Vernonanthura ferruginea	7.1	S	6	Act	D	Brush	Inf	Head	N	Violet	NE
Bignoneaceae											
Fridericia triplinervia	1.0	VL	1	Zyg	N	Bilabiate	Inf	Cymes	N	Rose	NE
Jacaranda caroba	2.8	VL	5	Zyg	D	Bilabiate	Inf	Cymes	N	Violet	NE
Bromeliaceae											
Bromelia antiacantha	4.0	L	1	Act	D	Tubular	Inf	Raceme	N	Rose	NE
Vriesea oligantha	12.1	L	4	Act	D	Tubular	Inf	Spike	N	Yellow	NE
Calophyllaceae											
Kielmeyera regalis	5.0	VL	5	Act	D	Rotate	Inf	Cymes	P	Rose	NE
Convolvulaceae											
Distimake flagellaris	5.3	VL	2	Act	N	Infundibular	Flo		N	White	NE
Evolvulus lithospermoides	2.9	L	6	Act	D	Infundibular	Inf	Spike	N	Violet	NE
Ipomoea procurrens	0.8	VL	4	Act	D	Infundibular	Flo		N	Rose	NE
Ipomoea rupestris	1.5	VL	1	Act	D	Infundibular	Flo		N	Rose	NE
Jacquemontia prostrata	1.9	L	13	Act	D	Infundibular	Flo		N	Violet	NE
Droseraceae											
Drosera hirtella	0.0	M	3	Act	D	Rotate	Inf	Raceme	P	Rose	NE
Drosera tomentosa	1.1	M	3	Act	D	Rotate	Inf	Raceme	P	Rose	NE
Ericaceae											
Agarista angustissima	5.7	M	1	Act	C	Urceolate	Inf	Raceme	N	Greenish	NE
Agarista duartei	22.1	M	6	Act	N	Urceolate	Inf	Raceme	N	Greenish	NE
Gaylussacia oleifolia	16.1	M	6	Act	D	Urceolate	Inf	Raceme	N	Greenish	EN
Gaylussacia reticulata	16.8	M	1	Act	D	Urceolate	Inf	Raceme	N	Greenish	NE
Eriocaulaceae											

Syngonanthus verticillatus	3.5	S	3	Zyg	D	Disk	Inf	Head	P	Orange	NE
Erythroxilaceae											
Erythroxylum campestre	100.0	S	1	Act	N	Rotate	Flo		N	White	NE
Euphorbiaceae											
Croton lundianus	4.2	M	1	Zyg	N	Rotate	Inf	Thyrse	N	White	NE
Fabaceae											
Aeschynomene paniculata	60.3	M	2	Zyg	D	Papilionaceous	Flo		N	Yellow	NE
Bowdichia virgilioides	60.0	M	1	Zyg	D	Papilionaceous	Inf	Panicle	N	Violet	NT
Calliandra dysantha	4.3	L	4	Act	D	Campanulate	Inf	Raceme	P	Red	NE
Calliandra fasciculata	11.7	VL	4	Act	D	Campanulate	Inf	Glomerule	P	Rose	NE
Calliandra linearis	7.5	VL	1	Act	D	Campanulate	Inf	Glomerule	P	Rose	VU
Centrosema virginianum	1.0	L	1	Zyg	D	Papilionaceous	Flo		N	Violet	NE
Chamaecrista desvauxii	2.7	L	14	Asy	D	Cucullate	Inf	Raceme	P	Yellow	NE
Chamaecrista ochnacea	3.5	L	13	Asy	D	Cucullate	Inf	Raceme	P	Orange	NE
Chamaecrista olesiphylla	2.0	L	2	Asy	D	Cucullate	Inf	Raceme	P	Yellow	NE
Chamaecrista ramosa	9.1	L	7	Asy	D	Cucullate	Inf	Raceme	P	Yellow	NE
Chamaecrista rotundifolia	1.8	L	4	Asy	D	Cucullate	Inf	Raceme	P	Yellow	NE
Chamaecrista vauthieri	42.7	L	7	Asy	D	Cucullate	Inf	Raceme	P	Yellow	EN
Clitoria guianensis	2.0	L	1	Zyg	D	Infundibular	Flo		N	Rose	NE
Leptolobium brachystachyum	2.0	S	1	Act	N	Campanulate	Inf	Raceme	N	White	NE
Lupinus coriaceus	6.8	M	3	Zyg	D	Papilionaceous	Inf	Raceme	P	Violet	VU
Mimosa macedoana	50.9	VL	6	Act	D	Brush	Inf	Glomerule	P	White	EN
Mimosa paucifolia	86.7	VL	6	Act	D	Brush	Inf	Glomerule	P	Rose	VU
Mimosa radula	40.9	VL	4	Act	D	Brush	Inf	Glomerule	P	Rose	NE
Periandra mediterranea	1.0	M	1	Zyg	D	Papilionaceous	Inf	Raceme	N	Violet	NE
Senna rugosa	8.8	VL	3	Asy	D	Cucullate	Inf	Panicle	P	Yellow	NE
Stylosanthes guianensis	7.1	S	7	Zyg	D	Papilionaceous	Flo		N	Yellow	NE

Zornia reticulata	5.0	S	1	Zyg	D	Papilionaceous	Inf	Spike	N	Yellow	NE
Gentianaceae											
Calolisianthus pedunculatus	2.1	VL	11	Act	D	Infundibular	Flo		P	Red	NE
Curtia diffusa	2.2	S	4	Act	N	Salverform	Inf	Cymes	P	White	NE
Curtia tenuifolia	2.2	M	1	Act	D	Infundibular	Inf	Cymes	N	Violet	LC
Iridaceae											
Pseudotrimezia juncifolia	1.2	VL	4	Zyg	D	Coronate	Flo		O	Yellow	NE
Pseudotrimezia truncata	1.0	VL	2	Zyg	D	Coronate	Flo		O	Violet	NE
Sisyrinchium vaginatum	1.0	L	1	Act	D	Coronate	Inf		P	Yellow	NE
Trimezia fistulosa	0.2	VL	3	Zyg	D	Coronate	Flo		O	Orange	NE
Trimezia rupestris	1.0	VL	1	Act	D	Coronate	Flo		O	Violet	NE
Lamiaceae											
Hypenia reticulata	12.7	M	12	Act	D	Bilabiate	Inf	Cymes	N	Red	NE
Hyptis lantanifolia	23.2	S	9	Zyg	D	Bilabiate	Inf	Thyrse	N	White	NE
Hyptis passerina	23.4	S	6	Zyg	D	Bilabiate	Inf	Thyrse	N	Violet	NE
Hyptis proteoides	10.8	S	12	Zyg	D	Bilabiate	Inf	Thyrse	N	White	NE
Lentibulariaceae											
Genlisea violacea	1.1	M	2	Zyg	D	Bilabiate	Flo		N	Violet	LC
Loganiaceae											
Spigelia linarioides	2.8	M	8	Act	D	Infundibular	Inf	Raceme	N	Rose	NE
Spigelia sellowiana	1.9	VL	1	Act	D	Infundibular	Inf	Raceme	N	Rose	LC
Loranthaceae											
Psittacanthus robustus	52.0	VL	2	Act	D	Tubular	Inf	Umbel	N	Yellow	NE
Lythraceae											
Cuphea diosmifolia	2.7	S	2	Zyg	D	Bilabiate	Inf	Raceme	N	Rose	NE
Cuphea ericoides	5.1	S	12	Zyg	D	Bilabiate	Inf	Raceme	N	Rose	NE
Cuphea micrantha	4.7	S	8	Zyg	D	Bilabiate	Inf	Raceme	N	Rose	NE

Cuphea pseudovaccinium	5.0	S	12	Zyg	D	Bilabiate	Inf	Raceme	N	Rose	NE
Diplusodon lanceolatus	6.0	M	10	Zyg	D	Campanulate	Flo		P	Rose	NE
Diplusodon orbicularis	2.7	M	10	Act	D	Campanulate	Flo		P	Rose	VU
Malpighiaceae											
Banisteriopsis argyrophylla	11.2	L	8	Zyg	D	Unguiculate	Inf	Thyrse	O	Yellow	NE
Banisteriopsis campestris	7.5	*L*	*3*	*Zyg*	*D*	*Unguiculate*	Inf	*Thyrse*	*O*	*Rose*	NE
Banisteriopsis malifolia	5.1	M	5	Zyg	D	Unguiculate	Inf	Thyrse	O	Rose	NE
Byrsonima dealbata	27.0	M	1	Zyg	D	Unguiculate	Inf	Thyrse	O	Yellow	NE
Byrsonima variabilis	10.0	M	1	Zyg	D	Unguiculate	Inf	Thyrse	O	White	LC
Byrsonima verbascifolia	3.5	M	1	Zyg	C	Unguiculate	Inf	Thyrse	O	Yellow	NE
Heteropterys pteropetala	6.2	M	13	Zyg	D	Unguiculate	Inf	Corymb	O	Yellow	NE
Peixotoa tomentosa	4.4	L	12	Zyg	D	Unguiculate	Inf	Thyrse	O	Yellow	NE
Tetrapterys microphylla	5.0	M	14	Zyg	D	Unguiculate	Inf	Thyrse	O	Yellow	LC
Malvaceae											
Wahlenbergia brasiliensis	20.5	S	1	Act	D	Campanulate	Inf	Panicle	N	Violet	NE
Melastomataceae											
Cambessedesia hilariana	1.4	S	3	Act	D	Rotate	Flo		P	Orange	LC
Cambessedesia semidecandra	5.1	S	8	Act	D	Rotate	Flo		P	Orange	VU
Chaetostoma armatum	2.5	M	1	Act	D	Rotate	Flo		P	Violet	NE
Fritzschia stenodon	1.2	M	3	Act	D	Cruciate	Inf	Raceme	P	Violet	NE
Lavoisiera caryophyllea	3.8	L	11	Act	D	Unguiculate	Flo		P	Violet	EN
Lavoisiera confertiflora	2.3	L	14	Act	D	Campanulate	Flo		P	Violet	NE
Lavoisiera cordata	3.6	VL	9	Act	C	Unguiculate	Flo		P	White	VU
Lavoisiera firmula	1.0	L	1	Act	D	Unguiculate	Flo		P	Rose	EN
Lavoisiera glandulifera	1.7	VL	10	Act	D	Rotate	Flo		P	Violet	NE
Lavoisiera imbricata	2.0	VL	2	Zyg	D	Campanulate	Flo		P	Rose	LC
Lavoisiera mucorifera	8.5	M	12	Act	D	Unguiculate	Flo		P	Rose	NT

Lavoisiera subulata	3.5	M	10	Act	D	Unguiculate	Flo		P	Rose	VU
Leandra aurea	7.3	S	2	Act	N	Rotate	Inf	Thyrse	P	White	NE
Marcetia taxifolia	14.1	S	14	Act	D	Rotate	Flo		P	Rose	NE
Miconia ferruginata	50.0	S	1	Act	N	Campanulate	Inf	Spike	P	Greenish	NE
Miconia irwinii	18.4	S	4	Act	D	Campanulate	Inf	Cymes	P	White	NE
Microlicia confertiflora	13.6	M	12	Act	D	Rotate	Flo		P	Rose	NE
Microlicia tenuifolia	8.5	M	2	Act	D	Rotate	Flo		P	Violet	EN
Microlicia tomentella	4.2	M	9	Act	D	Rotate	Flo		P	Violet	NE
Pleroma heteromallum	2.3	M	2	Act	D	Rotate	Inf	Thyrse	P	Violet	NE
Pleroma nodosum	11.8	M	5	Act	D	Rotate	Inf	Thyrse	P	Violet	NE
Pleroma villosissimum	5.2	L	7	Act	D	Rotate	Inf	Thyrse	P	Violet	NE
Siphanthera arenaria	2.4	M	14	Act	D	Rotate	Flo		P	Rose	NE
Trembleya laniflora	17.0	VL	5	Act	C	Rotate	Inf	Cymes	P	White	NE
Trembleya parviflora	15.2	M	13	Act	C	Rotate	Inf	Cymes	P	White	NE
Myrtaceae											
Campomanesia pubescens	8.8	S	1	Act	C	Rotate	Inf	Panicle	N	White	LC
Myrcia hartwegiana	2.4	S	5	Act	C	Rotate	Inf	Panicle	N	White	NE
Myrcia lasiantha	5.6	S	4	Act	C	Rotate	Inf	Panicle	N	White	NE
Ochnaceae											
Luxemburgia damazioana	3.0	L	1	Act	D	Rotate	Flo		P	Yellow	VU
Luxemburgia schwackeana	5.0	L	5	Act	D	Rotate	Flo		P	Yellow	NE
Ouratea floribunda	9.1	M	3	Act	D	Rotate	Inf	Panicle	P	Yellow	NE
Sauvagesia glandulosa	9.5	S	3	Act	D	Rotate	Inf	Panicle	P	Violet	NE
Sauvagesia linearifolia	1.9	M	2	Act	D	Rotate	Inf	Panicle	P	Rose	NE
Onagraceae											
Ludwigia octovalvis	2.7	M	1	Act	D	Rotate	Flo		N	Yellow	NE
Orchidaceae											

Cattleya caulescens	1.9	M	2	Zyg	D	Gullet	Inf	Raceme	N	Violet	NE
Cleistes paranaensis	0.7	VL	2	Zyg	D	Gullet	Flo		N	Violet	LC
Cyrtopodium parviflorum	6.6	L	6	Zyg	D	Gullet	Inf	Panicle	N	Yellow	LC
Epidendrum saxatile	18.9	L	2	Zyg	D	Gullet	Inf	Panicle	N	Violet	LC
Gomesa hydrophila	7.2	L	3	Asy	D	Gullet	Inf	Raceme	N	Yellow	NE
Gomesa spiloptera	6.8	VL	2	Zyg	D	Gullet	Inf	Raceme	N	Yellow	NE
Pseudolaelia geraensis	1.7	M	3	Zyg	D	Gullet	Inf	Raceme	N	Violet	LC
Orobanchaceae											
Agalinis brachyphylla	2.8	L	8	Zyg	D	Bilabiate	Flo		N	Violet	VU
Buchnera lavandulacea	8.0	S	3	Act	D	Tubular	Inf	Spike	N	Violet	NE
Buchnera sp	2.6	S	3	Act	D	Tubular	Inf	Spike	N	Violet	NA
Esterhazya nanuzae	3.2	L	1	Act	D	Bilabiate	Flo		N	Red	EN
Physocalyx aurantiacus	1.2	L	4	Act	D	Bilabiate	Flo		N	Orange	NT
Oxalidaceae											
Oxalis hirsutissima	1.0	M	3	Act	D	Rotate	Inf	Cymes	N	Yellow	NE
Phyllanthaceae											
Phyllanthus klotzschianus	8.5	S	11	Act	N	Urceolate	Flo		N	Greenish	NE
Polygalaceae											
Polygala exasperata	3.2	S	6	Zyg	D	Tubular	Inf	Spike	N	Rose	NE
Polygala glochidata	3.7	S	7	Zyg	D	Tubular	Inf	Spike	N	White	NE
Polygonaceae											
Coccoloba acrostichoides	29.0	S	1	Act	C	Urceolate	Inf	Raceme	N	Greenish	NE
Coccoloba cereifera	10.1	S	12	Act	D	Urceolate	Inf	Thyrse	N	Red	EN
Rapateaceae											
Cephalostemus ridelianus	1.0	M	1	Act	D	Rotate	Inf	Glomerule	P	Yellow	NE
Rhamnaceae											
Crumenaria erecta	3.3	S	1	Act	D	Tubular	Inf	Thyrse	P	Rose	NE

Rubiaceae											
Borreria capitata	15.8	S	3	Act	D	Bilabiate	Inf	Glomerule	N	White	NE
Borreria dasycephala	102.0	S	1	Act	D	Bilabiate	Inf	Glomerule	N	White	NE
Borreria schumannii	10.8	S	4	Zyg	D	Bilabiate	Inf	Glomerule	N	White	NE
Borreria warmingii	17.6	S	3	Act	N	Bilabiate	Inf	Glomerule	N	White	NE
Declieuxia deltoidea	5.7	S	3	Act	D	Tubular	Inf	Cymes	N	Violet	NE
Declieuxia diantheroides	3.5	S	1	Act	N	Tubular	Inf	Cymes	N	White	NE
Diodella apiculata	6.1	M	8	Act	D	Tubular	Flo		N	Rose	NE
Palicourea rigida	4.5	L	7	Act	D	Bilabiate	Inf	Cymes	N	Yellow	NE
Psyllocarpus laricoides	4.1	S	3	Act	N	Tubular	Inf	Cymes	N	White	NE
Remijia ferruginea	2.5	M	2	Act	N	Rotate	Inf	Cymes	N	White	NE
Tocoyena formosa	43.0	VL	2	Act	D	Tubular	Inf	Corymb	N	Yellow	NE
Salicaceae											
Casearia arborea	19.0	S	1	Act	N	Unguiculate	Inf	Glomerule	N	Greenish	NE
Sapindaceae											
Serjania erecta	4.6	S	1	*Act*	*N*	*Rotate*	Inf	*Thyrse*	*N*	White	NE
Serjania paradoxa	7.2	S	4	Act	D	Cruciate	Inf	Thyrse	N	White	NE
Solanaceae											
Solanum stenandrum	1.0	M	1	Act	D	Infundibular	Inf	Cymes	P	Violet	NE
Turneraceae											
Turnera oblongifolia	18.9	M	13	Act	D	Rotate	Inf	Raceme	N	Yellow	NE
Velloziaceae											
Barbacenia blackii	1.2	VL	2	Zyg	D	Tubular	Flo		N	Red	VU
Barbacenia flava	1.9	L	10	Act	D	Tubular	Flo		N	Yellow	NE
Barbacenia macrantha	0.9	L	4	Act	D	Tubular	Flo		N	Red	NE
Barbacenia rubrovirens	2.0	VL	2	Act	D	Tubular	Flo		N	Greenish	NE
Vellozia caruncularis	1.3	L	10	Act	D	Rotate	Flo		N	Violet	NE

Vellozia declinans	4.3	L	3	Act	D	Unguiculate	Flo		N	Violet	NE
Vellozia epidendroides	2.8	L	9	Act	D	Rotate	Flo		P	Rose	NE
Vellozia lilacina	1.0	VL	2	Act	D	Rotate	Flo		N	Violet	EN
Vellozia nivea	1.5	VL	1	Act	D	Rotate	Flo		N	Violet	NE
Vellozia patens	1.9	L	3	Act	D	Rotate	Flo		N	Violet	EN
Vellozia resinosa	0.9	L	3	Act	D	Rotate	Flo		N	Violet	NE
Vellozia variabilis	2.6	VL	5	Act	D	Rotate	Flo		N	Violet	LC
Verbenaceae											
Lippia corymbosa	104.3	S	2	Act	D	Tubular	Inf	Corymb	N	Rose	NE
Lippia lupulina	5.1	S	10	Act	D	Tubular	Inf	Corymb	N	Rose	NE
Stachytarpheta reticulata	3.7	M	7	Zyg	D	Tubular	Inf	Spike	N	Violet	NE
Vochysiaceae											
Qualea grandiflora	14.8	M	3	Zyg	D	Spurred	Inf	Raceme	N	Yellow	NE
Vochysia pygmaea	6.4	M	14	Zyg	D	Spurred	Inf	Raceme	N	Yellow	EN
Winteraceae											
Drimys brasiliensis	9.2	S	4	Act	C	Rotate	Inf	Panicle	P	White	LC
Xyridaceae											
Xyris asperula	1.5	L	7	Act	D	Cruciate	Inf	Head	P	Yellow	NE
Xyris bialata	1.6	M	7	Act	D	Cruciate	Inf	Head	P	Yellow	DD
Xyris nanuzae	1.0	S	2	Act	D	Cruciate	Inf	Head	P	Yellow	NE
Xyris nubigena	1.3	M	14	Act	D	Cruciate	Inf	Head	P	Yellow	NE

Table S2. Result of the chi-square test showing that flower morphological traits are distributed among the plant families sampled. Sampling between May/18 and August/19 in thirty *campo rupestre* vegetation plots at Serra do Cipó, Minas Gerais, Brazil.

Response variable	**Explanatory variable**	**χ2**	**p-value**	**N**
Corolla shape	Plant family	203.33	< 0.001	12,340
Floral reward		227.28	< 0.001	12,340
Flower symetry		177.25	< 0.001	12,340
Pollination unit		954.19	< 0.001	12,340
Time of anthesis		106.26	< 0.001	12,340
Prevailing corolla color		384.23	< 0.001	12,340
Flower size		625.77	< 0.001	12,340

Literature cited:

Adler, L.S. 2008. Selection by pollinators and herbivores on attraction and defense. In: Tilmon, K.J. (ed.). Specialization, speciation, and radiation-the evolutionary biology of herbivorous insects. University of California Press, Berkely, 1:162-173.

Ashman, T.L & Morgan, M.T. 2004. Explaining phenotypic selection on plant attractive characters: male function, gender balance or ecological context? Proceedings of the Royal Society of London. Series B: Biological Sciences, 271:553-559.

Ashman, T.L, Cole, D.H & Bradburn, M. 2004. Sex-differential resistance and tolerance to herbivory in a gynodioecious wild strawberry. Ecology, 85:2550-2559.

Althoff, D.M, Xiao, W., Sumoski, S. & Segraves, K.A: 2013. Florivore impacts on plant reproductive success and pollinator mortality in an obligate pollination mutualism. Oecologia, 173:1345-1354.

Amasino, R.M. 2005. Vernalization and flowering time. Current Opinions in Biotechnology, 16:154-158.

Barber, N.A., Adler, L.S. & Bernardo, H.L. 2011. Effects of above- and belowground herbivory on growth, pollination, and reproduction in cucumber. Oecologia, 165:377-386.

Barbosa, N.P.U. & Fernandes, G.W. 2016. Rupestrian Grassland: Past, Present and Future Distribution. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer. 1:531-544.

Barônio, G.J., Brito, V.L.G, Nogueira, A. & Rech, A. 2020. Beyond robbery: the role of upside-down behaviour performed by small oil-collecting bees in Malpighiaceae. Arthropod-Plant Interactions 14:613-621.

Barrett, S.C.H. & Harder, L.D. 1996. Ecology and evolution of plant mating. Trends in Ecology & Evolution, 11:73-79.

