UNIVERSIDADE FEDERAL DE MINAS GERAIS
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia, Conservação e Manejo de Vida Silvestre

Maria Gabriela Boaventura de Castro

A STUDY OF THE PROCESS AND PATTERNS THAT DRIVE FLORIVORY ACROSS PLANT LINEAGES AND ENVIRONMENTAL CONTEXTS

Belo Horizonte,
2023

Maria Gabriela Boaventura de Castro

A STUDY OF THE PROCESS AND PATTERNS THAT DRIVE FLORIVORY ACROSS PLANT LINEAGES AND ENVIRONMENTAL CONTEXTS

Tese apresentada ao programa de Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de doutora em Ecologia.

Orientadora: Drª Tatiana Cornelissen

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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

Ata da Defesa de Tese

Nº 220
Entrada: 2018/2

Maria Gabriela Boaventura de Castro

No dia 31 de maio de 2023, às 14:00 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) Maria Gabriela Boaventura de Castro, orientando(a) do Professor Tatiana Garabini Cornelissen, intitulada: **"A study of the processes and patterns that drive florivory across plant lineages and environmental contexts"**. Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Tatiana Garabini Cornelissen, 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: Geraldo Wilson Afonso Fernandes (UFMG), Irene Gélvez Zúñiga (UFMG), Milton Barbosa da Silva Júnior (UFMG), Lorena Ashworth (National University of Cordoba) 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;
( ) Reprovação da tese (marcar se é a primeira ou segunda reprovação): ( ) *primeira reprovação ( ) segunda reprovação

*Conforme o disposto no Artigo 80 da Resolução Complementar do CEPE/UFMG Nº 02/2017, de 04 de julho de 2017, caso seja a primeira reprovação, poderá ser concedido, a critério do Colegiado de Curso, um prazo para a realização de nova defesa de tese.

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, 31 de maio de 2023.

Assinaturas dos Membros da Banca Examinadora

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RESUMO

Este trabalho é o resultado de um estudo que teve como objetivo avaliar os padrões gerais e processos que determinam as interações entre flores e florívoros. No capítulo I nós sumarizamos as informações disponíveis até o momento sobre florívoria, através de uma revisão integrativa, que reuniu dados de estudos publicados até 2020 e dados inéditos, coletados em campo através de um protocolo padronizado. Nós comparamos os níveis de danos florais entre plantas tropicais e temperadas, examinamos os efeitos das características funcionais das plantas nos danos florais e exploramos a dinâmica eco-evolutiva das interações flor-florívoro para 180 espécies de plantas, em 64 famílias, distribuídas ao redor do mundo. Além disso, nós identificamos os principais caminhos de pesquisa que ajudarão a preencher lacunas persistentes de conhecimento, fornecemos o primeiro banco de dados global e de acesso livre com informações sobre interações flor-florívoro e propusemos um protocolo padronizado para medições de florívoria. Com flores de 61 espécies, distribuídas em 20 famílias e coletadas usando o protocolo padronizado para medições de florívoria supracitado, no capítulo II nós avaliamos a influência de alguns fatores abióticos (ambientais) e características florais nos níveis de florívoria. O objetivo deste capítulo II foi examinar se as mudanças ambientais causadas pela urbanização influenciam os níveis de florívoria e se os níveis de florívoria são impulsionados por atributos de plantas ligados a urbanização e a características funcionais e filogenéticas de flores e espécies. Neste capítulo nós fornecemos uma das primeiras avaliações de florívoria ao nível da comunidade de espécies, através de uma nova abordagem, no contexto das alterações ambientais que ocorrem devido a urbanização, preenchendo assim uma importante lacuna do conhecimento.

Palavras-chave: florívoria, herbívoria floral, dano floral, inimigos florais, florívoros, urbanização.

ABSTRACT

This work is the result of a study aimed at evaluating the general patterns and processes that determine the interactions between flowers and florivores. In Chapter I, we summarized the available information to date on florivory through an integrative review that brought together data from published studies up to 2020 and unpublished data collected in the field using a standardized protocol. We compared levels of floral damage between tropical and temperate plants, examined the effects of plant functional traits on floral damage, and explored the eco-evolutionary dynamics of flower-florivore interactions for 180 plant species in 64 families distributed worldwide. Additionally, we identified key research pathways that will help fill persistent knowledge gaps, provided the first global and freely accessible database with information on flower-florivore interactions, and proposed a standardized protocol for measuring florivory. In Chapter II, using flowers from 61 species belonging to 20 families and collected using the a standardized protocol for florivory collect and measurement's, we assessed the influence of abiotic (environmental) factors and floral traits on florivory levels. The aim of this Chapter II was to examine whether environmental changes caused by urbanization influence florivory levels and whether florivory levels are driven by plant attributes related to urbanization, as well as functional and phylogenetic traits of flowers and species. In this chapter, we provided one of the first assessments of florivory at the species community level through a novel approach, in the context of environmental changes occurring due to urbanization, thus filling an important knowledge gap.

Keywords: florivory, floral herbivory, floral damage, floral enemies, florivores, urbanization**.**

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INTRODUÇÃO GERAL

Interações entre insetos e plantas desempenham um papel fundamental na dinâmica das populações (Marquis, 1984), na estrutura das comunidades (Agrawal e Maron, 2022), nos processos evolutivos e serviços ecossistêmicos (Turcotte et al., 2014a; Kozlov et al., 2017). Essas interações compreendem processos que variam desde interações mutualísticas e positivas, como a polinização, ou interações antagônicas e negativas, como a herbívoria e a florívoria (Strauss et al. 1996; McCall e Irwin, 2006; Bronstein et al. 2007).

Os padrões gerais de herbívoria foliar vem sendo bem documentados nos últimos anos (Coley e Barone, 1996; Metcalfe et al., 2014; Turcotte et al., 2014b; Kozlov et a., 2015; Mendes et al., 2021), mas os padrões de florívoria, por outro lado, seguem amplamente pouco avaliados e indefinidos, já que a maioria dos estudos tende a se concentrar na herbívoria como relação antagonística e na polinização como relação mutualística (McCall e Irwin, 2006; McCall, 2008; Gorden e Adler, 2016). A florívoria é definida como qualquer tipo de dano a flores e envolve o consumo de tecidos florais por animais vertebrados ou invertebrados, como insetos (McCall e Irwin, 2006; Fig.1). Florívoros podem afetar as plantas tanto diretamente ao consumirem partes florais efetivamente ligadas à reprodução como pistilos, estames e óvulos, reduzindo o número de gametas produzidos – como indiretamente, quando ao consumirem pétalas, sépalas e botões florais eles modificam atributos florais relacionados à atratividade, interferindo na relação planta-polinizador (McCall e Irwin, 2006; Caruso et al., 2019, Fig.1). Como consequência, os florívoros podem causar uma pressão seletiva negativa sobre os atributos florais que atraem polinizadores, o que pode levar a uma redução no serviço ecológico prestados por eles (McCall e Irwin, 2006; Caruso et al., 2019; Rusman et al., 2019).

Fig.1. Florívoria e florívoros em algumas das espécies de plantas avaliadas no presente estudo. A- Flor e florívoros de *Solanum lycocarpum*. B- Florívoria em *Bauhinia variegata*. C- *Diabrotica speciosa* (Chrysomelidae), florívoro de *Turnera subulata*. D- Formiga florívora de *Periandra mediterranea*. E- Besouro Chrysomelidae alimentando-se de pétalas de *Chamaecrista* sp. F- Florívoria em *Ceiba speciosa*. G- Besouro *Conognatha compta* alimentando-se de pétalas de *Microliceae congestiflora*. H- Florívoria em *Trembleya laniflora*. I- Florívoria em *Aspilia* sp.