Belo, R.M., Negreiros, D., Fernandes, G.W., Silveira, F.A.O., Ranieri, B.D. & Morellato, L.P.C. 2013. Fenologia reprodutiva e vegetativa de arbustos endémicos de *campo rupestre* na Serra do Cipó, Sudeste do Brasil. Rodriguésia, 64:817-828.

Bernays, E. & Graham, M. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology, 69:886-892.

Bertness, M.D. & Shumway, S.W. 1992. Consumer driven pollen limitation of seed production in marsh grasses. American Journal of Botany, 79:288-293.

Brody, A.K. & Mitchell, R.J. 1997. Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. Oecologia, 110:86-93.

Bronstein, J.L., Huxman, T.E. & Davidowitz, G. 2007. Plant-mediated effects linking herbivory and pollination. Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press, 1:75-103.

Buchmann, S.L. & Hurley, J.P. 1978. A biophysical model for buzz pollination in angiosperms. Journal of Theoretical Biology, 72:639-657.

Buchmann, S.L. 1983. Buzz pollination in angiosperms. In: Jones, C.E. & Little, R.J. (eds.). Handbook of Experimental Pollination Biology. Van Nostrand Reinhold, New York, 1:73-113.

Canela, M.B.F. & Sazima, M. 2003. Florivory by the crab *Armases angustipes* (Grapsidae) influences hummingbird visits to *Aechmea pectinata* (Bromeliaceae). Biotropica, 35:289-294.

Cappellari, S.C., Melo, G.A., Aguiar, A.J.C. & Neff, J.L. 2010. Floral oil collection by male *Tetrapedia* bees (Hymenoptera: Apidae: Tetrapediini). Apidologie, 43:39-50.

Caruso, C.M., Eisen, K.E., Martin, R.A. & Sletvold, N. 2019. A meta-analysis of the agents of selection on floral traits. Evolution, 73:4-14.

Corllet, R.T. 2004. Flower visitors and pollination in the Oriental (Indomalayan) Region. Biological Reviews, 79:497-532.

Costa, F.V., Mello, M.A.R., Bronstein, J.L., Guerra, T.J., Muylaert, R.L., Leite, A.C. & Neves, F.S. 2016. Few ant species play a central role linking different plant resources in a network in rupestrian grasslands. PloS One, 11:e0167161.

Cunningham, S.A. 1995. Ecological constraints on fruit initiation by *Calyptrogyne ghiesbreghtiana* (Arecaceae): Floral herbivory, pollen availability, and visitation by pollinating bats. American Journal of Botany, 82:1527–1536.

Del-Claro, K., Rodriguez-Morales, D., Calixto, E.S., Martins, A.S. & Torezan-Silingardi, H.M. 2019. Ant pollination of *Paepalanthus lundii* (Eriocaulaceae) in Brazilian savanna. Annals of Botany, 123:1159-1165.

Dodd, M.E., Silvertown, J. & Chase, M.W. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. Evolution, 53:732-744.

Edlund, A.F., Swanson, R. & Preuss, D. 2004. Pollen and stigma structure and function: the role of diversity in pollination. The Plant Cell 16:84-97.

Ehrlich, P.R. & Raven, P.H. 1964. Butterflies and plants: a study in coevolution. Evolution, 18:586-608.

Faegri, K. & van der Pijl, L. 1979. Principles of pollination ecology. Pergamon Press, 3:244.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. 2004 Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution and Systematics 35:375-403.

Fernandes, G.W. & Ribeiro, S.P. 1990. Plant response to herbivory: Two examples from the neotropics. Ecotropicos, 2:77-86.

Fernandes, G.W. & Price, P.W. 1991. Comparisons of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. In: Price, P.W., Lewinsohn, T.M., Fernandes, G.W. & Benson, W.W. (eds.). Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, 252:91-115.

Fernandes, G.W. 2016. The megadiverse rupestrian grassland. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, 1:3–14.

Fernandes, G.W., Almeida, H.A., Nunes, C.A., Xavier, J.H.A., Coob, N.S., Carneiro, M.A.A., Cornelissen, T., Neves, F.S., Ribeiro, S.P., Nunes, Y.R.F., Pires, A.C.V. & Beirão, M.V. 2016. Cerrado to rupestrian grasslands: patterns of species distribution and the forces shaping them along an altitudinal gradient. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, 1:345-371.

Fernandes, G.W., Barbosa, N.P.U., Alberton, B., Barbieri, A., Dirzo, R., Goulart, F., Guerra, T.J., Morellato, L.P.C., Solar, R.R.C. 2018. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodiversity and Conservation, 27:2587-2603.

Fernandes, G. W., Arantes-Garcia, L., Barbosa, M., Barbosa, N. P., Batista, E. K., Beiroz, W., Resende, F. M., Abrahão, A., Almada, E. D., Alves, E., Alves, N. J., Angrisiano, P., Arista, M., Arooyo, J., Arruda, A. J., Bahia, T. O., Braga, L., Brito, L., Callisto, M., Caminha-Paiva, D., Carvalho, M., Conceição, A. A., Costa, L. N., Cruz, A., Cunha-Blum, J., Dagevos, J., Dias, B. F. S., Pinto, V. D., Dirzo, R., Domingos, D. Q., Echternacht, L., Fernandes, S., Figueira, J. E. C., Fiorini, C. F., Giulietti, A. M., Gomes, A., Gomes, V. M., Gontijo, B., Goulart, F., Guerra, T. J., Junqueira, P. A., Lima-Santos, D., Marques, J., Meira-Neto, J., Miola, D. T. B., Morellato, L. P. C., Negreiros, D., Neire, E., Neves, A. C., Neves, F. S., Novais, S., Oki, Y., Oliveira, E., Oliveira, R. S., Pivari, M. O., Junior, E. P., Ranieri, B. D., Ribas, R. P., Scariot, A., Schaefer, C. E., Sena, L., da Silva, P. G., Siqueira P. R., Soares, N. C., Soares-Filho, B., Solar, R., Tabarelli, M., Vasconcelos, R., Vilela, E. & Silveira, F. A. 2020. Biodiversity and ecosystem services in the Campo Rupestre: A road map for the sustainability of the hottest Brazilian biodiversity hotspot. Perspectives in Ecology and Conservation 18:213-222.

Frame, D. 2003. Generalist Flowers, Biodiversity and Florivory: Implications for Angiosperm Origins. Taxon, 52:681-685.

Galen, C. 1999. Why Do Flowers Vary? The functional ecology of variation in flower size and form within natural plant populations. BioScience, 49:631-640.

Galen, C. 2000. High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum*. American Naturalist, 156:72-83.

Galen, C. & Cuba, J. 2001. Down the tube: pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. Evolution, 55:1963-1971.

Galen, C. & Butchart, B. 2003. Ants in your plants: effects of nectar-thieves on pollen fertility and seedsiring capacity in the alpine wildflower, *Polemonium viscosum*. Oikos, 101:521-528.

Garcia, L.C. & Eubanks, M.D. 2019. Overcompensation for insect herbivory: a review and meta-analysis of the evidence. Ecology, 100:e02585.

Gélvez-Zúñiga, I., Teixido, A.L., Neves, A.C.O. & Fernandes, G.W. 2018a. Floral antagonists counteract pollinator-mediated selection on attractiveness traits in the hummingbird-pollinated *Collaea cipoensis* (Fabaceae). Biotropica, 50:797-804.

Gélvez-Zúñiga, I., Neves, A.C.O., Teixido, A.L. & Fernandes, G.W. 2018b. Reproductive biology and floral visitors of *Collaea cipoensis* (Fabaceae), an endemic shrub of the rupestrian grasslands. Flora, 238:129-137.

Gómez, J.M. 2003. Herbivory reduces the strength of pollinator-mediated selection in the mediterranean herb *Erysimum mediohispanicum*: consequences for plant specialization. The American Naturalist 162:242-256.

Gómez, J.M. 2000. Phenotypic selection and response to selection in *Lobularia maritima*: importance of direct and correlational components of natural selection. Journal of Evolutionary Biology, 13:689-699.

González-Browne, C., Murúa, M.M., Navarro, L., & Medel, R. 2016. Does Plant Origin Influence the Fitness Impact of Flower Damage? A Meta-Analysis. PlosOne, 11:e0146437.

Gottsberger, G. 1990. Flowers and Beetles in the South American Tropics. Botanica Acta, 103:360-365.

Guerra, T.J., Carstensen, D.W., Morellato, L.P.C., Silveira, F.A.O. & Costa, F.V. 2016. Mutualistic interactions among free-living species in rupestrian grasslands. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, 1:291-314.

Hargreaves, A.L., Harder, L.D. & Johnson, S.D. 2009. Consumptive emasuclation: the ecological and evolutionary consequences of pollen theft. Biological Reviews, 84:259-76.

Hassell, M.P. & Southwood, T.R.E. 1978. Foraging Strategies of Insects. Annual Review of Ecology and Systematics, 9:75-98.

Hoffmann, D., Vasconcelos, M.F. & Fernandes, G.W. 2020. The fate of endemic birds of eastern Brazilian mountaintops in the face of climate change. Perspectives in Ecology and Conservation, 18:257-266.

Hopper, S.D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. Plant Soil, 322:49-86.

Inouye, D.W. 1980. The Terminology of Floral Larceny. Ecology 61:1251-1253.

Irwin, RE., Brody, A.K. & Waser, N.M. 2001. The impact of floral larceny on individuals, populations, and communities. Oecologia, 129:161-168.

Irwin, R.E., Adler, L.S. & Brody, A.K. 2004. The dual role of floral traits: pollinator attraction and plant defense. Ecology, 85: 1503-1511.

Irwin, R.E., Galen, C., Rabenold, J.J., Kaczorowski, R. & McCutcheon, M.L. 2008. Mechanisms of tolerance to floral larceny in two wildflower species. Ecology, 89:3093-3104.

Irwin, R.E., Bronstein, J.L., Manson, J.S. & Richardson, L. 2010. Nectar Robbing: Ecological and Evolutionary Perspectives. Annual Review of Ecology, Evolution, and Systematics, 41:271-292.

Jacobi, C.M. & Carmo, F.F. 2011. The Contribution of Ironstone Outcrops to Plant Diversity in the Iron Quadrangle, a Threatened Brazilian Landscape. AMBIO A Journal of the Human Environment, 37:324-326.

Jacobi, C.M. & Antonini Y. 2008. Pollinators and defence of *Stachytarpheta glabra* (Verbenaceae) nectar resources by the hummingbird *Colibri serrirostris* (Trochilidae) on ironstone outcrops in South-East Brazil. Journal of Tropical Ecology, 24:301-308.

Jones, P.L. & Agrawal, A.A. 2017. Learning in insect pollinators and herbivores. Annual Review of Entomology, 62:53-71.

Karban, R. & Strauss, S.Y. 1993. Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. Ecology, 74:39-46.

Kearns, C.A. & Inouye, D.W. 1993. Techniques for Pollination Biologists. University Press of Colorado, 3:583.

Kolbek, J. & Alves, R.J.V. 2008. Impacts of cattle, fire and wind in rocky savannas, Southeastern Brazil. Acta Universitatis Carolinae Environmentalica, 22:111-130.

Kozlov, M.V., Lanta, V., Zverev, V. & Zvereva, E.L. 2015. Global patterns in background losses of woody plant foliage to insects. Global Ecology and Biogeography, 24:1126-1135.

Krupnick, G.A. & Weis, A.E. 1999. The effect of floral herbivory on male and female reproductive success in *Isomeris arborea*. Ecology, 80:135-149.

Krupnick, G.A., Weis, A.E. & Campbell, D.R. 1999. The consequences of floral herbivory for pollinator service to *Isomeris arborea*. Ecology, 80:125-134.

Labandeira, C.C. 2002. The history of associations between plants and animals. In: Herrera, C.M. & Pellmyr, O. (eds.) Plant-animal Interactions: An Evolutionary Approach. Blackwell Science, 2:26-261.

Labandeira, C.C. 2013. A paleobiologic perspective on plant-insect interactions. Current Opinion in Plant Biology, 16:414-421.

Lau, J.A. & Galloway, L.F. 2004. Effects of low-efficiency pollinators on plant fitness and floral trait evolution in *Campanula americana* (Campanulaceae). Oecologia, 141:577-583.

Lehtilä, K. & Strauss, S.Y. 1997. Leaf damage by herbivores affects attractiveness to pollinators in wild radish, *Raphanus raphanistrum*. Oecologia, 111:396-403.

Luo, Z., Zhang, S. & Renner, S.S. 2008. Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. Functional Ecology, 22:794-800.

Machado, I.C. & Lopes, A.V. 2004. Floral traits and pollination systems in the Caatinga, a Brazilian Tropical Dry Forest. Annals of Botany 94:365-376.

Madeira, J.A. & Fernandes, G.W. 1999. Reproductive phenology of sympatric taxa of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazilian Journal of Tropical Ecology, 15:463-479.

McCall, A.C. & Irwin, R.E. 2006. Florivory: the intersection of pollination and herbivory. Ecology Letters 9:1351-1365.

McCall, A.C. & Karban, R. 2006. Induced defense in *Nicotiana attenuata* (Solanaceae) fruit and flowers. Oecologia, 146:566-571.

McCall, A.C. & Fordyce, J.A. 2010. Can optimal defence theory be used to predict the distribution of plant chemical defences?. Journal of Ecology, 98:985-992.

McCall, A.C., Murphy, S.J., Venner, C. & Brown, M. 2013. Florivores prefer white versus pink petal color morphs in wild radish, *Raphanus sativus*. Oecologia, 172:189-195.

Mendes, G.M., Silveira, F.A.O., Oliveira, C., Dáttilo, W., Guevara, R., Ruiz-Guerra, B., Boaventura, M.G., Sershen, S. R., Phartyal, S.S., Ribeiro, S.P., Pinto, V.D., Vasconcelos, H., Tito R., Pereira, C.C., Carvalho, B., Carvalho, G.M., del Val, E., Buisson, E., Arruda, A., Toth, J.B., Roque, F., Souza, A.H., Bolzan, F., Neves, F.S., Kuchenbecker, J., Demetrio, G.R., Seixas, L., Romero, G., Omena, P.M., Silva, J.O., Paolucci, L., Queiroz, E., Ooi, M.K.J., Mills, C.H., Gerhold, P., Merzin, A., Massante, J.C., Aguilar, R., Carbone, L.M., Campos, R., Gomes, I., Zorzal, G., Solar, R., Ramos, L., Sobrinho, T., Sanders, P. & Cornelissen, T. 2021. How much leaf area do insects eat? A data set of insect herbivory sampled globally with a standardized protocol. Ecology, 102:e03301

Monteiro, B.L., Camargo, M.G.G., Loiola, P.P., Carstensen, D.W., Gustafsson, S. & Morellato, L.P.C. 2021. Pollination in the campo rupestre: a test of hypothesis for an ancient tropical mountain vegetation. Biological Journal of the Linnean Society, doi.org/10.1093/biolinnean/blaa205.

Moreira, X., Castagneyrol, B., Abdala-Roberts, L. & Traveset, A. 2019. A meta-analysis of herbivore effects on plant attractiveness to pollinators. Ecology, 100:e02707.

Mota, G.S., Luz, G.R., Mota, N.M, Coutinho, E.S., Veloso, M.D.M., Fernandes, G.W. & Nunes, Y.R.F. 2018. Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. Flora 238:32-42.

Mothershead, K. & Marquis, R.J. 2000. Fitness impacts of herbivory through indirect effects on plant–pollinator interactions in *Oenothera macrocarpa*. Ecology, 81:30-40.

Neal, P.R., Dafni, A. & Giurfa, M. 1998. Floral symmetry and its role in plant-pollinator systems: Terminology, Distribution, and Hypotheses. Annual Review of Ecology, Evolution, and Systematics, 29:345-373.

Ollerton, J., Killick, A., Lamborn, E., Watts, S. & Whiston, M. 2007. Multiple Meanings and Modes: On the Many Ways to Be a Generalist Flower. Taxon, 56:717-728

Ollerton, J., Winfree, R. & Tarrant, S. 2011. How many flowering plants are pollinated by animals?. Oikos 120:321–326.

Ollerton, J., Liede-Schumann, S., Endress, M.E., Meve, U., Rech, A.R., Shuttleworth, A., Keller, H.A., Fishbein, M., Alvarado-Cárdenas, L.O., Amorim, F.W., Bernhardt, P., Celep, F., Chirango, Y., Chiriboga-Arroyo, F., Civeyrel, L., Cocucci, A., Cranmer, L., da Silva-Batista, I.C., de Jager, L., Deprá, M.S., Domingos-Melo, A., Dvorsky, C., Agostini, K., Freitas, L., Gaglianone, M.C., Galetto, L., Gilbert, M., González-Ramírez, I., Gorostiague, P., Goyder, D., Hachuy-Filho, L., Heiduk, A., Howard, A., Ionta, G., Islas-Hernández, S.C., Johnson, S.D., Joubert, L., Kaiser-Bunbury, C.N., Kephart, S., Kidyoo, A., Koptur, S., Koschnitzke,, C., Lamborn E., Livshultz, T., Machado, I.C., Marino, S., Mema, L., Mochizuki, K., Morellato, L.P.C., Mrisha, C.K., Muiruri, E.W., Nakahama, N., Nascimento, V.T., Nuttman, C., Oliveira, P.E., Peter, C.I., Punekar, S., Rafferty, N., Rapini, A., Ren, Z.X., Rodríguez-Flores, C.I., Rosero, L., Sakai, S., Sazima, M., Steenhuisen, S.L., Tan, C.W., Torres, C., Trøjelsgaard, K., Ushimaru, A., Vieira, M.F., Wiemer, A.P., Yamashiro, T., Nadia, T., Queiroz, J. & Quirino, Z. 2019. The diversity and evolution of pollination systems in large plant clades: Apocynaceae as a case study. Annals of Botany, 123:311-325.

Parachnowitsch, A.L. & Kessler, A. 2010. Pollinators exert natural selection on flower size and floral display in *Penstemon digitalis*. New Phytologist, 188:393-402.

Pena, J.C., Goulart, F., Fernandes, G.W., Hoffmann, D., Leite, S.F.F., Britto, N.S., Soares-Filho, B., Sobral-Souza, T., Vancine, M.H. & Rodrigues, M. 2017. Impacts of mining activities on the potential geographic distribution of eastern Brazil mountaintop endemic species. Perspectives in Ecology and Conservation, 15:172-178.

Price, P.W. 1997. Insect Ecology. Jhon Wiley & Sons, 3:888.

R Core Team. 2021. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rapini, A., Ribeiro, P.L., Lambert, S. & Pirani, J.R. 2008. A flora dos campos rupestres da Cadeia do Espinhaço. Megadiversidade 4:16-24.

Rasmann, S., Alvarez, N. & Pellissier, L. 2014. The altitudinal niche-breadth hypothesis in insect-plant interactions. Annual Plant Reviews, 47:339-360.

Reddy, T.B., Rangaiah, K., Reddi,, E.U.B. & Reddi, C.S. 1992. Consequences of nectar robbing in the pollination ecology of *Vitex negundo* (Verbenaceae). Current Science Bangalore, 62:690-691

Riba-Hernández, P. & Stoner, K.E. 2005. Massive destruction of *Symphonia globulifera* (Clusiaceae) flowers by Central American spider monkeys (*Ateles geoffroyi*). Biotropica, 37:274-278.

Roddy A.B., Martínez-Perez C., Teixido A.L., Cornelissen T.G., Olson M.E., Oliveira R.S. & Silveira F.A.O. 2021. Towards the flower economics spectrum. New Phytologist, 229:665-672.

Rocha N.M.W.B., Carstensen D.W., Fernandes G.W., Le Stradic S., Buisson E. & Morellato L.P.C. 2016. Phenology patterns across a rupestrian grassland altitudinal gradient. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, 1:275-289.

Root, R.B.1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs,43:95-124.

Ruane, L.G., Rotzin, A.T. & Congleton, P.H. 2014. Floral display size, conspecific density and florivory affect fruit set in natural populations of *Phlox hirsuta*, an endangered species. Annals of Botany, 113:887-893.

Sargent, R.D. 2004. Floral symmetry affects speciation rates in angiosperms. Proceedings of the Royal Society of London, 271:603-608.

Silveira, F.A.O., Negreiros, D., Barbosa, N.P.U., Buisson, E., Carmo, F.F, Carstensen, D.W., Conceição, A.A., Cornelissen, T.G., Echternacht, L., Fernandes, G.W., Garcia, Q.S., Guerra, T.J., Jacobi, C.M., Lemos-Filho, J.P., Le Stradic, S., Morellato, L.P.C., Neves, F.S., Oliveira, R.S., Schaefer, C.E., Viana, P.L. & Lambers, H. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant Soil, 403:129-152.

Silva, J.O., Leal, C.R.O., Espírito-Santo, M.M. & Morais, H.C. 2017. Seasonal and diel variations in the activity of canopy insect herbivores differ between deciduous and evergreen plant species in a tropical dry forest. Journal of insect conservation, 21:667-676.

Simpson, M.G. 2019. Plant systematics. Elsevier Academic Press. 3:896.

Solís-Montero, L., Vergara, C.H. & Vallejo-Marín, M. 2015. High incidence of pollen theft in natural populations of a buzz-pollinated plant. Arthropod–Plant Interactions, 9:599-611.

Souza, C.S., Aoki, C., Ribas, A., Pott, A. & Sigrist, M.R. 2016. Floral traits as potential indicators of pollination vs. theft. Rodriguésia, 67:309-320

Strauss, S.Y., Conner, J.K. & Rush, S.L. 1996. Herbivory affects floral characters and plant attractiveness to pollinators: Implications for male and female plant fitness. The American Naturalist, 147:1098-1107.

Strauss, S.Y., Irwin, R.E. & Lambrix, V. 2004. Optimal defense theory and flower petal colour predict variation in the secondary chemistry of wild radish. Journal of Ecology, 92:132-141.

Strauss, S.Y & Whittall, J.B. 2006. Non-pollinator agents of selection on floral traits. In: Harder, L.D. & Barret, A.C.H. (eds.). Ecology and Evolution of Flowers. Oxford University Press, 1:120-138.

Teixido, A.L., Barrio, M. & Valladares, F. 2016. Size Matters: Understanding the Conflict Faced by Large Flowers in Mediterranean Environments. The Botanical Review, 82:204-228.

Turcotte, M.M., Davies, J., Thomsen, C.J.M. & Johnson, M.T.J. 2014. Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. Proceedings in Biological Sciences 281:20140555.

Vallejo-Marín, M., da Silva, E.M., Sargent, R.D. & Barrett, S.C. 2010. Trait correlates and functional significance of heteran-thery in flowering plants. New Phytologist, 188:418-425.

Zhao, Z.G. & Wang, Y.K. 2015. Selection by pollinators on floral traits in generalized *Trollius ranunculoides* (Ranunculaceae) along altitudinal gradients. PloS One 10:e0118299.

CHAPTER 2

The paradox of flowers at mountain ecosystems: flower attraction to pollinators vs attraction of unbidden florivores

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Keywords: *Campo rupestre*, Cerrado biome, elevation gradient, floral antagonists, floral visitors, flower attractivity, insect herbivory, insect-plant interactions, rupestrian grasslands.

Introduction

A large number of plants rely on animal-plant mutualisms for their persistence in evolutionary time. Interactions between plants and floral visitors are one of the main drivers of evolution since plants respond to selective pressures to maximize their attraction to pollinators to assure reproduction (Darwin 1877, Dodd et al. 1999, Fenster et al. 2004, Ollerton et al. 2019). The mutualisms of plants which depend on the services of pollinators have received attention since Darwin's time. Pollination is a widely documented interaction involving from generalist floral visitors pollinating several plant species to obligate specialists in which there exists a solely plant-pollinator pair of species (Waser 2006, Thompson 2005, Ollerton et al. 2007). World animal-pollinated species may represent 78% to 94% among the Angiosperms and tropical communities harbor a greater abundance of these species (Ollerton et al. 2011). Consequently, pollination is considered within the most important ecosystem services and its loss may result in catastrophic environmental, economic and social problems to humankind (Winfree et al. 2009, Potts et al. 2010, Novais et al. 2016, Porto et al. 2020). Therefore, shifts in flower visitor communities may not only have detrimental consequences for plant reproduction output, but also animals who depend on them are vulnerable to such changes (Senapathi1 et al. 2015, Körner et al. 2017).

Angiosperm morphology and flower visitor diversification is closely related (Dodd et al. 1999). However, entomophilous plants experience not only mutualistic interactions with pollinators and other floral visitors which may exert simultaneous opposite forces to selective pressures on floral attraction (Ruane et al. 2014, Lobo et al. 2016). These other visitors are considered floral antagonists and might behave as opportunists or strict florivores and/or robbers when foraging for nectar, pollen or floral tissues (Inouye 1980, McCall & Irwin 2006).

Floral antagonists incidence might be as extended and comprehensive as herbivory interactions, and in natural communities the consumption of flower organs might be as spread as leaf herbivory (Gélvez-Zúñiga et al. submitted, reviewed by Moreira et al. 2019). Thus, florivory effects have mostly been reported as detrimental to plant reproduction in both female and male components (Eliyahu et al. 2015, Bronstein et al. 2007, Jones & Agrawal 2017, Thompson & Fernandez 2006). Florivory can impact plant reproduction via direct trophic effects, due to insect consumption of floral structures (Krupnick & Weis 1999, Canela & Sazima 2003), or via indirect non-trophic effects, since floral attraction to pollinators diminish with the presence of florivory (Mothershead & Marquis 2000). Hence, the understanding of the dynamics between angiosperms and their flower visitors when coping with environmental changes may assure plant reproduction, insect food supplies and can help to prevent severe consequences in the near future (Liautaud et al. 2019).

Mountainous environments hold about a third of global plant species diversity and provide ecosystem services which are essential for the maintenance of human populations (Körner 2004, Colwell et al. 2008, Resende et al. 2013, Körner 2017, UNESCO 2017). Due to environmental changes over relatively short distances, mountains are excellent models to understand species responses in changing scenarios. Environmental variations along the elevation are linked to both plant and animal adaptive attributes and offer conditions to explore species responses in narrow geographic ranges (e.g., Fernandes & Price 1991, Fabbro & Körner 2004, Körner 2004, Nagano 2014, Fernandes et al. 2016b). Elevation-related changes in temperature, ambient humidity, solar radiation and land area reduction are among the most important factors globally associated to detectable changes in plant-animal dynamics (e.g. Humboldt 1817, Fernandes & Price 1988, 1991, Körner et al. 2017, Liautaud et al. 2019). So far, we are aware that climate change has provoked the contraction of endemic species distribution, extinction, and even homogenization in several mountain ecosystems around the globe due to upraise of lowland species and even opening up opportunities for biological invasions (Gilman et al. 2010, Tingley et al. 2012, Urban 2015, Hoffman et al. 2020). Therefore, such changes may deeply interfere with biotic interactions in mountainous environments (Lefebvre et al 2018, Lynn et al. 2019) with unforeseen catastrophic impacts.

Scenarios of environmental stress and limiting-resource habitats due to elevation gradients lead organisms to adjust and relocate resources to assure physiological functions and deal with the selective pressures in harsh environments such as *campo rupestre*. For instance, the growth and metabolic rates of insects have shown to decrease with elevation (Lefebvre et al. 2018). In addition, the size, abundance and richness of floral visitors also tend to decrease when the elevation increases (Nagano et al. 2014). Concomitantly, plant investments in vegetative and reproductive tissues are commonly reduced in species at upper elevations (Fabbro & Körner 2004, Hautier et al. 2009). For instance, a plant reduction in floral advertisements such as corolla size and quantity of nectar diminished with elevation in species from the Himalayan region (Basnett et al. 2019). Also, floral longevity reductions and shorter flowering periods have also been related to higher elevations (Primack 1985, Ashman & Arceo-Gómez 2013). Variations in flower number and size to match pollinator assemblages influenced by elevation have also been reported in several systems (Dohzono & Suzuki 2010, Parachnowitsch & Kessler 2010, Nagano et al. 2014, Zhao & Wang 2015). In tropical regions plants at mountainous environments may exhibit different strategies to fulfill pollination services when elevation increases. For instance, Arceo-Gómez et al. (2019) reported greater heterospecific pollen deposition performed primarily by vertebrates at upper elevations while insects furnish this function at lower elevations. This denotes the physiological costs of setting strategies to attract mutualist partners and guarantee plant reproductive success in less frequent pollinator contexts due to increased elevation constraints (Galen 1999, Carroll et al. 2001).

A set of morphological floral attributes (e.g. symmetry, corolla shape, floral reward, time of anthesis) has been broadly used when analyzing plant-insect interaction in pollination ecology or flower evolution contexts. Flowers with less restrictive morphological attributes, which are related to generalist flowers and generalized pollination systems (Ollerton et al. 2007), are predicted to allow a wide variety of visitors to access floral resources (e.g. pollen, nectar, tissue), increasing flower visitation likelihood when compared to restrictive flowers (Stang et al. 2006). Overall, flowers can be considered as less restrictive in morphology when rewards are open or exposed to be accessed by floral visitors (Frame 2003), regardless of their potential as pollinators or florivores. For instance, flowers with actinomorphic symmetry have shown to receive higher heterospecific pollen when compared to zygomorphic flowers at global scale (Arceo-Gómez et al. 2019). Additionally, non-pollinator visits have been related with floral attributes such as nectar rewards, small-sized flowers, greater number of open flowers and extended flowering periods in a Brazilian *palm swamp* plant community (Souza et al. 2016). The relationship between flower morphological attributes and investments in floral advertisement in plants that share or compete for pollinators are relatively clear, but since plants also set barriers against floral antagonists (Irwin et al. 2001, Gonzálvez et al. 2013) there is still a need for studies addressing the relationship between floral attributes and florivore insects.

The *campo rupestre* (rupestrian grassland) is a mega diverse, ancient, but highly threatened vegetation, which is mainly distributed in the Espinhaço Mountain Range, the second largest mountain chain in South America (Fernandes et al. 2020). For the first time, we addressed the variation of damages exerted by floral antagonist along the elevational gradient of *campo rupestre* and its relationship with floral advertisements and flower morphology. We hypothesized that increases in elevation will intensify plant susceptibility to floral antagonists since plant species are coping with harsher environmental conditions (Fernandes et al. 2016b, Mota et al. 2018) and because insect and plant diversity is negatively related to elevation increases in this mountain range (e.g., Perillo et al. 2017, Coelho et al. 2018, Nunes et al. 2018, Beirão et al. 2020, Castro et al. 2020). We expected: i) a decline in floral advertisement such as flower number, flower size, and number of flowering months as elevation increases; ii) an increase in the presence of florivory, proportion of attacked floral buds, open flowers, early fruits, and petal removal levels exerted by insects at upper elevations; and iii) a positive relationship between greater presence of florivory, attacked open flowers and levels of petal removal with both, plant investments in floral advertisement and elevation. Furthermore, we hypothesized that insect florivory will be triggered when flower resources are restricted in the community, since nectar, pollen and floral tissues represent important energetic and nutritional sources for insect herbivores (Nicolson 2011, Vaudo et al. 2020). We expected a greater proportion of attacked flowers and petal removal in months with lower production of flower resources in the community. Finally, we hypothesized that insect florivory in species with less limiting flower morphologies will exhibit greater damages by insect florivores, and that these damages will increase with the elevation. As less limiting flowers may enable several floral visitors groups to interact with floral structures and rewards, we expected a greater proportion of flowers attacked and petal removal levels as elevation increases in: i) nectariferous flowers; ii) flowers with actinomorphic symmetry; and iii) species with more than one potential pollinator group.

Material and methods:

Study site

This study was performed along the elevation variation in Serra do Cipó, southern portion of the Espinhaço mountain range, in southeastern Brazil. Broadly, the Serra do Cipó encompasses a *campo rupestre* landscape with patchy rocky outcrop vegetation dominated by grasslands with evergreen and sclerophyllous plants (Fernandes et al. 2016a, Silveira et al. 2016) (**Fig. 1a**). The region has humid subtropical climate type according to Köppen classification, and according to precipitation levels there are four seasons: warm rainy long-day summers between November and January; post-rainy transition period from February to April; dry cold short-day winters from May to September; and a post-dry period during October (Madeira & Fernandes 1999). Overall, the soils are predominantly nutrient-impoverished and covered by a highly adapted vegetation type (Negreiros et al. 2014). Across this environmental gradient in Serra do Cipó, the mean annual temperature, mean atmospheric pressure and soil temperature diminish with increasing elevation (Fernandes et al. 2016b). Conversely, mean wind speed and air humidity increases with increasing the elevation, while mean annual precipitation is higher at intermediate elevations (Fernandes et al. 2016b).

Landscape and habitats vary from Cerrado through *campo rupestre*, where plant species richness diminishes while increasing the number of individuals per species as elevation increases (Mota et al. 2018). Areas with lower elevation (~800 m a.s.l.) are characterized by sandy soils with small trees and shrubs from Cerrado vegetation, represented mainly by Fabaceae, Malpighyaceae, Asteraceae and Apocynaceae plant families. The species flowering periods in this community show some seasonality reaching a peak in the transition from dry to wet season (Rocha et al. 2016). As elevation increases, the landscape becomes a transition from Cerrado to *campo rupestre* vegetation (~900m) with rocky outcrops, small trees, shrubs and herbaceous plants represented by Verbecaceae, Rubiaceae, Nyctaginaceae, Malpighyaceae and Fabaceae (Mota et al. 2018). Flowering at this elevation belt is continuous over the year, making seasonality less explicit (Rocha et al. 2016). Habitats between 1000-1300m are predominantly sandy rocky grasslands, with intermittent dark clay soils and rocky outcrops, showing herbs and shrubs of *campo rupestre stricto sensu* vegetation with mainly Velloziaceae, Eriocaulaceae, Asteraceae, Poaceae and Melastomataceae species, and flowering and fruiting along the year (see Belo et al. 2013). Finally, the highest areas of the gradient (1300-1400m) are characterized by wet, organic clay substrate covered by sand and/or stones, and the prevailing vegetation are herbaceous plants from Eriocaulaceae, Asteraceae and Xyridaceae families and, a well defined flowering peak between February and March. Details on the flora and plant phenology can be found in Madeira & Fernandes (1999), Belo et al. (2013), Rocha et al. (2016) and Mota et al. (2018).

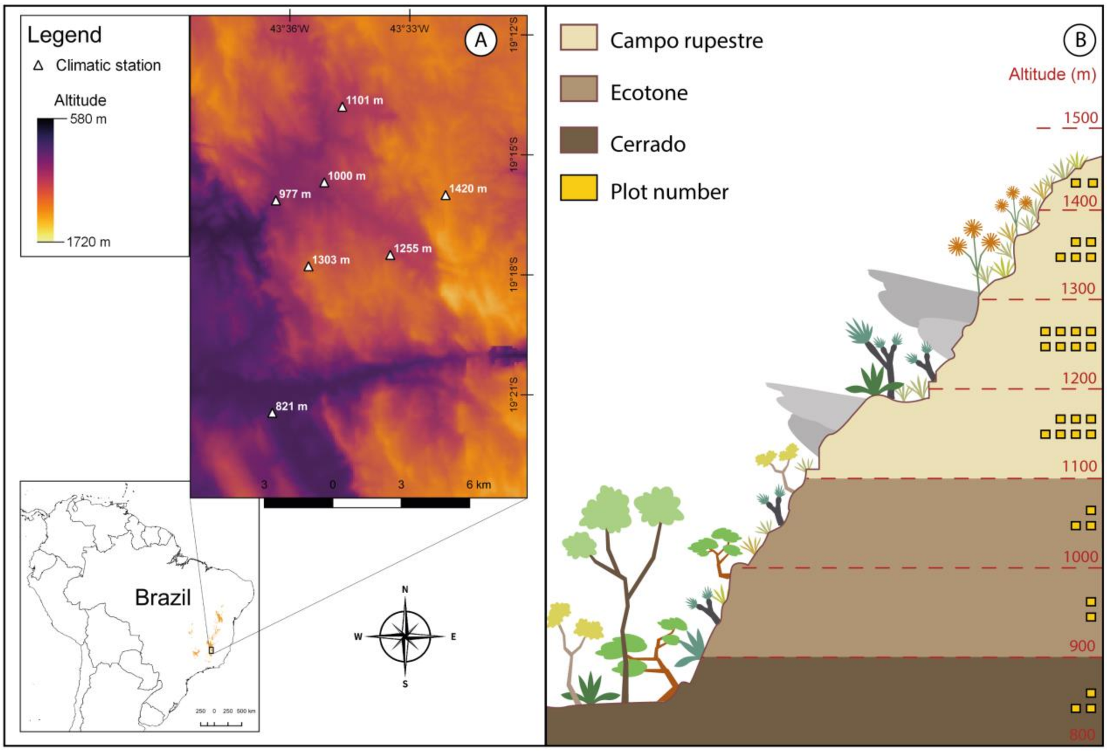

Figure 1. Study site within the Espinhaço mountain range and the elevation along the long-term ecological research site Serra do Cipó (LTER-CRSC), southeastern, Brazil. Data collection occurred monthly between May 2018 and August 2019. a) Area map and details of the elevation variation among the LTER-CRSC areas where flower damages exerted by insects was recorded; b) location of the thirty plots along the elevation in the dominant vegetation types, plots were approximately 500 m apart.

Data collection

Sampling was conducted between May 2018 and August 2019 along the elevation variation within the Long Term Ecological Research of Serra do Cipó LTER-CRSC, CNPq/Fapemig (PELD in portuguese abbreviation) sites between 800 and 1400 m a.s.l. Sites are located in the Serra do Cipó National Park and Morro da Pedreira Environmental Protection Area (See Fernandes 2016b and Silveira et al. 2019 for details). To address how the presence of damages exerted by florivore insects differ along the elevation variation, we performed a plant monthly census in 30 fixed plots (15m × 15m), spaced by 500 m from each other, with elevation varying from 823 to 1411 m a.s.l. (**Fig. 1b**); hence each plot represents a specific elevation value along the gradient. Up to ten individuals from the same species in plots were recorded at every campaign event. Despite of *campo rupestre* being a complex vegetation mosaic, we avoid setting plots nearby Atlantic forest patches (capão), and gallery forests. All plant material sampled was preserved for later identification by using literature, specialist's consultation and comparison with specimens from the Federal University of Minas Gerais

Herbarium (BHCB). Plant and insect material is currently in the Laboratório de Ecologia Evolutiva e Biodiversidade from the Federal University of Minas Gerais under the cataloging process.

To test if investments in flower advertisement decrease with elevation, we recorded three response variables. The first was the total number of open flowers (hereafter flower number) per plant individual, including attacked and non-attacked flowers. Second, the flower size of each plant species. Flowers with less than 10 mm were categorized as small, between 10-20 mm as medium, and with more than 20 mm were considered large flowers (adapted from Machado & Lopes 2004, see details in Gélvez-Zúñiga et al. submitted), and then the portion of each size category per plot was calculated. Third, the total number of months in which each plant species showed open flowers during the sampling period (hereafter flowering period). For all flowering individuals on plots the number of pre-anthesis floral buds, open flowers and early-stage fruits were recorded. Afterwards, the following response variables were quantified to test if florivore insect effects increase with elevation. The absence (**Fig. 2a**) or presence (**Fig. 2 b, c, d**) of floral damages by florivore insects (hereafter presence of florivory) per plant individual. The proportion of each individual pre-anthesis floral buds (hereafter attacked bud), open flowers (hereafter attacked flower) and early-stage fruits (hereafter attacked fruit) attacked by florivores. An organ (bud/flower/fruit) was considered attacked if exhibited any morphological modification resulting from insect feeding activities on any floral structures, as described for florivores in McCall & Irwin (2006). In this context, we included as florivore insect damages: i) pollen-robbing when anthers were removed or cutted to collect pollen (**Fig. 2b**), ii) any petal removal due to insect forage (**Fig. 2c**), and iii) nectar-robbing orifices in the flower calyx (**Fig. 2d**). Lastly, the proportion of petal area removed by insects (hereafter petal removal level) was estimated for every flower with signs of insect feeding in the corolla. The estimation of the amount of petal area removed was performed in a 0 to 100% scale at the field, where 0 represents flowers with intact corolla, 1 represents a 10% of, 2 represents a 20% and so on up to 10 which represents a completely (100%) removed corolla area by florivore insects.

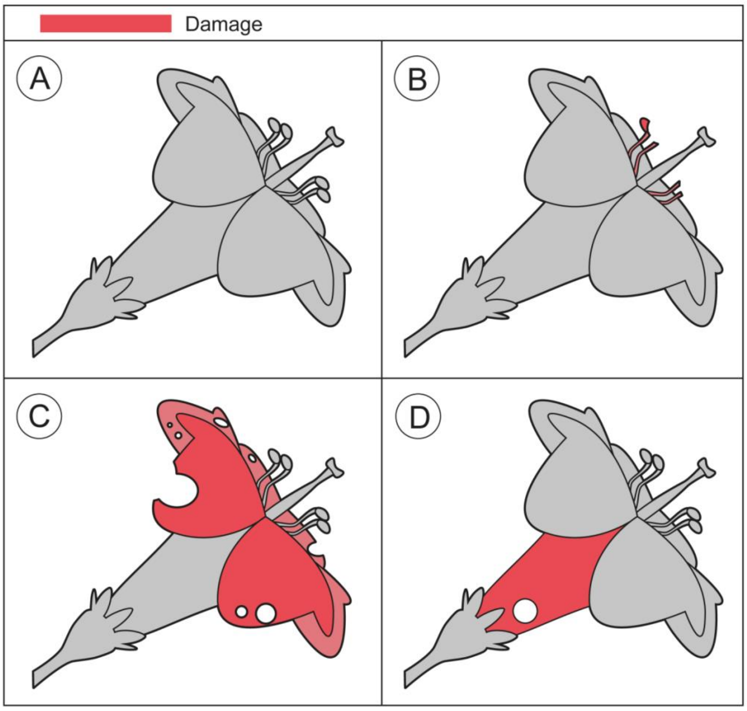

Figure 2. Damages exerted by floral antagonists recorded in flowers from the *campo rupestre* in the Espinhaço mountain range LTER-CRSC site, Brazil. Sampling events between May/18 and August/18. A) intact flower; B) pollen-robbing; D) petal removal; D) nectar-robbing holes. Sampling plots were approximately 500 m apart.

To assess if flowers with less limiting morphologies are more likely to show higher proportion of attacked flowers and petal removal levels along the elevation, we chose three variables commonly related with more accessible flowers to visitors (Frame 2003, Ollerton et al. 2007); floral reward, floral symmetry, and number of taxa reported for each plant species as potential pollination vectors (hereafter potential visitors). Each floral reward was classified as nectar, pollen, or oil according to field observations and/or literature searching for every plant species. The floral symmetry was categorized as actinomorphic, asymmetric, or zygomorphic according to Simpson (2006). Finally, the information about the potential visitors was gathered by linking our field observations, pollination systems and literature records for each plant species sampled in order to establish the number of potential visitors which visit or may be likely to visit the flowers of each species (Faegri & Pijl 1979, Freitas & Sazima 2006, Willmer 2011). Potential vectors were categorized as bat, bees, beetle, bird, butterfly, moth, wasp, and wind (adapted from Machado & Lopes 2004). Then, the total number of potential visitors for each plant species was calculated, ranging from 1 to 3.

Statistical analyses

To test if flower advertisements decrease with elevation Generalized Linear Models (GLMs) were performed using the elevation (m a.s.l.) as explanatory variable and flower number, flower size, and flowering period as response variables. The hypothesis that plant susceptibility to insect florivory increases with the elevation was tested using Generalized Linear Mixed Models (GLMMs) with elevation in m a.s.l. as unit as the explanatory variable and the proportion of attacked floral buds, flowers, fruits, and petal removal as response variables. Since plots were repeatedly measured, we considered them as random effects in all GLMMs, and for the models with the proportion of petal removal as response variable the plant individual was also added as a random effect because flowers with corolla removal from the same plant individual were repeatedly measured. The relationship between elevation, plant attractivity, and the presence of florivory was tested with GLMs using elevation (m a.s.l.), flower number, flowering period (months), and the interaction among them as explanatory variables, and the presence of florivory as response variable. GLMMs were constructed to test for the relationship between elevation (m a.s.l.), flower number, flowering period (months), and the interaction among them as explanatory variables and the proportion of attacked flowers and petal removal as response variables. To test for the variation in florivory by insects in months with greater number of species co-flowering we constructed GLMMs using the proportion of attacked open flowers and proportion of petal removal as response variables, and each sampling event (14 months) as the explanatory variable. Lastly, to test if less limiting flower morphologies show greater insect florivory effects at upper elevations, Generalized Linear Mixed Models (GLMMs) were constructed using floral reward, floral symmetry, and number of potential visitors and their interactions with the elevation (m a.s.l) as explanatory variables, and the proportion of attacked flowers and proportion of petal removal as response variables. When explanatory variables showed no significance in models they were removed from the analysis until the minimum adequate model (Crawley 2013). All GLMs and GLMMs were fitted for error distribution adequacy, and the *'lme4'* package was used to construct the GLMMs. In addition, when the effect of the random variable was 0 it was removed from the models. All the statistical analyses were performed using the R software v.4.0.2 (R Development Core Team, 2021).