Apesar do potencial impacto negativo da florívoria, ainda não temos uma compreensão completa sobre níveis gerais de dano floral ou, sobre como seus efeitos diretos e indiretos afetam as plantas e quais os mecanismos e processos que tornam certas espécies mais vulneráveis a esse antagonismo. Acreditamos que os efeitos da florívoria no *fitness* das plantas dependam de vários fatores como, da intensidade dos danos florais (quantidade de área floral removida), identidade das plantas e dos florívoros e a sua guilda alimentar e de fatores ligados ao ambiente onde plantas e florívoros estão inseridos. Entretanto, só conseguiremos avançar no conhecimento acerca da florívoria acumulando dados sobre níveis de danos e padrões de ocorrência deste antagonismo em várias linhagens de plantas e diferentes contextos ambientais e biogeográficos.

Considerando a falta de conhecimento sobre os padrões gerais que determinam as interações entre flores e florívoros, no **capítulo I** nós sumarizamos as informações disponíveis até o momento sobre florívoria, através de uma revisão integrativa, que reuniu dados de estudos publicados até 2020 e dados inéditos, coletados em campo através de um protocolo padronizado. Nós comparamos os níveis de danos florais entre plantas tropicais e temperadas, examinamos os efeitos das características funcionais das plantas nos danos florais e exploramos a dinâmica eco-evolutiva das interações flor-florívoro para 180 espécies de plantas, em 64 famílias, distribuídas ao redor do mundo. Além disso, nós identificamos os principais caminhos de pesquisa que ajudarão a preencher lacunas persistentes de conhecimento, fornecemos o primeiro banco de dados global e de acesso livre com informações sobre interações flor-florívoro e propusemos um protocolo padronizado para medições de florívoria.

Com flores de 61 espécies, distribuídas em 20 famílias e coletadas usando o protocolo padronizado para medições de florívoria supracitado, no **capítulo II** nós avaliamos a influência de alguns fatores abióticos (ambientais) e características florais nos níveis de florívoria. O objetivo deste capítulo II foi examinar se as mudanças ambientais causadas pela urbanização influenciam os níveis de florívoria e se os níveis de florívoria são impulsionados por atributos de plantas ligados a urbanização e a características funcionais e filogenéticas de flores e espécies. Neste capítulo nós fornecemos uma das primeiras avaliações de florívoria ao nível da comunidade de espécies, através de uma nova abordagem, no contexto das alterações ambientais que ocorrem devido a urbanização, preenchendo assim uma importante lacuna do conhecimento.

Capítulo I:

Revisiting florivory: an integrative review and global patterns of a neglected interaction

Running title: An integrative review of florivory and florivores

Revisiting florivory: an integrative review and global patterns of a neglected interaction

Maria Gabriela Boaventura[1], Nora Villamil[2], Alberto L. Teixido[3], Richard Tito[4], Heraldo L. Vasconcelos[5], Fernando A. O. Silveira[1], Tatiana Cornelissen[1]

1. Center for Ecological Synthesis and Conservation, Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, CP 486, Belo Horizonte, MG, Brazil.

2. Department of Ecology and Evolution, Université de Lausanne, CH-1015, Lausanne, Switzerland.

3. Departamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Av. Fernando Corrêa 2367, E-78060-900, Cuiabá, MT, Brazil.

4. Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Lima 15088, Peru.

5. Instituto de Biologia, Universidade Federal de Uberlândia, Av. Pará 1720, 38405-302, Uberlândia, MG, Brazil.

Corresponding author:
Maria Gabriela Boaventura
Center for Ecological Synthesis and Conservation
Universidade Federal de Minas Gerais
Belo Horizonte - MG, Brazil
+55(38)999119696
mgabiboaventura@ufmg.br