Results:

A total of 12,340 flowering individuals distributed among 207 species and 46 angiosperm families were recorded. The plant families Asteraceae, Fabaceae, Lythraceae and Melastomataceae were present along the entire elevation variation and altogether represented

51 % (6,269 out of 12,340) of the total individuals recorded. The plant families recorded in only one single elevation were Euphorbiaceae (810 m), Onagraceae (819 m), Salicaceae (963 m), Rapataceae (1227 m), Loranthaceae (1128 m), Erythroxylaceae (1230 m), Rhamnaceae (1257m), Lentibulariaceae (1364 m), and Solanaceae (1405 m). Altogether they represented 29 % (9 out of 46) of all plant families sampled. No plant species was recorded throughout the entire elevation variation. The plots with the greater flowering plant abundance were located at 1118 m elevation, with 663 out of 12,340 or 5.4% of the total individuals sampled, followed by the 1364 m elevation with 4.5% (571) of the individuals, and the 1178 m elevation with 4.4% (545) of the individuals. Interestingly, the plots at lower elevation, located in the Cerrado vegetation, showed the lowest plant abundances of flowering individuals (**Table 1**). Florivory damages exerted by insects were distributed throughout the entire elevation areas reaching higher frequency at the 1118 m elevation with 194 out of 3,164 (6 %) of attacked flowers, followed by 1364 m elevation with 152 out of 3,164 and 1201 m elevation with 152 out of 3,164. Damages caused by insect robbery were present along the elevation gradient with the exception of the 324 m and 1257 m elevations. Finally, thieving damages were present at eight elevations including plots located along the elevation gradient and altogether represented 0.2% or 8 out of 3348 of the total floral damages. Coleoptera and Hymenoptera were the most abundant and species rich insects found damaging flowers along the variation in elevation. Altogether, insect families Chrysomelidae, Curculionidae and Formicidae represented nearly 80% of the total insect sampled in flowers.

Table 1. Flowering plant abundance, species richness, and plant investments in floral advertisement (mean ± SD) recorded from May 2018 to August 2019 along the elevation variation in Serra do Cipó, southeastern Brazil.

Vegetation	Altitude	Families	Plant abundance	Species richness	Plant attraction	
					Flower number (mean ± SD)	Flowering months (mean ± SD)
Cerrado	810	17	182	40	14.989 ± 22.119	6.791 ± 4.922
	823	14	191	32	10.733 ± 25.759	9.377 ± 4.471
	824	14	78	32	7.051 ± 14.762	7.615 ± 4.078
Ecotone	955	13	397	46	8.683 ± 17.386	9.761 ± 3.132
	963	22	405	52	8.153 ± 14.026	9.232 ± 3.353
	1015	20	380	46	9.876 ± 17.333	9.095 ± 3.954
	1022	20	500	50	12.552 ± 21.006	10.038 ± 3.061
	1040	19	433	49	6.473 ± 9.252	10.637 ± 3.129
Campo rupestre	1104	21	396	60	5.997 ± 11.772	10.455 ± 3.623
	1118	21	663	59	6.308 ± 14.441	10.857 ± 3.393
	1124	19	439	42	7.105 ± 11.427	10.797 ± 3.194
	1127	22	373	54	8.249 ± 15.534	10.504 ± 3.363
	1128	17	243	40	9.868 ± 18.431	10.074 ± 3.917
	1151	19	357	51	6.793 ± 11.020	9.661 ± 3.943
	1178	22	545	58	6.336 ± 11.297	10.932 ± 3.722
	1201	17	510	46	9.510 ± 19.764	11.790 ± 3.077
	1220	22	526	55	5.875 ± 12.885	10.909 ± 2.879
	1227	23	475	46	7.600 ± 10.980	11.389 ± 3.688
	1230	17	435	54	9.425 ± 16.877	10.630 ± 3.563
	1242	20	527	51	12.004 ± 29.959	10.605 ± 3.772
	1250	21	412	49	5.721 ± 8.690	10.490 ± 3.921
	1257	19	447	41	5.917 ± 9.911	11.412 ± 3.283
	1285	19	419	47	9.442 ± 16.991	10.382 ± 3.865
	1306	20	417	46	9.331 ± 18.211	10.695 ± 3.671
	1313	21	425	58	5.459 ± 14.172	10.031 ± 3.812
	1327	23	409	49	5.677 ± 10.814	10.907 ± 3.323
	1329	18	424	51	6.300 ± 17.247	10.219 ± 4.314
	1364	23	571	55	10.270 ± 27.079	9.126 ± 3.959
	1405	14	367	38	5.597 ± 14.240	9.684 ± 4.404
	1411	14	394	33	6.071 ± 13.030	9.561 ± 3.856

The greater plant species richness was found in plots at 1104 m with 29% (60 out of 207 species) of the total plant species recorded, followed by 1118 m elevation with 28.5% (59 out of 207) and 1178 m and 1313 m elevations both with 58 out of 207 plant species each (see details on plant families, richness and abundance in **Table 1**). The most frequent plant species along the elevation gradient were *Chromolaena squalida* (Asteraceae) recorded in 90% of the elevations sampled (**Fig. S1a**). *Marcetia taxifolia* (Melastomataceae) and *Xyris nubigena* (Xyridaceae) were both present in 83% (25 out of 30 plots) of the elevation gradient (**Fig. S1b, c**), followed by *Cuphea ericoides* (Lythraceae) and *Lavoisiera confertiflora* (Melastomataceae) both present in 24 out of 30 plots or 80% of the elevation gradient (**Fig. S1d, e**).

Floral advertisement along the elevation

As expected, the number of flowers produced by plant individuals diminished with increasing elevation (χ^2= 62.498, p<0.001) (**Fig. 3a**). Greater flower number was found in the 810 m elevation with mean number of open flowers of 14.989 ± 22.119 (mean ± SD) flowers per plant individual, followed by the 1022 m elevation with mean of 12.552 ± 21.006 flowers per plant, and 1242 m elevation with mean of 12.004 ± 29.959 flowers per plant. Overall, individuals in the 1327 m, 1329 m, and 1405 m elevation showed lower investments in flower numbers (**Table 1**). The effect of elevation on the proportion of plant species flower size varied depending on the size category (χ^2= 16.845, p <0.001). While the small-sized flowers proportion decreased with the elevation, the proportion of medium and large flowers increased with elevation (**Fig. 3b**). Opposite to expected, the species flowering period at higher elevations were greater than in species at lower elevations (χ^2=60.707, p<0.001) (**Fig. 3c**).

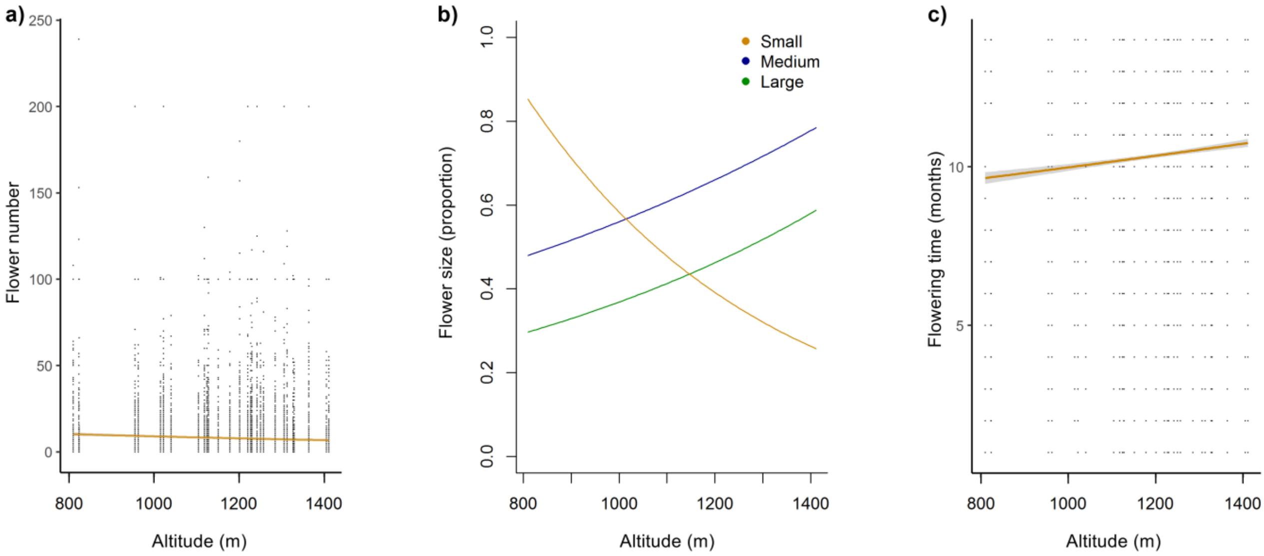

Figure 3. Investments in floral advertisement along the 824-1411 m a.s.l elevation variation showing that a) number of open flowers decreases with elevation, b) proportion of species with medium and large flowers increase and small flowers decrease with elevation, c) number of months each species flowered increased with elevation. Sampling between May 2018 and August 2019 in Serra do Cipó, Southeastern Brazil.

Flower damages exerted by insects along the elevation

The plant species that showed greater signs of florivory and proportion of attacked flowers at higher elevation plots were *Microlicia confertiflora* (**Fig. 4a**), *Lavoisiera caryophyllea* and *Pleroma villosissimum*, all belonging to Melastomataceae, along with *Vellozia epidendroides* (**Fig. 4b**) and *Barbacenia flava* (**Fig. 4c**) both from Velloziaceae. At intermediate elevations the flowers attacked the most by florivores were *Marcetia taxifolia* (**Fig. 4d**), *Microlicia* *tomentella* and *Lavoisiera glandulifera* from Melastomataceae, followed by *Cuphea micrantha* (Lythraceae) (**Fig. 4e**), *Vellozia variabilis* (**Fig. 4f**) and *Vellozia caruncularis* from Velloziaceae. Finally, at lower elevations, the species with greater proportion of floral damages were *Tetrapterys microphylla* (Malpighiaceae) (**Fig. 4g**), *Chamaecrista desvauxii* (Fabaceae), *Lavoisiera glandulifera* (**Fig. 4h**) and *Fritzschia stenodon* both from the Melastomataceae family, and *Peixotoa tomentosa* (Malpighiaceae) (**Fig. 4i**).

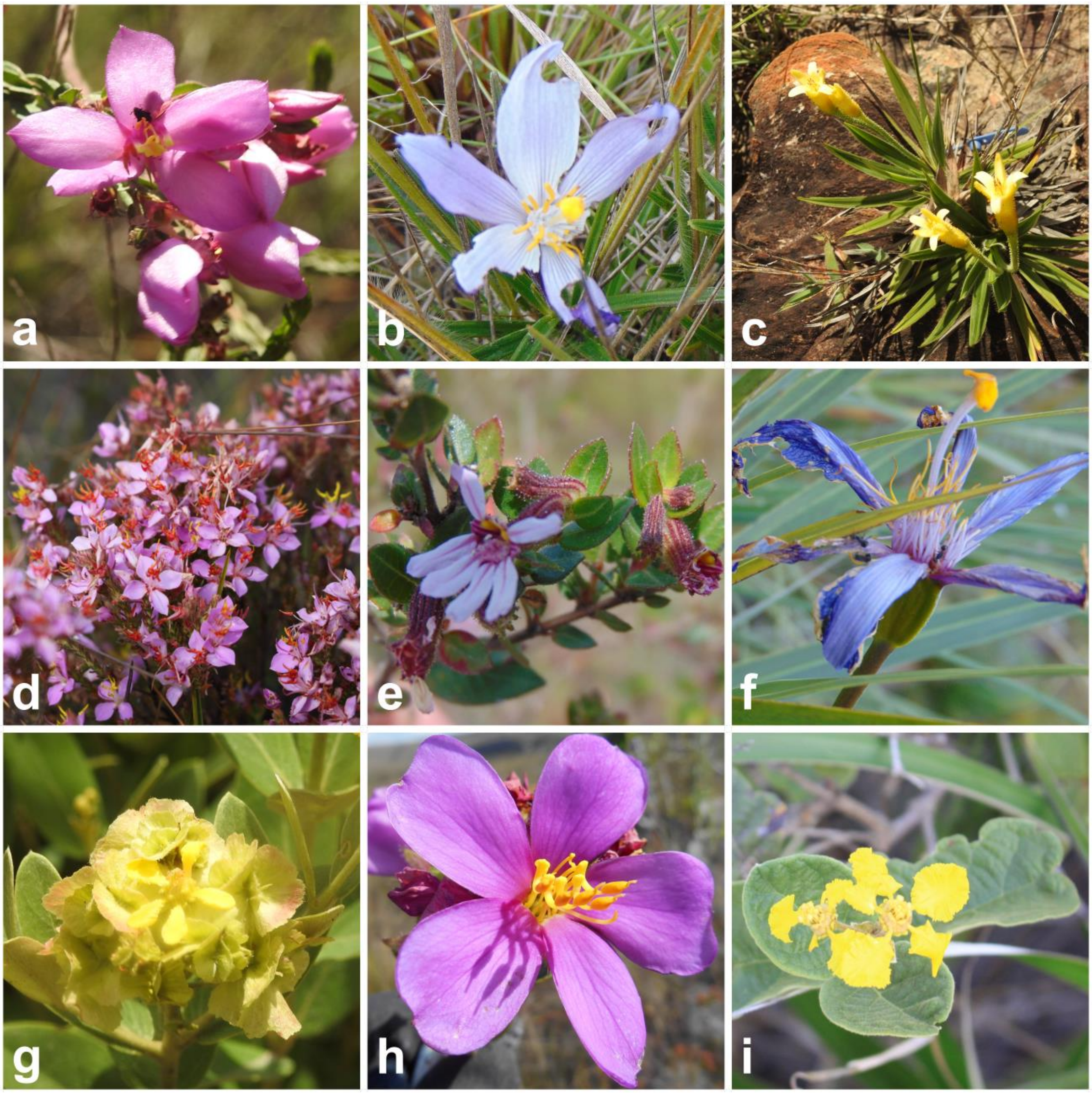

Figure 4. Plant species with greater presence of damages and proportion of attacked flowers by insect florivores along 823 to 1411 m a.s.l. elevation in Serra do Cipó, Southeastern Brazil. Upper plots -from 1364-1411 m a.s.l.- a) *Microlicia confertiflora*, b) *Vellozia epidendroides*, c) *Barbacenia flava*. Intermediate plots -between 1151 and 1201 m a.s.l.- d) *Marcetia taxifolia*, e) *Cuphea micrantha*, f) *Vellozia variabilis*. Lower plots -from 810 to 824 m a.s.l.- g) *Tetrapterys microphylla*, h) *Lavoisiera glandulifera*, i) *Peixotoa tomentosa*.

As expected by the hypothesis of greater plant susceptibility to insect florivory when increasing the elevation, the presence of florivory was slightly greater in plant individuals from upper elevations when compared to individuals at lower elevations (χ^2=5.7018, p=0.01695, **Table 3**). The greatest proportion of attacked flowers was found in the 1313 m a.s.l. elevation with an average of 0.273 ± 0.428 (mean ± SD), followed by the 1220 elevation with an average of 0.212 ± 0.385, and the 1201 elevation with 0.205 ± 0.356. Additionally, the proportion of attacked flowers by insect florivores in plant individuals at upper elevations was also greater than in plants at lower elevations (χ^2= 57.535, p<0.001, **Fig. 5a**). On the other hand, the elevation solely did not influence the proportion of pre-anthesis floral buds (p= 0.8141), early-stage fruits (p= 0.8892) and petal removal levels (p= 0.1216) (**Table 3**). The greatest proportion of pre-anthesis floral buds attacked was found in the 1327 m elevation with an average of 0.064 ± 0.214, followed by the 823 m elevation with an average of 0.056 ± 0.195, and the 1201 m elevation with 0.054 ± 0.184 (**Table 2**). The greatest proportion of early-stage fruits attacked was found in the 823 m elevation with an average of 0.043 ± 0.195, followed by the 1327 m elevation with an average of 0.016 ± 0.124, and the 1364 m elevation with an average of 0.015 ± 0.113 (**Table 2**). Finally, the greatest proportion of petal removal was found at the 1040 m elevation with an average of 0.482 ± 0.277, followed by the 824 m elevation with an average of 0.419 ± 0.291, and the 1285 m elevation with 0.358 ± 0.216 of mean petal removal level (**Table 2**).

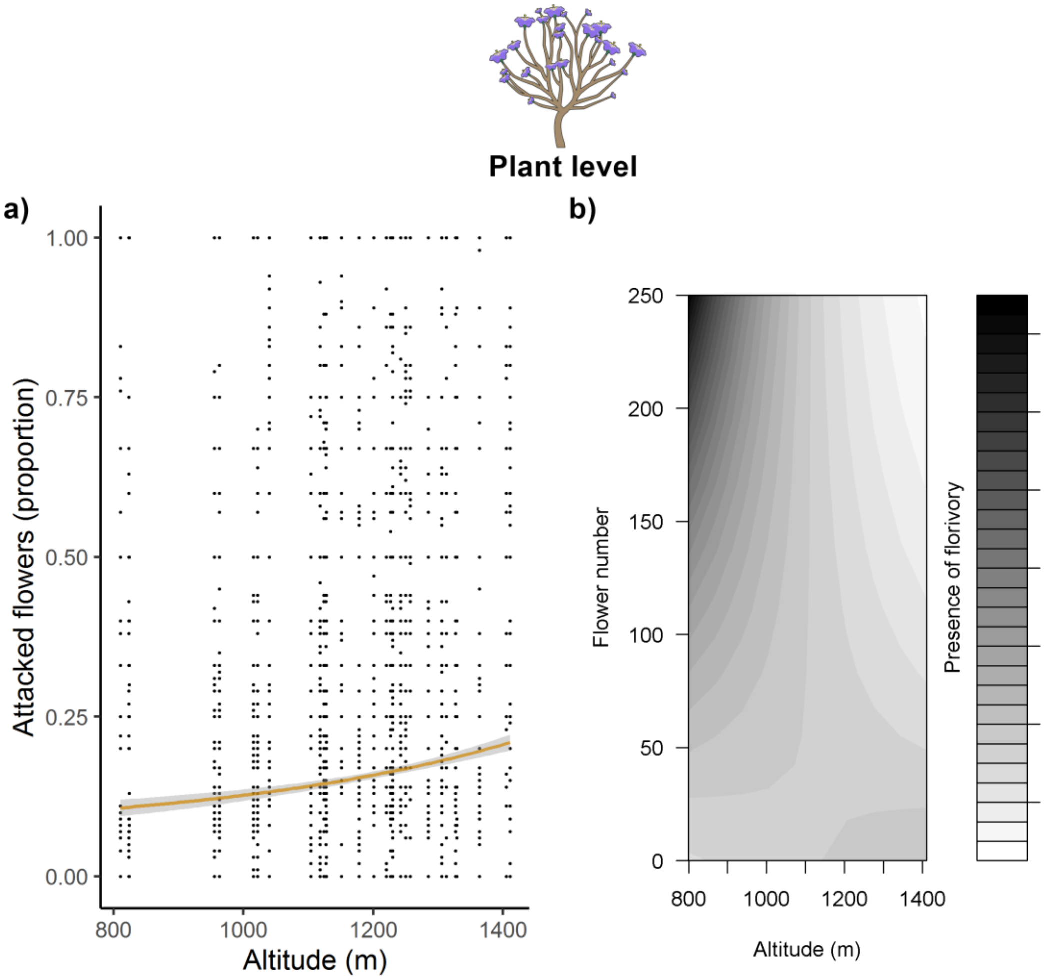

Figure 5. Florivory exerted by insect florivores along thirty plots ranging from 823 to 1411 m a.s.l. in *campo rupestre* plant community, southeastern, Brazil. Data collection occurred between May 2018 and August 2019. a) The proportion of attacked open flowers increases along the elevation; b) effect of the elevation in the presence of florivory, showing that at lower elevations in plants individuals with greater flower number.

Table 2. Floral damages exerted by insects along the elevation gradient in *campo rupestre* plant community in Serra do Cipó, Brazil between May 2018 and August 2019. Main vegetation type, plot elevation (N=30), proportion (mean ± SD) of attacked pre-anthesis floral buds, open flowers, early-stage fruits, and proportion of petal removal.

Vegetation	Altitude (m)	Proportion of floral damages on			
		floral buds (mean ± SD)	open flowers (mean ± SD)	early fruits (mean ± SD)	petal remotion (mean ± SD)
Cerrado	810	0.048 ± 0.151	0.108 ± 0.252	0.004 ± 0.034	0.247 ± 0.186
	823	0.056 ± 0.195	0.168 ± 0.325	0.007 ± 0.074	0.279 ± 0.181
	824	0.047 ± 0.183	0.094 ± 0.240	0.043 ± 0.195	0.419 ± 0.291
Ecotone	955	0.048 ± 0.152	0.104 ± 0.245	0	0.269 ± 0.190
	963	0.035 ± 0.143	0.116 ± 0.256	0.002 ± 0.037	0.343 ± 0.242
	1015	0.017 ± 0.100	0.100 ± 0.228	0.005 ± 0.009	0.287 ± 0.219
	1022	0.036 ± 0.144	0.090 ± 0.223	0.004 ± 0.049	0.260 ± 0.187
	1040	0.047 ± 0.188	0.132 ± 0.294	0.004 ± 0.007	0.482 ± 0.277
Campo rupestre	1104	0.042 ± 0.159	0.099 ± 0.247	0.008 ± 0.087	0.304 ± 0.207
	1118	0.040 ± 0.158	0.180 ± 0.335	0.002 ± 0.040	0.328 ± 0.256
	1124	0.048 ± 0.195	0.180 ± 0.350	0.005 ± 0.064	0.335 ± 0.225
	1127	0.044 ± 0.159	0.140 ± 0.286	0.001 ± 0.026	0.268 ± 0.217
	1128	0.052 ± 0.186	0.117 ± 0.253	0.001 ± 0.018	0.310 ± 0.220
	1151	0.029 ± 0.147	0.159 ± 0.306	0.002 ± 0.044	0.355 ± 0.274
	1178	0.019 ± 0.118	0.146 ± 0.319	0	0.311 ± 0.197
	1201	0.054 ± 0.184	0.205 ± 0.356	0.001 ± 0.014	0.324 ± 0.230
	1220	0.031 ± 0.161	0.212 ± 0.385	0	0.328 ± 0.230
	1227	0.050 ± 0.185	0.120 ± 0.282	0.005 ± 0.067	0.312 ± 0.235
	1230	0.033 ± 0.147	0.144 ± 0.285	0.003 ± 0.049	0.266 ± 0.212
	1242	0.054 ± 0.196	0.161 ± 0.315	0.003 ± 0.045	0.310 ± 0.233
	1250	0.037 ± 0.152	0.181 ± 0.326	0.002 ± 0.030	0.352 ± 0.237
	1257	0.025 ± 0.123	0.153 ± 0.313	0.011 ± 0.088	0.285 ± 0.190
	1285	0.030 ± 0.150	0.160 ± 0.317	0.002 ± 0.049	0.358 ± 0.216
	1306	0.054 ± 0.188	0.194 ± 0.335	0.001 ± 0.018	0.328 ± 0.218
	1313	0.025 ± 0.135	0.273 ± 0.428	0.001 ± 0.016	0.273 ± 0.178
	1327	0.064 ± 0.214	0.189 ± 0.331	0.016 ± 0.124	0.323 ± 0.219
	1329	0.027 ± 0.145	0.160 ± 0.353	0.002 ± 0.049	0.316 ± 0.212
	1364	0.038 ± 0.168	0.193 ± 0.365	0.015 ± 0.113	0.358 ± 0.256
	1405	0.039 ± 0.174	0.166 ± 0.351	0.007 ± 0.068	0.289 ± 0.188
	1411	0.026 ± 0.120	0.196 ± 0.350	0.001 ± 0.025	0.299 ± 0.218

Plant individuals with greater flower numbers exhibited greater presence of florivory at lower elevations, and florivory incidence decreased simultaneously in individuals with fewer open flowers (lower flower number) and as elevation increased (χ^2= 69.061, p<0.001, **Fig. 5b**). The proportion of attacked flowers was greater in plants at upper elevations and with longer flowering periods and decreased gradually with decreasing elevation and in species with shorter flowering periods (χ^2=69.17, p<0.001, **Fig 6a**). In addition, the proportion of attacked flowers in individuals with more than 100 flowers was very low regardless of the elevation, but gradually increased in individuals with fewer open flowers and with increasing elevation (χ^2=208.7, p<0.001, **Fig. 6b**). Lastly, the proportion of petal removal was greater on individuals with greater flowering periods at lower elevations and decreased with the elevation. Overall, petal removal levels increased with elevation regardless the species flowering period (χ^2=0.00177, $p<0.001$, **Fig. 6c**).

Table 3. Results of Generalized Linear Models and Generalized Linear Mixed Models showing the effect of the elevation on the presence of florivory, proportion of attacked flowers, pre-anthesis floral buds and early-stage-fruits attacked and petal removal levels exerted by florivore insects in *campo rupestre* in Serra do Cipó, between May 2018 and August 2019.

Response variable	**Explanatory variable**	**Random factor**	**p**	**χ^2**	**df**	**Error distribution**
Presence of florivory	Altitude		**0.01695**	5.701	1	Binomial
	Altitude + display + altitude:display		**<0.001**	69.061	6	Quasibinomial
Attacked flowers	Altitude	Plot	**<0.001**	57.535	1	Binomial
	Altitude + Flower number		**<0.001**	208.7	2	Binomial
	Altitude + Flowering time		**<0.001**	69.17	2	Binomial
	Altitude + Flower size		**<0.001**	528.53	3	Binomial
Attacked floral buds	Altitude	Plot	0.8141			
	Altitude : Flower number		0.0834			
	Altitude + Flowering time		0.6490			
Attacked early fruits	Altitude	Plot	0.8892			
	Altitude: Flower number		0.9930			
	Altitude: Flowering time		0.5260			
Petal removal level	Altitude	Plot & Individual	0.1216			
	Altitude: Flower number		0.08336			
	Altitude: Flowering time		**0.00177**	15.051	3	Binomial
	Altitude: Flower size		**0.005584**	19.994	7	Binomail

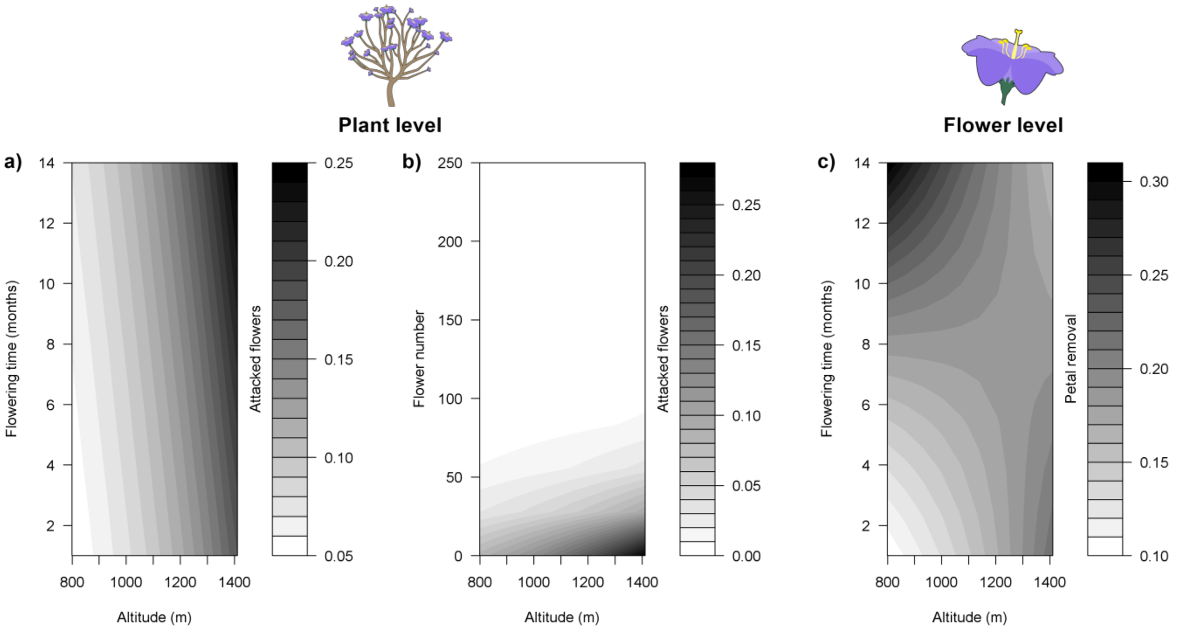

Figure 6. Influence of the elevation (823-1411 m a.s.l.) in florivory exerted by insect in a *campo rupestre* plant community, southeastern, Brazil. a) Greater proportion of attacked flowers in species with longer flowering periods at upper elevations; b) greater proportion of attacked flowers in individuals with larger flower numbers regardless of the elevation; c) greater proportion of petal removal in species with longer flowering periods at lower elevations.

Overall, 13% (27 out of 207) of the total plant species recorded flowered during 11 months or more. Nine species produced flowers throughout the 14-month sampling events: *Aspilia jolyana* (Asteraceae), *Chamaecrista desvauxii* (Fabaceae), *Gomphrena incana* (Amaranthaceae), *Tetrapterys microphylla* (Malpighiaceae), *Vochysia pygmaea* (Vochysiaceae), *Xyris nubigena* (Xyridaceae) and form the Melastomataceae *Lavoisiera confertiflora*, *Marcetia taxifolia* and *Siphanthera arenaria*. Interestingly, 20% (N= 41) of the plant species flowered exclusively during one sampling event. The greatest species flowering abundance occurred in early February and accounted for the 10% (1,227 out of 12,340) of all sampled plant individuals, followed by early March with 953 out of, and November with 913 out of flowering individuals. On the other hand, the lowest flower abundances were registered in July/19 with 612 individuals or 5% of flowering individuals recorded, followed by June with 732 individuals, and October with 745 individuals, each one representing 6% of the total flowering individuals recorded.

Greater number of plant individuals flowering occurred in February/18 (1227 out of 12,340), September/18 (1110 individuals), and August/18 (1071 individuals), and altogether accounted for 27% of the total flowered plants sampled. On the other hand, lower numbers of flowering individuals were in July/19 (612 individuals), June/19 (723 individuals) and July/18 (744 individuals), altogether accounting for the 16% of the total individuals flowering during the sampling events. Interestingly, the greater number of total flowers (independent of the abundance of individuals) occurred in August/19 (9152 flowers), followed by September/18 (9288 flowers), and August/18 (8637 flowers). The greater proportion of open flowers attacked by insect florivores occurred in both sampling events corresponding to July -18 and /19- (χ^2=215.93, p<0.001). The proportion of flowers attacked by insect florivores showed no differences in the months of August/18, February, March, May, June and August/19, while the lower attack occurred in October and April (**Fig. 7a**). Remarkably, the lowest proportion of petal removal in single flowers occurred in June/19 and August/19 (χ^2=213.95, p<0.001), which are also the months with greater flower abundance in the plant community. The greater proportion of petal removal on single flowers occurred in May/19 and March while the proportion of petal removal by insect florivores showed no differences in the months of July/18, April and May (**Fig. 7b**).

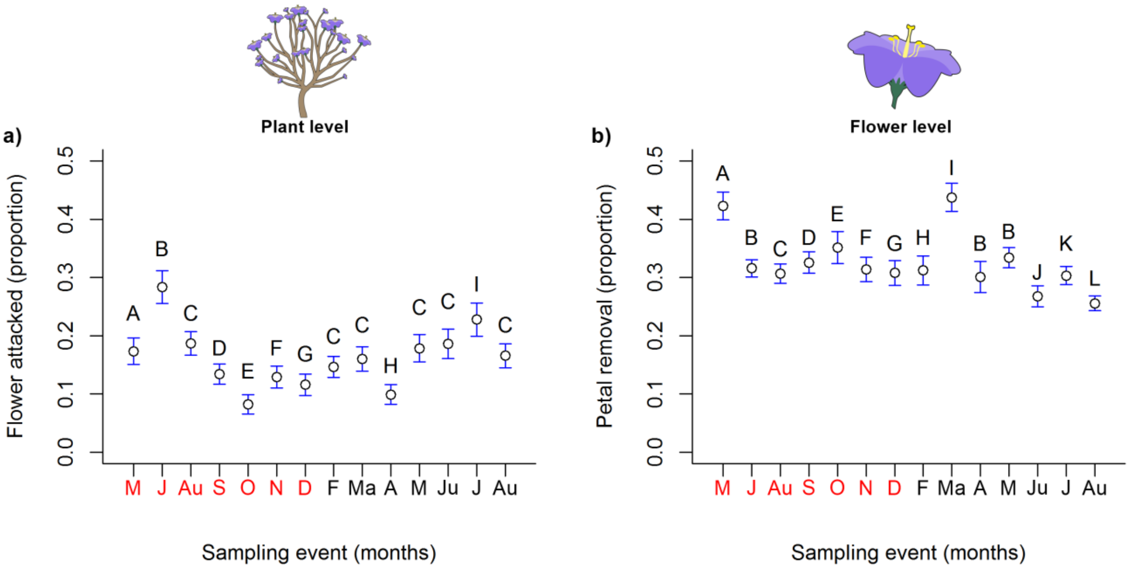

Figure 7. Variation on the a) average proportion of attacked open flowers and b) and average proportion of petal removal exerted by florivores in *campo rupestre* plant community, southeastern, Brazil. Data collection between May 2018 (red letters in the x label axis) and August 2019 (black letters in the x label axis). Sampling event numbers represent: M: May/18; J: early July/18; Au: August/18; S: September/18; O: October/18; N: November/18; D: December/18; F: early February/19; Ma: March/19; A: April/19; M: May/19; Ju: June/19; J: July/19, and Au: August/19. Different letters mean statistical differences between each month average value.

Flower morphology and insect florivore attack

Individuals with nectariferous flowers were more common in the 1022 m, 1178 m, 1220 m elevation plots and altogether represented 17% (915 individuals) of the total individuals with nectar producing flowers along the elevation variation. Pollen flowers were more frequent in the 1118 m, 1242 m and 1313 m elevation plots and altogether accounted for the 18% (1182 individuals) of the total pollen-rewarded individuals. The greatest abundance of oil-rewarded flowers was in the 1127 m, 1128 m and 1015 m elevation plots, and altogether represented the 27% (310 individuals) of the total individuals with oil flowers. Flowers with nectar and pollen rewards showed greater proportion of attacked flowers at higher elevations, while oil flowers showed no differences and (χ^2= 239.79, p<0.001, **Fig. 8a**). Additionally, the proportion of petal removal exerted by insect florivores in nectariferous and oil-flower species increased with elevation, while the petal removal in pollen-rewarded flowers slightly decreased with elevation (χ^2= 68.725, p<0.001, **Fig. 8b**).

Flowers with actinomorphic symmetry were more frequent in the 1118 m, 1364 m, and 1242 elevation plots, and altogether accounted for 1498 out of 7717 (20%) of the total radial symmetry flowers. Zygomorphic flowers were more abundant in the 1040 m, 1230 m, and 1178 m elevation plots and altogether represented 648 out of 3901 (16%) of the total bilateral symmetry flowers. Species with asymmetric flowers were more frequent in 1327 m, 823 m, and 1285 and altogether accounted for 212 out of 722 (29%) of the total species with asymmetric corolla. As expected by the hypothesis of less limiting flower morphologies, the attack by insect florivores in different flower symmetries was affected by the elevation (χ^2= 189.66, p<0.001). The greatest proportion of attacked flowers occurred in flowers with actinomorphic symmetry, followed by asymmetric and zygomorphic flowers (**Fig. 8c**). Interestingly, the proportion of petal removal on actinomorphic flowers slightly decreased with elevation, while petal removal in zygomorphic flowers increased with elevation and petal removal on asymmetric flowers was not affected by the elevation (χ^2= 61.771, p<0.001, **Fig. 8d**).

Species with limiting morphologies to flower visitors were more frequent in plots with 1118 m, 1022 m, and 955 m elevation, and altogether accounted for 14% or 1,138 out of 8,091 of the total individuals visited solely by one potential visitor. Species visited by two potential visitor groups were more abundant in plots at 1364 m, 1118 m and 1405 m, and altogether represented 20% or 655 out of 3,291 of the total plants with two groups of visitors. Finally, species with less limiting morphologies to visitors were more frequent in plots at 1201 m, 1227 m, and 1124 m elevations and altogether accounted for 37% or 358 out of 958 of the total individuals visited by three or more groups. The proportion of attacked flowers increased along the elevation for species with one, two and three or more potential visitors, however species visited just by one visitor group showed greater attack than less limiting morphologies species (χ^2= 371.52, p<0.001, **Fig. 8e**). Interestingly, the greater proportion of petal removal occurred in species with a single (1) potential visitor group and was negatively related with increased elevation (χ^2=16.201, p= 0.006293). Lastly, the proportion of petal removal increased in species with less limiting morphologies as elevation increased, while flowers from species with two potential visitors were not affected by the elevation (**Fig. 8f**).

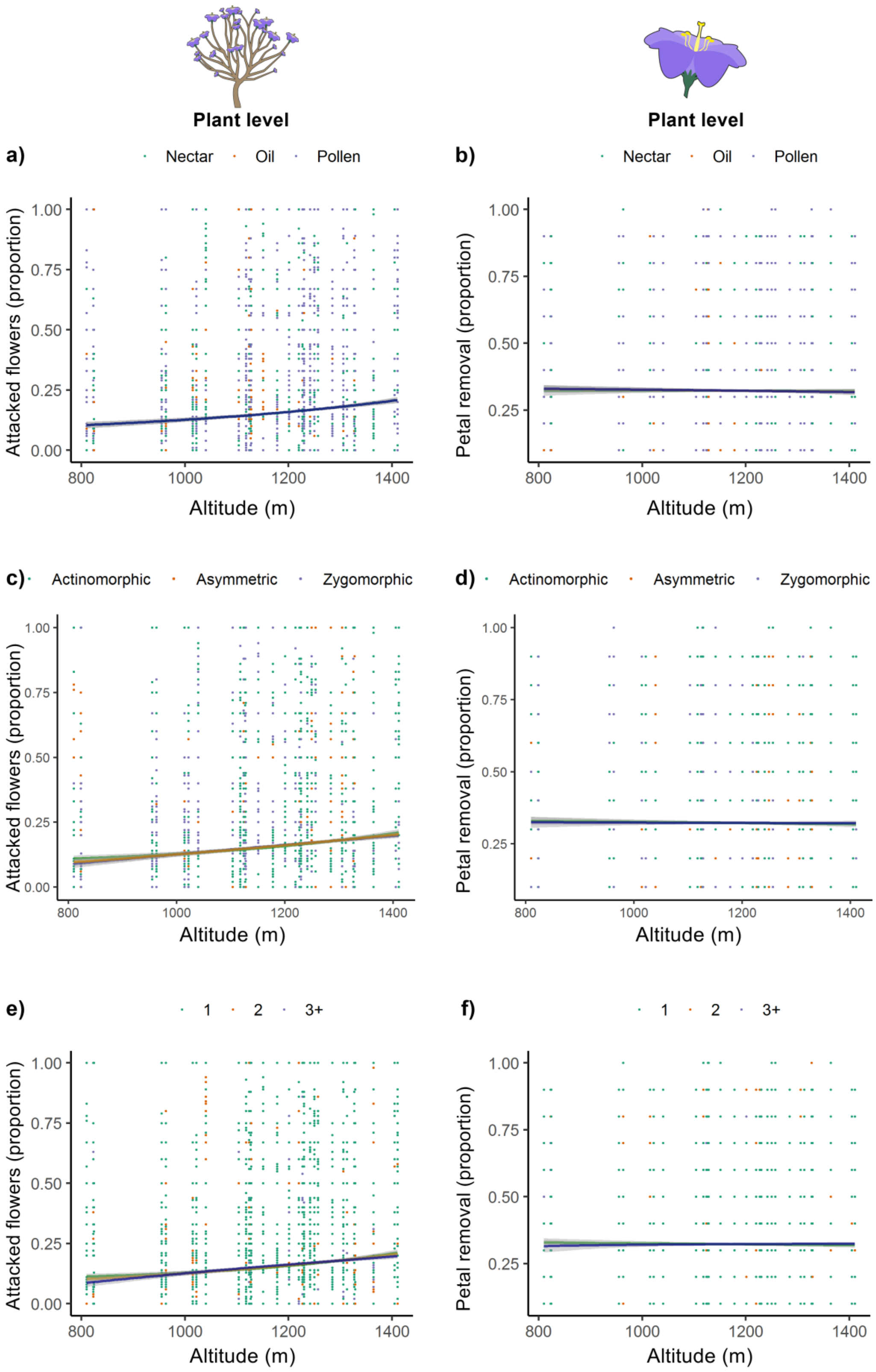

Figure 8. Floral damages exerted by insects along the elevation variation (800 m a.s.l. to 1400 m a.s.l) in the *campo rupestre* in Serra do Cipó, Brazil. a) The proportion of attacked flowers in nectar and pollen species increased with the elevation, b) Proportion of petal removal according to plant species floral reward, c) Proportion of attacked flowers according to plant species flower symmetry, d) Proportion of petal removal according to plant

species flower symmetry, e) Proportion of attacked flowers according to plant species potential visitors, f) Proportion of petal removal according to plant species potential visitors. In e) and f): one potential visitor: 1; two potential visitors: 2; and three or more potential visitors: 3+.

Discussion:

This study reports novel information about the spacio-temporal variation of damages exerted by floral antagonists along an elevation gradient in a tropical mountaintop ecosystem. The total number of open flowers per individual and the proportion of small-sized flowers were negatively affected when elevation increased. In addition, the presence of insect florivory and the proportion of attacked flowers were positively related with increases in elevation, and higher presence of florivory occurred on plants with greater flower number. The proportion of attacked flowers by insect florivores increases with both elevation and longer flowering periods. Moreover, the proportion of petal removal raises progressively when increasing elevation, and it was greater in species with longer flowering periods. In months with fewer flowers available in the community we demonstrated a greater proportion of attacked flowers by insect florivores. Ultimately, we report novel data in the relationship between insect florivores and less restrictive flower morphologies along the elevation gradient in the ancient and speciose *campo rupestre* landscape. Species with nectariferous flowers showed greater proportion of petal removal by florivores and it increased with elevation. Furthermore, the proportion of attacked flowers increased with elevation in flowers with actinomorphic symmetry, while the proportion of petal removal in species with several potential visitors was positively related to increased elevation.

Asteraceae, Fabaceae, Lythraceae and Melastomataceae plant families were the most abundant in terms of individuals along the elevation and altogether represented 51% of the total plant community. These four plant families were also reported among the most species-rich in the floristic survey performed in this mountain range (Mota et al. 2018) and other *campo rupestre* plant communities (Conceição et al. 2016, Silveira et al. 2016). Interestingly, we found greater species richness in the Velloziaceae family than Mota et al. (2018), which was also among the most attacked by insect florivores (Gélvez-Zúñiga et al. submitted). Our results show the lowest abundance and species richness of flowering plants at lower elevations, in Cerrado vegetation areas, which differs from the findings of Rocha et al. (2016) and Mota et al. (2018) for overall floristic composition in the same study area. This lower plant diversity at lower elevations can be related with the fact that we targeted to record only plants with open flowers (or at least floral pre-anthesis buds floral buds) which may have caused an underestimation of abundance in these areas. Also, species from Cerrado vegetation exhibit annual or even biannual flowering phenologies and this fluctuate greatly between flowering from one year to another (Batalha et al. 1997, Oliveira & Gibbs 2000, Batalha & Martins 2004).