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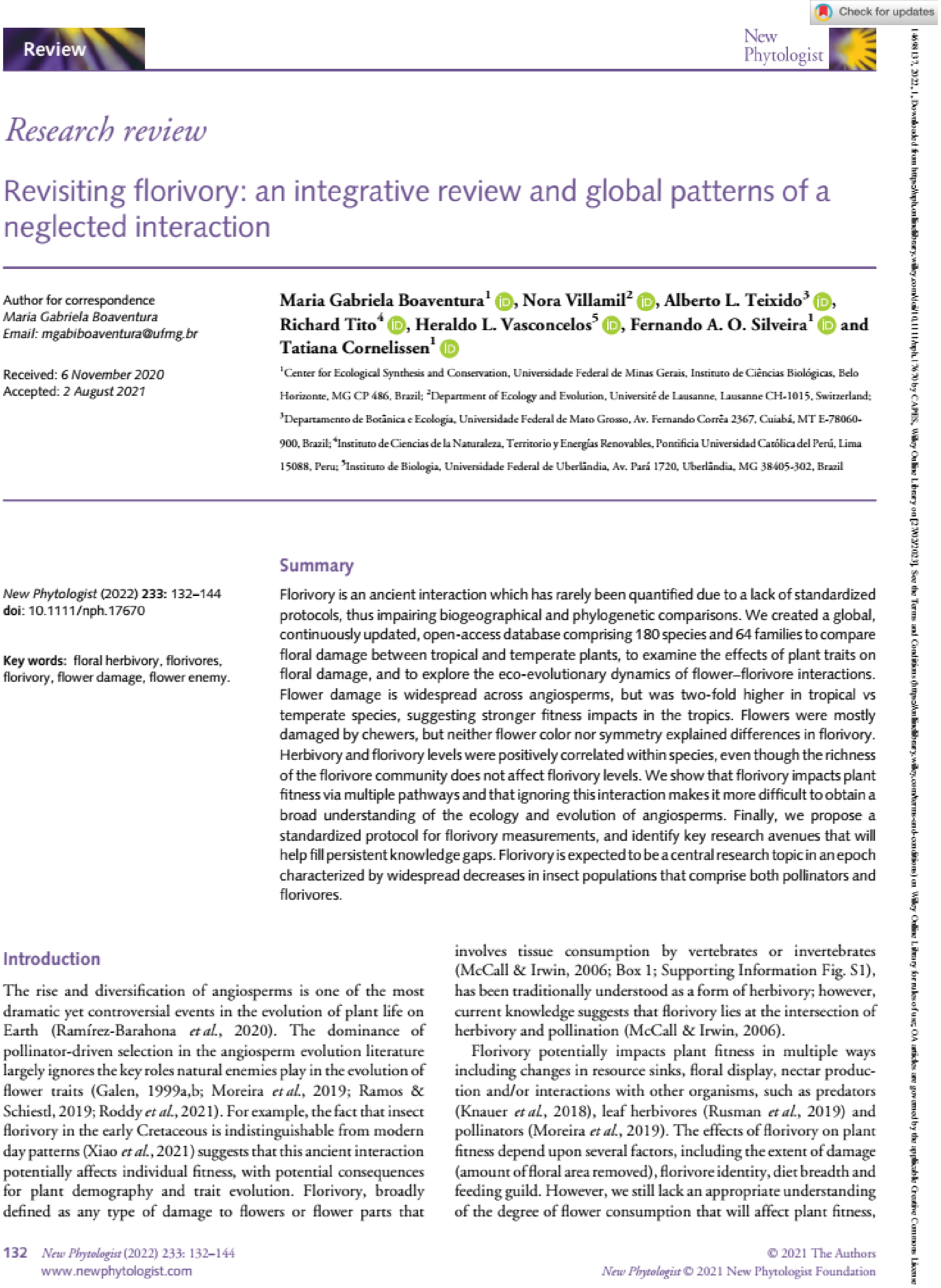

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Revisiting florivory: an integrative review and global patterns of a neglected interaction

Author for correspondence
Maria Gabriela Boaventura
Email: mgabiboaventura@ufmg.br

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Maria Gabriela Boaventura[1], **Nora Villamil**[2], **Alberto L. Teixido**[3], **Richard Tito**[4], **Heraldo L. Vasconcelos**[5], **Fernando A. O. Silveira**[1] and **Tatiana Cornelissen**[1]

[1]Center for Ecological Synthesis and Conservation, Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Belo Horizonte, MG CP 486, Brazil; [2]Department of Ecology and Evolution, Université de Lausanne, Lausanne CH-1015, Switzerland; [3]Departamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Av. Fernando Corrêa 2367, Cuiabá, MT E-78060-900, Brazil; [4]Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Lima 15088, Peru; [5]Instituto de Biologia, Universidade Federal de Uberlândia, Av. Pará 1720, Uberlândia, MG 38405-302, Brazil

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Key words: floral herbivory, florivores, florivory, flower damage, flower enemy.