Floral damages exerted by insects were differently distributed along the elevation. Florivory and robbery damages occurred throughout the entire elevation, while thieving was much less frequent in the plant community but occurred along the elevation gradient. Chrysomelidae and Curculionidae beetles along with Hymenoptera represented nearly the 90% of insects damaging the flowers in *campo rupestre* and they behave as florivores, robbers and/or thieves (Gélvez-Zúñiga et al. 2018b, Gélvez-Zúñiga et al. submitted). Insect florivory along the elevation may be largely influenced by these two extensive groups of insect herbivores since flowers represent high energy nutritious sources for beetles (Nicolson 2011, Gottsberger & Webber 2018, Vaudo et al. 2020). Probably, the beetle abundance and its ability to tolerate harsh environmental conditions at higher elevations are related to the extension of florivory damages along the elevation gradient. For instance, the abundance of Chrysomelidae was positively related to increasing elevation regardless of the season in the same study area (Ribeiro et al. 1994). Chrysomelidae species can occupy wide elevation ranges and there are species well adapted to harsh mountaintop conditions (Ribeiro et al. 1994, Bouzan et. al 2015) while feeding mainly in Angiosperms (Konstantinov & Vandenberg 1996). Concomitantly, Curculionidae beetles also occupy wide ranges of microhabitats along elevations in temperate regions (Williams et al. 2008) and in tropical mountains (Musthafav & Abdulla 2019). However, patterns of decreasing Hymenoptera abundance when increasing elevation in *campo rupestre* areas have also been reported for ants (Castro et al. 2020), Aculeata Hymenoptera (Perillo et al. 2017) and euglossine bees (dos Santos et al. 2020). Since insect-flower interactions are highly context-dependent and because each mountainous environment presents its particularities, the presence of species along elevation gradients is a combination between the regional environmental scenario and the general elevation phenomena (Körner et al. 2017). Hence, studies embracing the beetle-flower interactions, especially Chrysomelidae (but see Ribeiro et al. 1994) and Curculionidae species, may help to understand the variation of florivory in environmental gradients.

Floral advertisement along the elevation

At lower elevations plant individuals produced greater carbon investments in flower number when compared to individuals at higher elevations and this number diminished when increasing the elevation. An overall reduction in plant size has been related to physiological responses due to variations in environmental conditions in elevation gradients (Hautier et al. 2009, Parachnowitsch & Kessler 2010, Nagano et al. 2014, Zhao & Wang 2015). For instance, in alpine plant species the total flower area diminished when increasing elevation and this reduction was greater in species with inflorescences than with solitary flowers (Fabbro & Körner 2004). Plant investments in floral advertisement can vary according to differences in geographic pollinator assemblages, body size and/or abundance at different elevations (Herrera et al. 2006, Gomez et al. 2008, Newman et al. 2014, Nagano et al. 2014, Sun et al. 2014). Although single plant populations may respond rapidly to changes in the pollinator assemblage by adapting its flower size (Galen l996), it remains to be explored the resulting influence on florivory levels.

The size of the species flower determines its variation along the elevation gradient in *campo rupestre*. Species with small-sized flowers were negatively affected by increasing the elevation. Interestingly, this trend for small-sized flowers matches the findings reported by Basnett et al. (2019) where the corolla length and the average stamen-stigma distance decreased with elevation in ten *Rhododendron* (Ericaceae) species. These changes were also correlated with shifts in pollinator assemblages and nectar robbing by bumblebees along the elevation (Delmas et al. 2014, Basnett et al. 2019). In general, a reduction in plant size when increasing elevation has been documented mostly in alpine ecosystems (Körner 2003, Alexander et al. 2009, Hautier et al. 2009, Nagano 2014). Indirect biotic interactions such as florivory by insects may also influence plant attributes in elevation gradients (Dohzono & Suzuki 2010), however, florivore choices and their impacts in floral attributes at large scales are still scarce.

On the other hand, species with medium-sized and large-sized flowers were positively related with elevation. The fact that species with medium-sized and large-sized flowers increased along the elevation might be related to: i) greater plant investments to overcome scenarios with less pollinators and lower flower visitation rates at higher elevations (Kelly 1998, Galen 1999, Kiełtyk 2021); ii) growing investments in flower advertisemnts to counteract increased pollen limitation at upper elevations (Larson & Barrett 2000, Knight et al. 2005, Arroyo et al. 2017, Black et al. 2019). Larger floral size has usually been related to favor plant attraction to pollinators (Barrett & Harder 1996, Aigner 2005, Fenster et al. 2004, Teixido & Valladares 2014); however, the benefits of being more attractive to pollinators may trigger an energetic trade-off between the high energetic costs of producing larger flowers and also increase attraction to insect florivores (Strauss & Whittall 2006).

Opposite to our expectations, we detected a positive relationship between the flowering duration (species flowering period) and increasing elevation. In average, plant species at lower elevations produced flowers for about nine months, while plant species at upper elevations produced flowers from ten to eleven months. This pattern of increased flowering periods at higher elevations have been also reported for other systems. For instance, plant species in alpine ecosystems invest three times more in biomass allocation to floral structures at upper elevations than species at lower elevations (Fabbro & Körner 2004). Conversely, an average trend of decreasing flowering period with increasing elevation in herbaceous species from southern Germany was reported by Bucher & Römermann (2020), but interestingly insect-pollinated species in this elevation gradient showed the capacity to extend their flowering periods to favor cross-pollination. Since nearly 60% of *campo rupestre* plant species are pollinated by insects (Monteiro et al. 2021), this could suggest a potential plasticity of plants to extend their flowering periods at higher elevations to assure reproduction. However, studies testing specific investments in flower attraction to pollinators at upper elevations in *campo rupestre* should be addressed.

Florivory along the elevation

The presence of florivory and the proportion of flower attack by insect florivores increased with elevation, however elevation did not affect the proportion of pre-anthesis floral buds, early-stage fruits or proportion of petal removal. The elevation variation in Serra do Cipó shows clear patterns of reduction in mean temperature and intensifications in air humidity from 69 to 88 % when elevation increased (Fernades et al. 2016b). Also, species abundance, richness, diversity and/or ecological functions diminish with increasing elevation for floristic communities (Rocha et al. 2016, Mota et al. 2018), free-living herbivores in xeric habitats (Ribeiro et al. 1998), Aculeata hymenopterans (Perillo et al. 2017), galling insects (Fernandes & Price 1991, Coelho et al. 2018), dung beetles (Nunes et al. 2018), euglossine bees (dos Santos et al. 2020) and ants (Castro et al. 2020) in *campo rupestre* elevation gradients. Along the elevation variation in *campo rupestre* plant species are predominantly pollinated by biotic vectors and bees are considered the most important pollinators (Carstensen et al. 2016). Bee and wind pollination systems are not affected by elevation, while the proportion of hummingbird-pollinated species diminishes as elevation increases, and the proportion of fly-pollinated species increases at higher elevations (Monteiro et al. 2021). Our results represent, to our knowledge, the first broadly record showing the patterns of insects feeding on floral rewards and/or tissues without providing pollination services along an environmental gradient along.

The most interesting scenarios considering insect florivory along the elevation in *campo rupestre* were found when the interaction between elevation and floral advertisements (flower number and flowering period) were considered. Remarkably, plants with less number of flowers at upper elevations showed little to zero presence of florivory exerted by insects. This suggests that the physiological cost of producing and maintaining a greater quantity of simultaneous open flowers (Galen et al. 1999, Roddy 2019) when elevation increases might be advantageous when avoiding floral herbivores. Concurring with our results, overall greater presence of insect florivores is also associated with fewer simultaneously open flowers (Mosleh Arany et al. 2009, Penet al. 2009, Ruane et al. 2014, Gélvez-Zúñiga et al. 2018). In addition, when the elevation increased, a greater proportion of attacked flowers by florivore insects occurred in species with longer flowering periods. In which species at lower elevations and flowering for less than six months were the least attacked by florivores. Finally, plant species with fewer number of open flowers were more likely to have flowers attacked by insect florivores, and this trend becomes stronger as the elevation increases. This suggests that at upper elevations there are fewer flowers available in the community and because of this the attack by insect florivores might be more severe. For instance, species of *Bombus*, which are frequently reported at higher elevations, usually forage for pollen on the species from the wind-pollinated genus *Festuca* (Poaceae) when floral resources are scarce in Alpine ecosystems (Rasmann et al. 2014).

The elevation did not affect the proportion of petal removal by insect florivores in the *campo rupestre* plant community. However, when addressing the petal removal in species with longer flowering periods an overall increase of petal removal was detected, reaching its greater intensity at lower elevations. Plant species with a single flowering event (1 month) showed the lesser petal removal levels occurred at lower elevations. A plausible explanation for this trend of less petal removal in species with shorter flowering periods might be that short-bloom species at lower elevations end up avoiding florivory when compared to species that have longer flowering periods (McCall & Irwing 2006). However, there is still much to understand regarding the mechanisms of floral herbivory in plant community’s dynamics, especially in environments without a marked flowering seasonality, such as *campo rupestre* (Rocha et al. 2016). The results reported here represent a framework to go further in the understanding of insect florivory dynamics in the speciose and threatened *campo rupestre*.

Variation of insect florivory according to flower availability

The greater proportion of attacked flowers by insect florivores was in July-18 and July-19 respectively, which correspond to the months with fewer flowers available in the community. Generally, July is characterized by low temperatures and dry weather in the region (Madeira & Fernandes 1999, Rocha et al. 2016). In tropical regions insects are more abundant during the rainy season (Wolda 1980, Novais et al. 2018) and this matches the greater Chrysomelidae abundances in several Brazilian ecosystems (Nogueira-de-Sá et al. 2004, Flinte et al. 2009, Linzmeier & Ribeiro-Costa 2013). However, Ribeiro et al. (1994) found that abundance of Chrysomelidae did not differ between rainy or dry seasons along the elevation gradient at Serra do Cipó. Overall, temperature is the most accurate predictor of temporal beetle abundance and species richness, while precipitation show less influence (Wardhaugh et al. 2018) This may indicate that greater floral herbivory is occurring when there are less abundance of inter-specific competitors and may represent an open opportunity to use flower resources more extensively. Furthermore, the fact that floral herbivory peaks occurred in the dry season, represent an additional constraint for plant species with reproductive strategies in this time of the year, and may constitute a great model to test floral herbivory consequences in plant fitness for *campo rupestre* species. Yet, no clear patterns were detected for temporal variation in the proportion of petal removal by insect florivores since both the highest and the lowest levels of petal removal occurred in the dry season. Finally, these temporal patterns of variation in floral herbivory must be addressed by longer sampling periods since flowering dynamics may change rapidly from one year to another.

Less restrictive flower morphologies along the elevation

Our results partially confirm the hypothesis that less limiting flower morphologies are more attacked by insect florivores in the ancient and speciose *campo rupestre*. We verified that petal removal by insects is greater in nectariferous flowers as elevation increases. While petal removal levels in pollen-rewarded flowers, which are most commonly related to specialized pollination systems (Ollerton et al. 2007), decreased along the elevation. Nectar is an essential nutritional resource not only for pollinators but also for florivores (Wäckers et al. 2007), and bees forage more frequently on flowers associated with higher nectar concentrations (Nicolson 2011). Since, bees are the main pollinator in *campo rupestre* (Carstensen et al. 2016, Monteiro et al. 2021), the fact that nectariferous flowers are more attacked by insect florivores may add an ecological constraint to plant reproduction at upper elevations.

Flowers with actinomorphic symmetry showed greater proportion of attacked flowers by insect florivores, and this attack increased with elevation. Surprisingly, flowers with zygomorphic symmetry showed greater petal removal as elevation increased. At global scale, actinomorphic flowers are related to exhibit higher floral visitors rates than to zygomorphic flowers (Neal et al. 1998, Arceo-Gómez et al. 2019). In Alpine ecosystems, zygomorphic flowers with bilabiate corollas, which are mainly pollinated by bees, are replaced by actinomorphic disk-like flowers as elevation increased, raising the chances of floral visitation at upper elevations (Rasmann et al. 2014). Accordingly, in our study species with zygomorphic corollas were more frequent at lower elevations reaching the maximum values at intermediate elevations, while actinomorphic flowers were more frequent at higher elevations, but also reached a peak in-between elevation. Lastly, greater petal removal levels occurred in less restrictive flowers in terms of potential flower visitors at upper elevations. Petal removal in species with less limiting flower morphologies increased along the elevation, while petal removal in species with just one potential visitor group were greater at lower areas and negatively related with the elevation.

This study shows novel records on the variation of florivory exerted by insects in a whole plant community along an environmental gradient. Also, it is the first formal quantification of overall plant investments in floral advertisement and how these are related to variations in insect florivory, floral reward and flower morphology in the speciose *campo rupestre*. The trends and mechanisms underlying insect florivory at a community level are of great importance since florivory may ultimately impact, via direct or indirect effects, plant reproduction output and overall plant fitness over time. In this regard, the findings of this study constitute a first step in the understanding of overall insect florivory in ancient habitats, where plant species are highly adapted to impoverished soils with low water retention, dispersal constraints, harsh environmental conditions and with predominantly insect pollinated species (Silveira et al. 2019, Fernandes et al. 2020, Monteiro et al. 2021). Our results strengthen the idea that biotic insect-plant interactions are strongly dependent on the context and that simultaneous selective pressures imposed by both biotic and abiotic components, are ultimately tracing floral attributes (Parachnowitsch & Kessler 2010, Ruane et al. 2014, Zhao & Wang 2015, Caruso et al. 2019). Collective efforts to address broader studies on insect florivory are highly needed and future studies should explore deeper the mechanisms underlying environmental fluctuations of insect florivory dynamics since plants share and compete for pollinators while setting barriers against floral enemies (Irwin et al. 2001, Gonzálvez et al.

2013). Insect florivory represents an avenue of opportunities to access plant-pollinator-florivore interactions in landscapes facing environmental degradation, excessive natural resources exploitation and changing scenarios such as tropical mountains and its speciose habitats.

Acknowledgements:

We thank JE Santos-Junior, PR Siqueira, L Migliore, G Biffi, LR Vasconcellos, SA Vanin, FS Castro, L Perillo, LA de Moura, L Massutti, ACM Jacobina, A Lima, GC Pereira, CA Ferreira Júnior, Júlio JL, B Monteiro L for assistance with species identification. IGZ thanks A Elbakyan for her contribution to public access of research papers. IGZ received a scholarship from CNPq. Thanks to Reserva Vellozia, Parque Nacional da Serra do Cipó, Cedro Textil, Pousada Pedra do Elefante, Pousada Serra Morena, and Pousada Rancho Cipó for logistical support. This study was funded by PELD/CNPq, Fapemig, ComCerrado, CAPES, and CNPq.

Supplementary material

Figure S2. Most frequent *campo rupestre* flowering species along thirty plots ranging from 823 to 1411 m a.s.l. between May 2018 and August 2019 at Serra do Cipó, Brazil. a) *Chromolaena squalida* (Asteraceae), b) *Marcetia taxifolia* (Melastomataceae), c) *Xyris nubigena* (Xyridaceae), d) *Cuphea ericoides* (Lythraceae), e) *Lavoisiera confertiflora* (Melastomataceae).

Literature cited:

Aigner, P.A. 2005. Variation in pollination performance gradients in a *Dudleya* species complex: can generalization promote floral divergence? Functional Ecology 19:681.689.

Alexander, J.M., Edwards, P.J., Poll, M., Parks, C.G. & Dietz, H. 2009. Establishment of parallel altitudinal clines in traits of native and introduced forbs. Ecology 90:612-622.

Arany, A. M., de Jong, T. J. & van der Meijden, E. 2009. Herbivory and local genetic differentiation in natural populations of Arabidopsis thaliana (Brassicaceae). Plant Ecology 201:651-659.

Araújo, L.M., Fernandes, G.W. 1993. Padrões de distribuição de formigas arborícolas ao longo do gradiente altitudinal da Serra do Cipó. In: IX Congresso da Sociedade Botânica de São Paulo, 1992, Ilha Solteira. Resumos do IX Congresso da Sociedade Botânica de São Paulo, 1992. p. 155-155.

Arceo-Gómez, G., Schroeder, A., Albor, C., Ashman, T.L., Knight, T.M., Bennett, J.M., Suarez, B. & Parra-Tabla, V. 2019. Global geographic patterns of heterospecific pollen receipt help uncover potential ecological and evolutionary impacts across plant communities worldwide. Scientific Reports 9:8086.

Arroyo, M.T.K., Pacheco, D.A. & Dudley, L.S. 2017. Functional role of long-lived flowers in preventing pollen limitation in a high elevation outcrossing species. AoB Plants 9:plx050.

Ashman, T.L. & Arceo-Gómez, G. 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. American Journal of Botany 100:1061-1070.

Baker, H.G. & Baker, I. 1983. A brief historical review of the chemistry of floral nectar. In: Bentley, B. & Elias, T. (Ed) The Biology of Nectaries. New York: Columbia Univ.Press p 126–52.

Barrett, S. C. H. & Harder, L. D. 1996. Ecology and evolution of plant mating. Trends in Ecology & Evolution 11:73-79.

Basnett, S., Ganesan, R. & Devy, S.M. 2019. Floral traits determine pollinator visitation in *Rhododendron* species across an elevation gradient in the Sikkim Himalaya. Alpine Botany 129:81-94.

Batalha, M. A., Aragaki, S. & Mantovani, W. 1997. Phenological variations of the Cerrado species in Emas-Pirassununga, SP. Acta Botanica Brasilica 11:61-78.

Batalha, M.A. & Martins, F.R. 2004. Reproductive phenology of the Cerrado plant community in Emas National Park (central Brazil). Australian Journal of Botany 52:149-161.

Beirão, M.V., Neves, F.S. & Fernandes, G.W. 2020. Climate and plant structure determine the spatiotemporal butterfly distribution on a tropical mountain. Biotropica 53:191-200.

Belo, R.M., Negreiros, D., Fernandes, G.W., Silveira, F.A.O., Ranieri, B.D. & Morellato, L.P.C. 2013. Fenologia reprodutiva e vegetativa de arbustos endémicos de campo rupestre na Serra do Cipó, Sudeste do Brasil. Rodriguésia 64:817-828.

Black, H.N., Harrison, J.D.G. & Cron, G.V. 2019. Do breeding system and pollen limitation vary with altitude in the widespread herb, *Cineraria erodioides* (Asteraceae)? South African Journal of Botany 121:377-385.

Bouzan, A.M., Flinte, V., Macedo, M.V. & Monteiro, R.F. 2015. Elevation and temporal distributions of Chrysomelidae in southeast Brazil with emphasis on the Galerucinae. ZooKeys 547:103-117.

Bucher, S.F. & Römermann, C. 2020. Flowering patterns change along elevational gradients and relate to life-history strategies in 29 herbaceous species. Alpine Botany 130:41-58.

Bronstein, J.L., Huxman, T.E. & Davidowitz, G. 2007. Plant-mediated effects linking herbivory and pollination. In: Ohgushi, T., Craig, T.P. & Price, P.W. (eds). Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press 1:75-103

Canela, M.B.F. & Sazima, M. 2003. Florivory by the crab *Armases angustipes* (Grapsidae) influences hummingbird visits to *Aechmea pectinata* (Bromeliaceae). Biotropica 35:289-294.

Carroll, A.B., Pallardy, S.G. & Galen, C. 2001. Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). American Journal of Botany 88:438-446.

Carstensen, D. W., Sabatino, M., Trøjelsgaard, K., Morellato, L. P. C. 2016. Betadiversity of plant-pollinator networks and the spatial turnover of pairwise interactions. PLoS One 9 e112903.

Caruso, C.M., Eisen, K.E., Martin, R.A. & Sletvold, N. 2019. A meta-analysis of the agents of selection on floral traits. Evolution, 73:4-14.

Castro, F.S., Silva, P.G., Solar, R., Fernandes, G.W. & Neves, F.S. 2020. Environmental drivers of taxonomic and functional diversity of ant communities in a tropical mountain. Insect Conservation and Diversity 13:393-403.

Coelho, M.S., Carneiro, M.M.A., Branco, C.A., Borges, R.A.X. & Fernandes, GW. 2018. Species turnover drives *β*-diversity patterns across multiple spatial scales of plant-galling interactions in mountaintop grasslands. PloS One 13:e0195565.

Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C. & Longino, J.T. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258-261.

Conceição, A.A., Rapini, A., Carmo, F.F., Brito, J.C., Silva, G.A., Neves, S.P.S. & Jacobi, C.M. 2016. Rupestrian grassland vegetation, diversity, and origin. In: Fernandes, G.W. (ed.). Ecology and conservation of mountain-top grasslands in Brazil. Springer Chan, 1:105-123.

Crawley, M.J. 2013. The R book. Second edition, John Wiley & Sons Ltd. 975p.

Darwin, C.R. 1877. The various contrivances by which orchids are fertilised by insects. John Murray. London. UK.

Delmas, C.E.L., Escaravage, N., Pornon, A. 2014. Massive floral display affects insect visits but not pollinator-mediated pollen transfer in *Rhododendron ferrugineum*. Plant Biology 16:234-243.

Dodd, M.E., Silvertown, J. & Chase, M.W. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. Evolution 53:732-744.

Dohzono, I. & Suzuki, K. 2010. Morphological and genetic differentiation in *Isodon umbrosus* by altitudinal variation in bumblebee pollinator assemblages. Plant Species Biology 25:20-29.

dos Santos, F.M., Beiroz, W., Antonini, Y., Martén-Rodríguez, S., Quesada, M. & Fernandes GW. 2020. Structure and composition of the euglossine bee community along an elevational gradient of rupestrian grassland vegetation. Apidologie 51, 675-687.

Eliyahu, D., McCall, A.C., Lauck, M. & Trakhtenbrot, A. 2015. Florivory and nectar-robbing perforations in flowers of pointleaf manzanita *Arctostaphylos pungens* (Ericaceae) and their effects on plant reproductive success. Arthropod Plant Interactions 9:613-622.

Fabbro, T. & Körner, C. 2004. Altitudinal differences in flower traits and reproductive allocation. Flora, 199:70-81.

Faegri, K. & van der Pijl, L. 1979. The principles of pollination ecology. Pergamon Press, Oxford 3:244p.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. 2004 Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution and Systematics 35:375-403.

Fernandes, G.W., Price, P.W. 1991. Comparisons of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. In: Price, P.W., Lewinsohn, T.M., Fernandes, G.W. & Benson, W.W. (eds.). Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, 1:91-115.

Fernandes, G.W. 2016a. The megadiverse rupestrian grassland. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, Cham, 1:3–14.

Fernandes, G.W., Almeida, H.A., Nunes, C.A., Xavier, J.H.A., Coob, N.S., Carneiro, M.A.A., Cornelissen, T., Neves, F.S., Ribeiro, S.P., Nunes, Y.R.F., Pires, A.C.V. & Beirão, M.V. 2016b. Cerrado to rupestrian grasslands: patterns of species distribution and the forces shaping them along an altitudinal gradient, In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, Cham, 1:345-371.

Fernandes, G. W., Arantes-Garcia, L., Barbosa, M., Barbosa, N. P., Batista, E. K., Beiroz, W., Resende, F. M., Abrahão, A., Almada, E. D., Alves, E., Alves, N. J., Angrisiano, P., Arista, M., Arooyo, J., Arruda, A. J., Bahia, T. O., Braga, L., Brito, L., Callisto, M., Caminha-Paiva, D., Carvalho, M., Conceição, A. A., Costa, L. N., Cruz, A., Cunha-Blum, J., Dagevos, J., Dias, B. F. S., Pinto, V. D., Dirzo, R., Domingos, D. Q., Echternacht, L., Fernandes, S., Figueira, J. E. C., Fiorini, C. F., Giulietti, A. M., Gomes, A., Gomes, V. M., Gontijo, B., Goulart, F., Guerra, T. J., Junqueira, P. A., Lima-Santos, D., Marques, J., Meira-Neto, J., Miola, D. T. B., Morellato, L. P. C., Negreiros, D., Neire, E., Neves, A. C., Neves, F. S., Novais, S., Oki, Y., Oliveira, E., Oliveira, R. S., Pivari, M. O., Junior, E. P., Ranieri, B. D., Ribas, R. P., Scariot, A., Schaefer, C. E., Sena, L., da Silva, P. G., Siqueira P. R., Soares, N. C., Soares-Filho, B., Solar, R., Tabarelli, M., Vasconcelos, R., Vilela, E. & Silveira, F. A. 2020. Biodiversity and ecosystem services in the Campo Rupestre: A road map for the sustainability of the hottest Brazilian biodiversity hotspot. Perspectives in Ecology and Conservation 18:213-222.

Flinte, V., Macedo, V.M. & Monteiro, F.R. 2009. Chrysomelids and their host plants along an altitudinal gradient in a tropical Atlantic Rain Forest in Rio de Janeiro, Brazil. In: Jolivet, P., Santiago-Blay, J. & Schmitt, M. (Eds) Research on Chrysomelidae 2. Brill, Leiden, 31-56p.

Freitas, L. & Sazima, M. 2006. Pollination biology in a tropical high-altitude grassland in Brazil: interactions at the community level. Annals of the Missouri Botanical Garden 93:465-520.

Frame, D. 2003. Generalist Flowers, Biodiversity and Florivory: Implications for Angiosperms. Taxon 52:681-685.

Galen, C. 1996. Rates of floral evolution: Adaptation to bumblebee pollination in an alpine wildflower, *Polemonium viscosum*. Evolution 50:120-25.

Galen, C. 1999. Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. Bioscience 49:631-640.

Galen, C., Sherry, R.A. & Carroll, A.B. 1999. Are Flowers Physiological Sinks or Faucets? Costs and Correlates of Water Use by Flowers of *Polemonium viscosum*. Oecologia 118:461-470.

Gélvez-Zúñiga, I., Teixido, A.L., Neves, A.C.O. & Fernandes, G.W. 2018a. Floral antagonists counteract pollinator-mediated selection on attractiveness traits in the hummingbird-pollinated *Collaea cipoensis* (Fabaceae). Biotropica 50:797-804.

Gélvez-Zúñiga, I., Neves, A.C.O., Teixido, A.L. & Fernandes, G.W. 2018b. Reproductive biology and floral visitors of *Collaea cipoensis* (Fabaceae), an endemic shrub of the rupestrian grasslands. Flora 238:129-138.

Gélvez-Zúñiga, I., Novais S. N., Santiago J. C., Quesada M. & Fernandes, G.W. Submitted. Florivory in a biodiversity hotspot: trends, mechanisms and damages. Ecology 2021.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. 2010. A framework for community interactions under climate change. Trends in Ecology and Evolution 25:325-331.

Gómez, J. M., Bosch, J., Perfectti, F., Fernández, J. D., Abdelaziz, M. & Camacno, J. P. M. 2008. Association between floral traits and rewards in *Erysimum mediohispanicum* (Brassicaceae). Annals of Botany 101:1413-1420.

González, F.G., Santamaría, L.L., Corlett, R.T. & Rodríguez-Gironés, M.A. 2013. Flowers attract weaver ants that deter less effective pollinators. Journal of Ecology 101:78-85.

Gottsberger, G. & Webber, A.C. 2018. Nutritious tissue in petals of Annonaceae and its function in pollination by scarab beetles. Acta Botanica Brasilica 32:279-286.

Hautier, Y., Randin, C.F., Stoecklin, J. & Guisan, A. 2009. Changes in reproductive investment with altitude in an alpine plant. Journal of Plant Ecology 2:125-134.

Herrera, C.M., Castellanos, M.C. & Medrano, M. 2006. Geographical context of floral evolution: toward an improved research programme in floral diversification. In: Harder, L.D. & Barrett, S.C.H. (eds.). Ecology and evolution of flowers. Oxford University Press, 1:278-294

Hoffmann, D., Vasconcelos, M.F. & Fernandes, G.W. 2020. The fate of endemic birds of eastern Brazilian mountaintops in the face of climate change. Perspectives in Ecology and Conservation 18:257-266.

Humboldt, von A. 1817. De distributione geographica plantarum secundum coeli temperiem et altitudinem montium, prolegomena. Libraria Graeco-Latino-Germanica, Paris 244p.

Inouye, D.W. 1980. The Terminology of Floral Larceny. Ecology 61:1251-1253.

Irwin, R.E., Brody, A.K. & Waser, N.M. 2001. The impact of floral larceny on individuals, populations, and communities. Oecologia 129:161-168.

Jones, P.L., Agrawal, A.A. 2017. Learning in insect pollinators and herbivores. Annual Review of Entomology 62:53-71.

Kelly, C.A. 1998. Effects of variable life history and insect herbivores on reproduction in *Solidago macrophylla* (Asteraceae) on an elevational gradient. The American Midland Naturalist Journal 139:243-254.

Kiełtyk, P. 2021. Patterns of floral allocation along an elevation gradient: variation in *Senecio subalpinus* growing in the Tatra Mountains. Alpine Botany 1-8 (https://doi.org/10.1007/s00035-021-00247-w).

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J. & Ashman, T.L. 2005. Pollen limitation of plant reproduction: Pattern and process Annual Review of Ecology, Evolution and Systematics 36:467-497.

Konstantinov, A.S. & Vandenberg, N.J. 1996. Handbook of Palearctic Flea Beetles (Coleoptera: Chrysomelidae: Alticinae). Associated Publishers, 1:273-439.

Körner, C. 2003. Growth dynamics and phenology. In: Körner, C. (ed.). Alpine plant life: functional plant ecology of high mountain ecosystems, Springer 2:221-233.

Körner, C. 2004. Mountain biodiversity, its causes and function. Ambio: A Journal of the Human Environment 33:11-17.

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K. & Spehn, E.M. 2017. A global inventory of mountains for bio-geographical applications. Alpine Botany 127:1-15.

Krupnick, G.A. & Weis, A.E. 1999. The effect of floral herbivory on male and female reproductive success in *Isomeris arborea*. Ecology 80:135-1149.

Larson, B.M.H. & Barrett, S.C.H. 2000. A comparative analysis of pollen limitation in flowering plants. Biological Journal of the Linnean Society 69:503-520.

Liautaud, K., van Nes, E.H., Barbier, M., Scheffer, M. & Loreau, M. 2019. Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. Ecology Letters 22:1243-1252.

Lefebvre, V., Villemant, C., Fontaine, C. & Daugeron, C. 2018. Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. Scientific Reports 8:4706.

Linzmeier, A.M. & Ribeiro-Costa, C.S. 2013. Seasonal pattern of Chrysomelidae (Coleoptera) in the state of Paraná, southern Brazil. Biota Neotropica 13:153-162.

Lobo, J.A., Lacerda-Ramos, D. & Cabral-Braga, A. 2016. Visitation rate of pollinators and nectar-robbers to the flowers and inflorescences of *Tabebuia aurea* (Bignoniaceae): effects of floral display size and habitat fragmentation. Botanical Journal of the Linnean Society 181:667-681.

Lynn, J.S., Kazenel, M.R., Kivlin, S.N. & Rudgers, J.A. 2019. Context-dependent biotic interactions control plant abundance across altitudinal environmental gradients. Ecography 42:1600-1612.

Machado, I.C. & Lopes, A.V. 2004. Floral traits and pollination systems in the Caatinga, a Brazilian Tropical Dry Forest. Annals of Botany 94:365-376.

Madeira, J.A. & Fernandes, G.W. 1999. Reproductive phenology of sympatric taxa of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazil. Journal of Tropical Ecology 15:463-479.

McCall, A.C. & Irwin, R.E. 2006. Florivory: the intersection of pollination and herbivory. Ecology Letters 9:1351-1365.

Monteiro, B.L., Camargo, M.G.G., Loiola, P.P., Carstensen, D.W., Gustafsson, S. & Morellato, L.P.C. 2021. Pollination in the campo rupestre: a test of hypothesis for an ancient tropical mountain vegetation. Biological Journal of the Linnean Society blaa205. (https://doi.org/10.1093/biolinnean/blaa205).

Moreira, X., Castagneyrol, B., Abdala-Roberts, L. & Traveset, A. 2019. A meta-analysis of herbivore effects on plant attractiveness to pollinators. Ecology 100:e02707.

Mota, G.S., Luz, G.R., Mota, N.M., Coutinho, E.S., Veloso, M.D.M., Fernandes G.W. & Nunes, Y.R.F. 2018. Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. Flora 238:32-42.

Mothershead, K. & Marquis, R.J. 2000. Fitness impacts of herbivory through indirect effects on plant–pollinator interactions in *Oenothera macrocarpa*. Ecology 81:30-40.

Musthafa, M.M. & Abdullah, F. 2009. Beetles species richness along environmental gradients at montane ecosystem in Fraser's Hill, Peninsular Malaysia. Sains Malaysiana 48: 1395-1407.

Nagano, Y., Abe1, K., Kitazawa, T., Hattori, T., Hirao, A.S. & Itino, T. 2014. Changes in pollinator fauna affect altitudinal variation of floral size in a bumblebee-pollinated herb. Ecology and Evolution 4:3395-3407.

Neal, P.R., Dafni, A. & Giurfa, M. 1998. Floral symmetry and its role in plant-pollinator systems: Terminology, Distribution, and Hypotheses. Annual Review of Ecology, Evolution, and Systematics, 29:345-373.

Negreiros, D., Le Stradic. S., Fernandes, G.W. & Rennó, H.C. 2014. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecology 215:379-388.

Newman, E., Manning, J. & Anderson, B. 2014. Matching floral and pollinator traits through guild convergence and pollinator ecotype formation. Annals of Botany 113:373-384.

Nicolson, S.W. 2011. Bee Food: The Chemistry and Nutritional Value of Nectar, Pollen and Mixtures of the Two. African Zoology 46:197-204.

Nogueira, F.S., Medeiros, L. & Macedo, M.V. 2004. Phenology of populations of tortoise beetles (Cassidinae) in Brazil. In: Jolivet, P., Santiago-Blay, J.A. & Schmitt, M. (Eds) New Developments in the Biology of Chrysomelidae. SPB Academic Publishing, The Hague, 647-658p.

Novais, S.M.A., Nunes, C.A., Santos, N.B., D`Amico, A.R., Fernandes, G.W., Quesada, M., Braga, R.F. & Neves, A.C.O. 2016. Effects of a Possible Pollinator Crisis on Food Crop Production in Brazil. PloS One 13:e0197396.

Novais, S.M.A., Macedo-Reis, L.M., Cristobal-Peréz, E.J., Sánchez-Montoya, G., Janda, M., Neves, F. & Quesada, M. Positive effects of the catastrophic Hurricane Patricia on insect communities. Scientific Reports 8:15042

Nunes, C.A., Braga, R.F., Resende, F.M., Neves, F.S., Figueira, J.E.C. & Fernandes, G.W. 2018. Linking biodiversity, the environment and ecosystem, functioning: ecological functions of dung beetles along a tropical elevational gradient. Ecosystems 21:1244-1254.

Oliveira, P.E. & Gibbs, P.E. 2000. Reproductive biology of woody plants in a Cerrado community of Central Brazil. Flora 195:311-329.

Ollerton, J., Killick, A., Lamborn, E., Watts, S. & Whiston, M. 2007. Multiple Meanings and Modes: On the Many Ways to Be a Generalist Flower. Taxon 56:717-728.

Ollerton, J., Winfree, R. & Tarrant, S. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Ollerton, J., Liede-Schumann, S., Endress, M.E., Meve, U., Rech, A.R., Shuttleworth, A., Keller, H.A., Fishbein, M., Alvarado-Cárdenas, L.O., Amorim, F.W., Bernhardt, P., Celep, F., Chirango, Y., Chiriboga-Arroyo, F., Civeyrel, L., Cocucci, A., Cranmer, L., Silva-Batista, I.C., Jager, L., Deprá, M.S., Domingos-Melo, A., Dvorsky, C., Agostini, K., Freitas, L., Gaglianone, M.C., Galetto, L., Gilbert, M., González-Ramírez, I., Gorostiague, P., Goyder, D., Hachuy-Filho, L., Heiduk, A., Howard, A., Ionta, G., Islas-Hernández, S.C., Johnson, S.D., Joubert, L., Kaiser-Bunbury, C.N., Kephart, S., Kidyoo, A., Koptur, S., Koschnitzke, C., Lamborn, E., Livshultz, T., Machado, I.C., Marino, S., Mema, L., Mochizuki, K., Morellato, L.P.C., Mrisha, C.K., Muiruri,, E.W., Nakahama N., Nascimento, V.T., Nuttman, C., Oliveira, P.E., Peter, C.I., Punekar, S., Rafferty, N., Rapini, A., Ren, Z.X., Rodríguez-Flores, C.I., Rosero, L., Sakai, S., Sazima,, M., Steenhuisen S.L., Tan, C.W., Torres, C., Trøjelsgaard, K., Ushimaru, A., Vieira, M.F., Wiemer, A.P., Yamashiro, T., Nadia, T., Queiroz, J. & Quirino, Z. 2019. The diversity and evolution of pollination systems in large plant clades: Apocynaceae as a case study. Annals of Botany 123:311-325.

Parachnowitsch, A.L. & Kessler, A. 2010. Pollinators exert natural selection on flower size and floral display in *Penstemon digitalis*. New Phytologist 188:393-402.

Penet, L., Collin, C.L. & Ashman, T.L. 2009. Florivory increases selfing: an experimental study in the wild strawberry, *Fragaria virginiana*. Plant Biology 11:38-45.

Perillo, L.N., Neves, F.D.S., Antonini, Y. & Martins, R.P. 2017. Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient. PloS One 12:e0182054.

Porto, R.G., de Almeida, R.F., Cruz-Neto, O., Tabarelli, M., Viana, B.F., Peres, C.A. & Lopes, A.V. 2020. Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. Food Security 1-18.

Potts, S.G., Roberts, S.P., Dean, R., Marris, G., Brown, M., Jones, R., Neumann P. & Settele, J. 2010. Declines of managed honeybees and beekeepers in Europe? Journal of Apicultural Research 49:15-22.

Primack, R. 1985. Longevity of individual flowers. Annual Review of Ecology, Evolution, and Systematics 16:15-37.

R Core Team. 2021. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rasmann, S., Alvarez, N. & Pellissier, L. 2014. The altitudinal niche-breadth hypothesis in insect-plant interactions. Annual Plant Reviews 47:339-360.

Resende, F.M., Fernandes, G.W. & Coelho, M.S. 2013. Economic valuation of plant diversity storage service provided by Brazilian rupestrian grassland ecosystems. Brazilian Journal of Biology 73: 709-716.

Ribeiro, S.P, Carneiro, M.M.A. & Fernandes, G.W. 1994. Distrmution of Brachypnoea (Coleoptera: Chrysomelidae) in an altitudinal gradient in a Brazilian savanna vegetation. Phytophaga 6:29-33.

Ribeiro, S.P., Carneiro, M.M.A. & Fernandes, G.W. 1998. Free-feeding insect herbivores along environmental gradients in Serra do Cipó: basis for a management plan. Journal of Insect Conservation 2:107-118.

Rocha, N.M.W.B., Carstensen, D.W., Fernandes, G.W., Le Stradic, S., Buisson, E. & Morellato, L.P.C. 2016. Phenology patterns across a rupestrian grassland altitudinal gradient. In: Fernandes, G.W. (ed.). Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, Chan, 1:275-289.

Roddy, A.B. 2019. Energy balance implications of floral traits involved in pollinator attraction and water balance. International Journal of Plant Sciences 180:944-953.

Ruane, L., Rotzin, A.T. & Congleton, P.H. 2014. Floral display size, conspecific density and florivory affect fruit set in natural populations of *Phlox hirsuta*, an endangered species. Annals of Botany 113:887-893.

Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G. & Carvalheiro, L.G. 2015. Pollinator conservation — the difference between managing for pollination services and preserving pollinator diversity. Current Opinion in Insect Science 12:93-101.

Sun, M., Gross, K. & Schiestl, F.P. 2014. Floral adaptation to local pollinator guilds in a terrestrial orchid. Annals of Botany 113:289-300.

Stang, M., Klinkhamer, P.G.L. & van der Meijden, E. 2006. Size constraints and flower abundance determine the number of interactions in a plant flower visitor web. Oikos 112:111-121.

Silveira, F.A.O., Negreiros, D., Barbosa, N.P.U., Buisson, E., Carmo, F.F., Carstensen, D.W., Conceição, A.A., Cornelissen, T.G., Echternacht, L., Fernandes, G.W., Garcia, Q.S., Guerra, T.J., Jacobi, C.M., Lemos-Filho, J.P., Le Stradic, S., Morellato, L.P.C., Neves, F.S., Oliveira, R.S., Schaefer, C.E., Viana, P.L. & Lambers, H. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant Soil 403:129-152.

Silveira, F.A.O., Barbosa, M., Beiroz, W., Callisto, M., Macedo, D.R., Morellato, L.P.C., Neves, F.S., Nunes, Y.R.F., Solar, R.R. & Fernandes, G.W. 2019. Tropical mountains as natural laboratories to study global changes: A long-term ecological research project in a megadiverse biodiversity hotspot. Perspectives in Plant Ecology, Evolution and Systematics 38:64-73.

Simpson, M.G. 2019. Plant systematics. Elsevier Academic Press. 3:896.

Souza, C.S., Aoki, C., Ribas, A., Pott, A. & Sigrist, M.R. 2016. Floral traits as potential indicators of pollination vs. theft. Rodriguésia 67:309-320.

Strauss, S.Y. & Whittall, J.B. 2006. Non-pollinator agents of selection on floral traits. In: Harder, L.D. & S. Barrett, S.C.H. (eds.). Ecology and evolution of flowers. Oxford University Press 1:120-138.

Teixido, A.L. & Valladares, F. 2014. Pollinator-mediated phenotypic selection does not always modulate flower size and number in the large-flowered mediterranean shrub *cistus ladanifer* (Cistaceae). Botanical Journal of the Linnean Society 176:540-555.

Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Global Change Biology 18:3279-3290.

Thompson, J.N. 2005. The geographic mosaic of coevolution. The Universtity of Chicago Press, Chicago & Londres, 400p.

Thompson, J.N., Fernandez, C.C. 2006. Temporal dynamics of antagonism and mutualism in a geographically variable plant–insect interaction. Ecology 87:103-112.

UNESCO 2017. Mountain Ecosystem Services. In: Egan, P.A. & Price, M.F. (eds.). Mountain Ecosystem Services and Climate Change: A Global Overview of Potential Threats and Strategies for Adaptation. United Nations Educational, Scientific and Cultural Organization, 1:10-18.

Urban, M.C. 2015. Climate change. Accelerating extinction risk from climate change. Science,348:571-573.

Vaudo, A.D., Tooker, J.F., Patch, H.M., Biddinger, D.J., Coccia, M., Crone, M.K., Fiely, M., Francis, J.S., Hines, H.M., Hodges, M., Jackson, S.W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E.D., Vanderplanck, M., Yip, E., Leonard, A.S. & Grozinger, C.M. 2020. Pollen Protein: Lipid Macronutrient Ratios May Guide Broad Patterns of Bee Species Floral Preferences. Insects 11:132.

Wäckers, F.L., Romeis, J. & van Rijn, P. 2007. Nectar and Pollen Feeding by Insect Herbivores and Implications for Multitrophic Interactions. Annual Review of Entomology 52:301-23.

Wardhaugh, C.W., Stone, M.J. & Stork, N.E. 2018. Seasonal variation in a diverse beetle assemblage along two elevational gradients in the Australian Wet Tropics. Scientific Reports 8:8559

Waser, N.M. 2006. Specialization and generalization in plant–pollinator interactions: an historical perspective. In: Waser, N.M & Ollerton, J. (eds.). Plant-pollinator interactions: from specialization to generalization. Chicago: University of Chicago Press 1:3-17.

Williams, K.K., McMillin, J.D., DeGomez, T.E., Clancy, K.M. & Miller, A. 2008. Influence of elevation on bark beetle (Coleoptera: Curculionidae, Scolytinae) community structure and flight periodicity in ponderosa pine forests of Arizona. Environmental Entomology 37:94-109.

Willmer, P. 2011. Types of Flower visitors: syndromes, constancy, and Effectiveness. In: Willmer, P. Pollination and floral ecology. Princeton University Press, 1:261-288.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G. & Aizen, M.A. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068-2076.