Summary

Florivory is an ancient interaction which has rarely been quantified due to a lack of standardized protocols, thus impairing biogeographical and phylogenetic comparisons. We created a global, continuously updated, open-access database comprising 180 species and 64 families to compare floral damage between tropical and temperate plants, to examine the effects of plant traits on floral damage, and to explore the eco-evolutionary dynamics of flower–florivore interactions. Flower damage is widespread across angiosperms, but was two-fold higher in tropical vs temperate species, suggesting stronger fitness impacts in the tropics. Flowers were mostly damaged by chewers, but neither flower color nor symmetry explained differences in florivory. Herbivory and florivory levels were positively correlated within species, even though the richness of the florivore community does not affect florivory levels. We show that florivory impacts plant fitness via multiple pathways and that ignoring this interaction makes it more difficult to obtain a broad understanding of the ecology and evolution of angiosperms. Finally, we propose a standardized protocol for florivory measurements, and identify key research avenues that will help fill persistent knowledge gaps. Florivory is expected to be a central research topic in an epoch characterized by widespread decreases in insect populations that comprise both pollinators and florivores.

Introduction

The rise and diversification of angiosperms is one of the most dramatic yet controversial events in the evolution of plant life on Earth (Ramírez-Barahona *et al.*, 2020). The dominance of pollinator-driven selection in the angiosperm evolution literature largely ignores the key roles natural enemies play in the evolution of flower traits (Galen, 1999a,b; Moreira *et al.*, 2019; Ramos & Schiestl, 2019; Roddy *et al.*, 2021). For example, the fact that insect florivory in the early Cretaceous is indistinguishable from modern day patterns (Xiao *et al.*, 2021) suggests that this ancient interaction potentially affects individual fitness, with potential consequences for plant demography and trait evolution. Florivory, broadly defined as any type of damage to flowers or flower parts that involves tissue consumption by vertebrates or invertebrates (McCall & Irwin, 2006; Box 1; Supporting Information Fig. S1), has been traditionally understood as a form of herbivory; however, current knowledge suggests that florivory lies at the intersection of herbivory and pollination (McCall & Irwin, 2006).

Florivory potentially impacts plant fitness in multiple ways including changes in resource sinks, floral display, nectar production and/or interactions with other organisms, such as predators (Knauer *et al.*, 2018), leaf herbivores (Rusman *et al.*, 2019) and pollinators (Moreira *et al.*, 2019). The effects of florivory on plant fitness depend upon several factors, including the extent of damage (amount of floral area removed), florivore identity, diet breadth and feeding guild. However, we still lack an appropriate understanding of the degree of flower consumption that will affect plant fitness,

Summary

Florivory is an ancient interaction which has rarely been quantified owing to a lack of standardized protocols, thus impairing biogeographical and phylogenetic comparisons. We created a global, continuously-updated, open-access database comprising 180 species and 64 families to compare floral damage between tropical and temperate plants, to examine the effects of plant traits on floral damage, and to explore the eco-evolutionary dynamics of flower-florivore interactions. Flower damage is widespread across angiosperms but was two-fold higher in tropical vs. temperate species, suggesting stronger fitness impacts in the tropics. Flowers were mostly damage by chewers, but neither flower color nor symmetry explained differences in florivory. Herbivory and florivory levels were positively correlated within species even though the richness of the florivore community does not affect florivory levels. We show that florivory impacts plant fitness through multiple pathways and that ignoring this interaction hampers a broad understanding on the ecology and evolution of angiosperms. Finally, we propose a standardized protocol for florivory measurements, and identify key research avenues that will help fill persistent knowledge gaps. Florivory is expected to be a central research topic in an epoch characterized by widespread decreases in insect populations that comprise both pollinators and florivores.

Keywords

Florivores, flower damage, flower enemy, florivory, floral herbivory

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***Box 1.* Flowers beyond pollinators: the role of flower enemies**

Florivory has been broadly defined as flower consumption by animals or flower herbivores, although the different flower enemies involved in this interaction have different impacts on plant fitness and floral evolution. Nectar robbers and florivores have been the most frequent enemies evaluated, both through natural observations as well as through experiments manipulating flower damage artificially. We compiled definitions of terms regarding flower enemies (Galen, 1999a,b; McCall & Irwin, 2006), bearing in mind the challenges of labelling species behavior in such entangled, intermingled interactions. For example, in some plant families, flower parts are offered as the reward for legitimate pollinators, which are not included in our definition of florivores due to their overall positive outcome for plant fitness (Gottsberger, 1999):

1. Florivores: animals that cause damage and consume flower buds, flowers and floral rewards, before fruit and seed formation. Included in this category are vertebrates and invertebrates that damage petals, sepals, bracts, pistils, stamens and/or ovules. These florivores consume floral parts or, in some cases, the whole flower. We excluded from this definition, pollen-eating pollinators which consume flower parts but act as legitimate pollinators.

2. Nectar robbers: Nectar robbers damage flowers, usually without aiming to consume the perianth tissue. They are considered flower enemies, but not florivores.

2.1. Primary nectar robbers: illegitimate flower visitors who usually pierce flower parts to obtain nectar without exerting any pollen removal or deposition.

2.2. Secondary nectar robbers: illegitimate flower visitors who use perforations made by previous robbers to obtain nectar, but who exert no pollen removal or deposition functions.

3. Nectar thieves: animals that use the natural flower opening to obtain nectar, but do not exert any pollen removal or deposition due to incompatible morphology between body and flower. Nectar thieves do not pierce flowers. Together with nectar robbers, nectar thieves are sometimes called nectar larcenists.

4. Pre-dispersal seed or ovule predators: animals that prey upon seeds or ovules before they are dispersed. The main predators are insect larvae and adults, birds, and mammals. Their impacts on plant fitness vary widely.

5. Flower parasites: pathogens that are transported to flowers by pollinators or other visitors, such as spores, viruses or bacteria. Infections caused by these parasites can lead to plant diseases and lower nectar production and/or sterile flowers.

6. Saproflorivory: consumption of flowers already shed by the mother-plant. This is unlikely to have major negative impacts on plant fitness.

This suggests that florivores may have an underappreciated role in impacting female fitness. Thus, evaluating the impacts of florivores on plant fitness needs to extend beyond estimating floral tissue loss and start embracing the multitude of paths by which florivores impact host plant fitness, such as their indirect effects.

Florivory resembles herbivory in that it involves the consumption of plant tissues with direct (damaging reproductive structures) and indirect (affecting the attractiveness of damaged flowers to pollinators) negative effects on plant performance (see González-Browne *et al.,* 2016; Soper-Gorden & Adler, 2016; Soper-Gorden *et al.,* 2016). However, florivory also resembles pollination in that flowers are a crucial resource to florivores in the similar ways as they are to pollinators (Genini *et al.,* 2010). Many pollinator-attractive traits also attract floral enemies (Jacobsen & Raguso, 2018; Rusman *et al.,* 2019), establishing a complex mosaic of selective forces shaping flower traits. However, florivory goes beyond these mere resemblances, and stand alone as an interaction linking both herbivory and pollination (Table 1). Florivory also shapes interactions with plant herbivores generating cascading and community-wide effects (Soper-Gorden *et al.,* 2016).

Distinguishing between foliar and floral herbivores as well as generalist consumers of both flowers and leaves is important due to their different consequences for plant fitness (McCall & Irwin, 2006). Induced plant responses to florivory against generalist insects might be common (McCall & Karban, 2006), and may trigger responses in other plant organs. For example, flower damage by generalist flower eating katydids (Orthoptera) induces mechanical defenses in leaves of *Lantana camara* (Goh *et al.,* 2019). Generalist herbivores that simultaneously feed upon leaves and flowers might cause greater reductions in plant performance due to the combined and direct effects of tissue consumption and the indirect effects of flower consumption on pollinators (Cardel & Koptur, 2010). By accounting for both leaf and flower damage, we depict a more realistic picture, as ecological communities involve the simultaneous occurrence of antagonistic and mutualistic species on a single resource (e.g., leaf or flower) rather than as isolated pairwise mutualistic or antagonistic interactions (Tscharntke & Hawkins, 2002).