Wolda, H. 1980. Seasonality of tropical insects. I. Leafhoppers (Homoptera) in las Cumbres, Panamá. The Journal of Animal Ecology 4:277-290.

Zhao, Z.G. & Wang, Y.K. 2015. Selection by pollinators on floral traits in generalized *Trollius ranunculoides* (Ranunculaceae) along altitudinal gradients. PloS One 10:e0118299.

Final remarks and future perspectives

This was a formal study on the florivory exerted by insects on a variety of flowers in a speciose *campo rupestre* plant community. This study began with a simple observation of a Velloziaceae flower and from that day on, several questions emerged gradually. Eventually, that list of inquiries turned into a project proposal and, inevitably, in a long-term research initiative. The first inquiries included a natural history approach; to repeatedly observe and write down. That is how the results summarized in **Table S1** and Table 2 from the **Chapter 1** were obtained. Here we presented a list of 207 plant species with detailed information about floral rewards, flower morphology, shape of the corolla and pollination unit, among others. Also, three commonly measured floral advertisements were quantified for each plant species: flower number, category of floral size and the species flowering period along 14-motnh samplings. Simultaneously, in **Chapter 1** were reported the 120 insect morphospecies which interacted with the observed flowers, its behavior as flower visitors (potential pollinator, robber, thieve, florivore or a combination of those categories), number of plant species visited and the floral rewards they targeted.

After gathering this basic information about florivores and flowers, the natural incidence of this insect-plant interaction were measured leading to some interesting results; i) 26% of the plants from *campo rupestre* in Serra do Cipó present signs of damages by florivore insects, ii) strict florivory, understood as damages resulted from insect chewing of floral structures, is far more frequent than nectar-robbing or thieving in this plant community. However, nectar-robbing have received much more attention on scientific studies than florivory (Irwin et al. 2010), may be due to its direct, and in some cases diffuse, relationship with pollination. Another, valuable information gathered in the present study is that 7% of the total flowers produced in this plant community (nearly 99,000 flowers recorded) has showed levels of petal removal by insect florivores during the 14-month sampling events. The information gathered in this study open research opportunities for future hypothesis testing in pollination ecology, plant reproduction, insect behavior, functional ecology, among others.

Details on the relationship between floral attributes and the proportion of attack by insect florivores (**Chapter 1**), and the variation of attacks by florivore insects in an environmental gradient (**Chapter 2**) have answered many other inquiries about insect florivores and its flower preferences. Yet, as part of the science method dynamics, there are always other inquiries to address, or pathways to go further. One of them is the relation between phylogeny and florivory, this highly context-depend biotic interaction. In the Figure 1 is presented the phylogeny of the plants recorded in this study, with the plant families attacked the most by insect florivores (from left to right: Fabaceae, Malpighiaceae, Melastomataceae and Lythraceae) highlighted with green lines. Plant species with greater average flowers attacked by insect florivores are denoted with light orange boxes, and plant species with greater frequency of attack by insect florivores are denoted in light blue boxes. These trends suggest that greater susceptibility to insect florivory may not necessarily be occurring in close related plant families, but there may by some characteristics inside plant genus, e.g. *Vellozia* (Vellozciaceae) and *Lavoisiera* (Melastomataceae), which favor insect feeding on flowers in this plant community. However, this is a purely exploratory analysis and formal testes should be addressed in the future to unravel the relations between phylogeny and florivory by insects in this *campo rupestre* plant community.

As the general trends found for the proportion of petal removal by florivores differed from the rest of the variables measured for some of the floral attributes analyzed. We explored the average petal removal by plant species (light orange boxes) and the plant species where proportion of petal removal was more frequent for this subset of the data (light blue boxes) in the Figure 2. In this case, we found that *Vochysia pygmaea* from the Vochysiaceae family showed both high average petal removal proportion and frequency, and interestingly this species is not grouped within the most attacked plant families. Overall petal removal average and frequencies are not densely distributed in certain plant genera, as occurred for the plant level attack and frequencies. Hence, phylogeny represents a promising approach to better understand florivory by insects in the ancient *campo rupestre* plant community in Serra do Cipó. However, future formal analyses should be addressed to detect reliable and statistically robust patterns. Furthermore, the presence of phylogenetic signal in the florivory variables quantified in this study will allow a better understanding of the legacy of evolution in this biotic interaction. Hence, to test if there is a phylogenetic signal in the incidence and intensity of insect florivory represents the next step in the task of unveiling florivory by insect in tropical speciose communities. Synthesizing, I specifically intend to finish this document with an inquiry since as in the scientific method, and in nature itself, the end of a cycle represents as well a new window of opportunities.

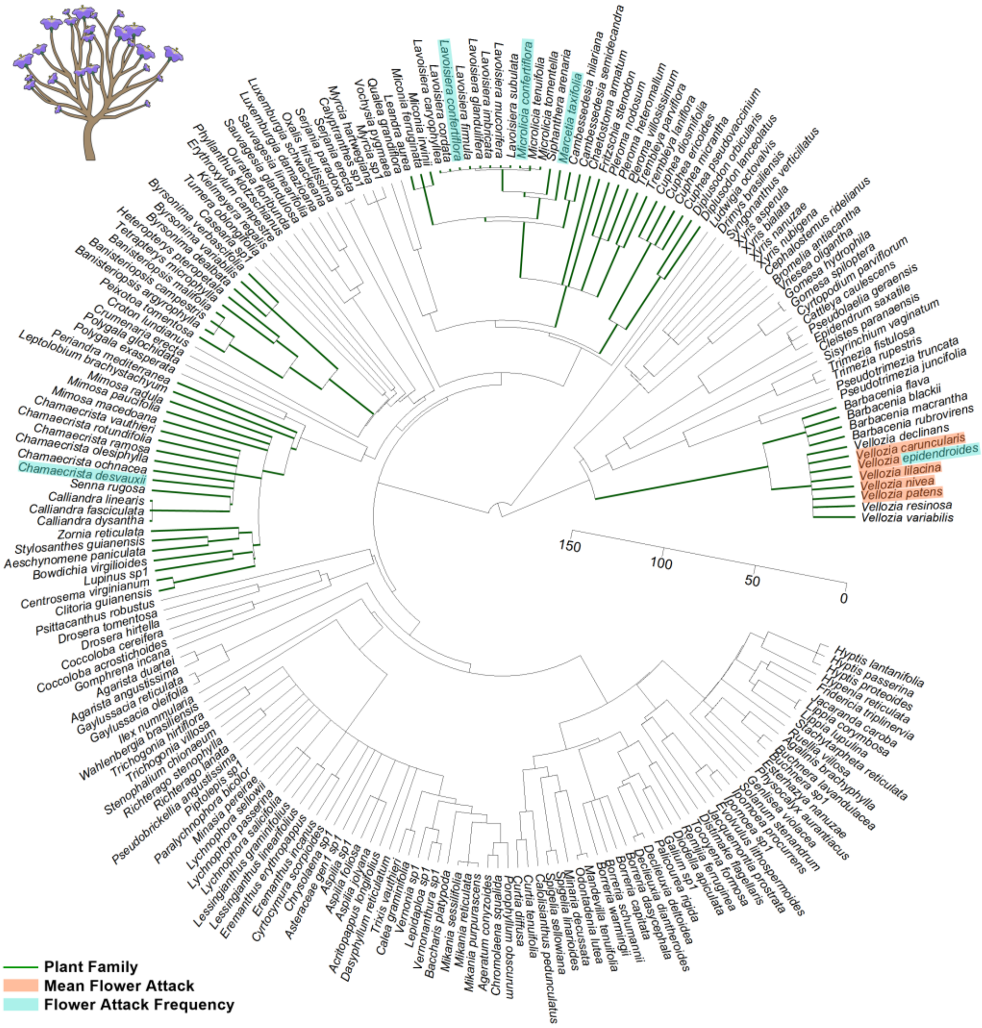

Figure 1. Angiosperm phylogeny of the plants species recorded to address damages by insect florivores in a *campo rupestre* plant communty in Serra do Cipó, Southeastern, Brazil. Samplings occurred between May/18 and August/19. Plant level approach showing: the five plant families most attacked by insect florivores (from left to right: Fabaceae, Malpighiaceae, Melastomataceae and Lythraceae) in gren solid lines. Plant species with greater mean flowers attacked by insect florivores in light orange boxes. Plant species with greater frequency of attack by insect florivores in light blue boxes.

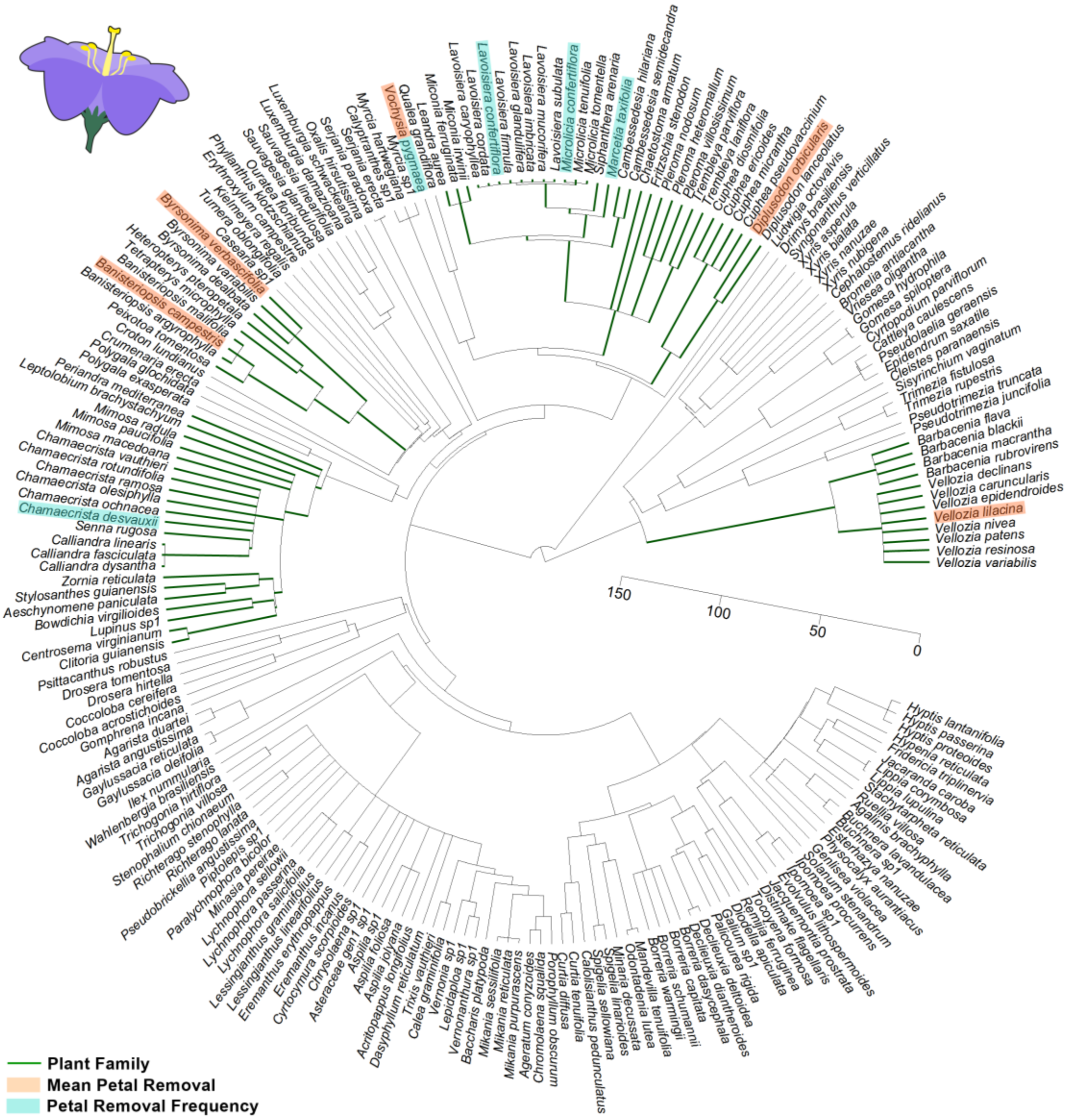

Figure 2. Angiosperm phylogeny of the plant species recorded to address damages by insect florivores in a *campo rupestre* plant communty in Serra do Cipó, Southeastern, Brazil. Samplings occurred between May/18 and August/19. Flower level approach showing: the five plant families most attacked by insect florivores (from left to right: Fabaceae, Malpighiaceae, Melastomataceae and Lythraceae) in gren solid lines. Plant species with greater mean flowers attacked by insect florivores in light orange boxes. Plant species with greater frequency of attack by insect florivores in light blue boxes.

General references:

Aigner, P.A. 2005. Variation in pollination performance gradients in a *Dudleya* species complex: can generalization promote floral divergence? Functional Ecology 19:681-689.

Arista, M. & Ortiz, P.L. 2007. Differential gender selection on floral size: an experimental approach using *Cistus salviifolius*. Journal of Ecology 95:973-982.

Bronstein, J.L., Huxman, T.E. & Davidowitz, G. 2007. Plant-mediated effects linking herbivory and pollination. In: Ohgushi, T., Craig, T.P. & Price, P.W. (eds). Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press 1:75-103

Bronstein, J.L., Huxman, T.E. & Davidowitz, G. 2007. Plant-mediated effects linking herbivory and pollination. In: Ohgushi, T., Craig, T.P., Price, P.W. (Eds), Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press, Cambridge, UK p 75-103.

Burgess, KH. 1991. Florivory: the ecology of flower feeding insects and their host plants. PhD Thesis, Harvard University, Cambridge, MA.

Castro, S., Silveira, P. & Navarro L. 2008. Consequences of nectar robbing for the fitness of a threatened plant species. Plant Ecology 199:201-208.

Delmas, C.E.L., Escaravage, N. & Pornon A. 2014. Massive floral display affects insect visits but not pollinator-mediated pollen transfer in *Rhododendron ferrugineum*. Plant Biology 16:234-243.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. 2004 Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution and Systematics 35:375-403.

Fernandes, G.W. 2016. The megadiverse rupestrian grassland. In: Fernandes GW (Ed), Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, Cham, pp. 3–14.

Fernandes, G.W., Barbosa, N.P.U., Alberton, B., Barbieri, A., Dirzo, R., Goulart, F., Guerra, T.J., Morellato, L.P.C., Solar, R.R.C. 2018. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodiversity and Conservation, 27:2587-2603.

Fernandes, G. W., Arantes-Garcia, L., Barbosa, M., Barbosa, N. P., Batista, E. K., Beiroz, W., Resende, F. M., Abrahão, A., Almada, E. D., Alves, E., Alves, N. J., Angrisiano, P., Arista, M., Arooyo, J., Arruda, A. J., Bahia, T. O., Braga, L., Brito, L., Callisto, M., Caminha-Paiva, D., Carvalho, M., Conceição, A. A., Costa, L. N., Cruz, A., Cunha-Blum, J., Dagevos, J., Dias, B. F. S., Pinto, V. D., Dirzo, R., Domingos, D. Q., Echternacht, L., Fernandes, S., Figueira, J. E. C., Fiorini, C. F., Giulietti, A. M., Gomes, A., Gomes, V. M., Gontijo, B., Goulart, F., Guerra, T. J., Junqueira, P. A., Lima-Santos, D., Marques, J., Meira-Neto, J., Miola, D. T. B., Morellato, L. P. C., Negreiros, D., Neire, E., Neves, A. C., Neves, F. S., Novais, S., Oki, Y., Oliveira, E., Oliveira, R. S., Pivari, M. O., Junior, E. P., Ranieri, B. D., Ribas, R. P., Scariot, A., Schaefer, C. E., Sena, L., da Silva, P. G., Siqueira P. R., Soares, N. C., Soares-Filho, B., Solar, R., Tabarelli, M., Vasconcelos, R., Vilela, E. & Silveira, F. A. 2020. Biodiversity and ecosystem services in the Campo Rupestre: A road map for the sustainability of the hottest Brazilian biodiversity hotspot. Perspectives in Ecology and Conservation 18:213-222.Frame D. 2003. Generalist Flowers, Biodiversity and Florivory: Implications for Angiosperms. Taxon, 52:681-685.

Galen, C. 1996. Rates of floral evolution: Adaptation to bumblebee pollination in an alpine wildflower, *Polemonium viscosum*. Evolution 50:120-25.

Galen, C. 1999. Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. Bioscience 49:631-640.

Harder, L.D. & Johnson SD. 2005. Adaptive plasticity of floral display size in animal pollinated plants. Proceedings of the Royal Society of London Biological Sciences 272:2651-2657.

Inouye, D.W. 1980. The Terminology of Floral Larceny. Ecology 61:1251-1253.

Irwin, R.E. & Brody, A.K. 1998. Nectar robbing in *Ipomopsis aggregata*: effects on pollinator behavior and plant fitness. Oecologia 116:519-527.

Irwin, R.E. 2006. The consequences of direct versus indirect species interactions to selection on traits: pollination and nectar robbing in *Ipomopsis aggregata*. American Naturalist 167:315-328.

Irwin, R.E., Brody, A.K. & Waser, N.M. 2001. The impact of floral larceny on individuals, populations, and communities. Oecologia 129:161-168.

Irwin, R.E., Bronstein, J.L., Manson, J.S. & Richardson, L. 2010. Nectar robbing: ecological and evolutionary perspectives. Annual Review of Ecology, Evolution, and Systematics 41:271-292.

Jones, P.L. & Agrawal, A.A. 2017. Learning in insect pollinators and herbivores. Annual Review of Entomology 62:53-71.

Kudoh, H. & Whigham, D.F. 1998. The effect of petal size manipulation on pollinator/seed-predator mediated female reproductive success of *Hibiscus moscheutos*. Oecologia 117:70-79.

Lobo, J.A., Lacerda-Ramos, D. & Cabral-Braga, A. 2016. Visitation rate of pollinators and nectar robbers to the flowers and inflorescences of *Tabebuia aurea* (Bignoniaceae): effects of floral display size and habitat fragmentation. Botanical Journal of the Linnean Society 181: 667-681.

McCall, A.C. & Irwin, RE. 2006. Florivory: the intersection of pollination and herbivory. Ecology Letters 9:1351-1365.

Moreira, X., Castagneyrol, B., Abdala-Roberts, L. & Traveset, A. 2019. A meta-analysis of herbivore effects on plant attractiveness to pollinators. Ecology 100:e02707.

Mothershead, K. & Marquis, R.J. 2000. Fitness impacts of herbivory through indirect effects on plant–pollinator interactions in *Oenothera macrocarpa*. Ecology 81:30-40.

Navarro, L. & Medel, R. 2009. Relationship between floral tube length and nectar robbing in *Duranta erecta* L. (Verbenaceae). Botanical Journal of the Linnean Society 96:392-398.

Neves, A.C.O., Barbieri, A.F., Pacheco, A.A., Resende, F.M., Braga, R.F., Azevedo, A.A. & Fernandes, G.W. 2016. The human dimension in the Espinhaço Mountains: land conversion and ecosystem services. In: Fernandes GW (Ed.) Ecology and Conservation of Mountaintop Grasslands in Brazil, Springer, Switzerland, pp 501-530.

Ollerton, J., Killick, A., Lamborn, E., Watts, S. & Whiston, M. 2007. Multiple Meanings and Modes: On the Many Ways to Be a Generalist Flower. Taxon 56:717-728.

Roddy, A.B. 2019. Energy balance implications of floral traits involved in pollinator attraction and water balance. International Journal of Plant Sciences 180:944-953.

Roddy A.B., Martínez-Perez C., Teixido A.L., Cornelissen T.G., Olson M.E., Oliveira R.S. & Silveira F.A.O. 2021. Towards the flower economics spectrum. New Phytologist, 229:665-672.

Rosas-Guerrero, V., Aguilar, R., Martén-Rodríguez, S., Ashworth, L., Lopezaraiza-Mikel, M., Bastida, J.M. & Quesada, M. 2014. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? Ecology Letters 17:388-400.

Ruane, L., Rotzin, A.T. & Congleton, P.H. 2014. Floral display size, conspecific density and florivory affect fruit set in natural populations of *Phlox hirsuta*, an endangered species. Annals of Botany 113:887-893

Shykoff, J., Bucheli, E. & Kaltz, O. 1996. Flower lifespan and disease risk. Nature 379:779-780.

Silveira, F.A.O., Negreiros, D., Barbosa, N.P.U., Buisson, E., Carmo, F.F., Carstensen, D.W., Conceição, A.A., Cornelissen, T.G., Echternacht, L., Fernandes, G.W., Garcia, Q.S., Guerra, T.J., Jacobi, C.M., Lemos-Filho, J.P., Le Stradic, S., Morellato, L.P.C., Neves, F.S., Oliveira, R.S., Schaefer, C.E., Viana, P.L. & Lambers, H. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant Soil 403:129-152.

Stebbins, G.L. 1970. Adaptive radiation of reproductive characteristics in angionsperms, I: pollination mechanisms. Annual Review of Ecology, Evolution, and Systematics 1:307-326.

Strauss SY, Irwin RE. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. Annual Review of Ecology, Evolution, and Systematics, 35: 435-466.

Strauss, S.Y. & Whittall, J.B. 2006. Non-pollinator agents of selection on floral traits. In: Harder, L.D. & S. Barrett, S.C.H. (eds.). Ecology and evolution of flowers. Oxford University Press 1:120-138.

Teixido, A.L., Méndez, M. & Valladares, F. 2011. Flower size and longevity influence florivory in the large-flowered shrub *Cistus ladanifer*. Acta Oecologica 37: 418-421.

Teixido, A.L. & Valladares, F. 2014. Pollinator-mediated phenotypic selection does not always modulate flower size and number in the large-flowered mediterranean shrub *cistus ladanifer* (Cistaceae). Botanical Journal of the Linnean Society 176:540-555.

Thompson, J.N. 2005. The geographic mosaic of coevolution. The Universtity of Chicago Press, Chicago & Londres, 400p.

Thompson, J.N., Fernandez, C.C. 2006. Temporal dynamics of antagonism and mutualism in a geographically variable plant–insect interaction. Ecology 87:103-112.

Wang, O., Li, Y., Pu, X., Zhu, L., Tang, Z. & Liu, Q. 2013. Pollinators and nectar robbers cause directional selection for large spur circle in *Impatiens oxyanthera* (Balsaminaceae). Plant Systematics and Evolution 299:1263-1274.