Table 1 - The tangled nature of the ecology, evolution and biogeography of widely-studied herbivores and pollinators, and overlooked florivores.

Characteristic	**Herbivores**	**Pollinators**	**Florivores**	**Key References**
Interaction outcome	Parasitism, predation, or commensalism	Mutualism, rarely parasitism	Parasitism, rarely mutualism	Herrera & Pellmyr, 2002; McCall & Irwin, 2006
Impact on host	Negative or neutral	Positive	Unknown	Herrera & Pellmyr, 2002; McCall & Irwin, 2006
Plant organ/resource	Roots, stems, leaves, seeds	Pollen, nectar, oil, more rarely petals	Sepals, tepals, stamens, ovules, nectar	Coley & Barone, 1996; McCall & Irwin, 2006
Frequency of interaction	Year-round	During plant reproduction	During plant reproduction	McCall & Irwin, 2006
Specialization degree	From generalists to specialists	From generalists to specialists	Most likely generalists	Forister *et al.,* 2015; Wash & Ollerton, 2006; McCall & Irwin, 2006; Caruso *et al.,* 2019
Selective force	On leaves and flowers	On flowers	On flowers?	Lorange *et al.,* 2013; Schiestl & Johnson, 2013; Caruso *et al.,* 2019
Latitudinal gradient	Specialization towards tropics	Specialization towards temperate areas	Unknown	Coley & Barone, 1996; Kozlov *et al.,* 2015b; Waser & Ollerton, 2006; Keith & Mitchell-Olds, 2017

Furthermore, the presence of a third agent can affect the likelihood, type or intensity of interactions within a given pairwise interaction, influencing patterns of trait evolution through diffuse selection (Strauss & Irwin, 2004). Generalist ants – which usually defend plants when herbivores are abundant (Rosumek *et al.,* 2009) – turn into florivores when neither leaves or herbivores are present (Smallegange *et al.,* 2007; Bandeili & Müller, 2010). The impacts of herbivory and florivory on plant fitness can lead to different population, community and ecosystem-wide outcomes (McCall & Irwin, 2006), and it is therefore crucial to start distinguishing between damage caused by both generalist and specialist florivores and herbivores.

Another knowledge gap preventing a broader understanding of flower-florivore interactions is the understanding on how plant traits affect florivory levels. The remarkable variation in flower traits is generally attributed to pollinator-mediated selection (van der Kooi & Ollerton, 2020). However, floral traits that originally evolved to protect gametes from predators (Chanderbali *et al.,* 2016) may also attract flower enemies (see refs in Roddy *et al.*, 2021), creating a mosaic of complex, multilayered interaction networks (Strauss & Irwin, 2004; Lucas-Barbosa, 2016). Unfortunately, morphological flower traits are underrepresented in plant trait databases. A search into TRY database (www.try-db.org) (Kattge *et al.,* 2020) retrieved only 22 morphological flower traits; other traits such as flower rewards, were much more common (more than 3,500 entries) than traits relevant for florivore attraction, including flower size (Teixido *et al.,* 2011; McCall & Barr, 2012; Gélvez-Zúñiga *et al.,* 2018), floral display (Krupnick *et al.*, 1999; Oguro & Sakai, 2015), longevity (McCall & Irwin, 2006; Teixido *et al.,* 2011), secondary metabolites in petals (Jacobsen & Raguso, 2018, Kessler *et al.,* 2019) and in pollen and nectar (Adler, 2000).

Changes in plant apparency (Feeny, 1976; Smilanich *et al.*, 2016) involve strategies to reduce damage from herbivores and plants may also escape florivory by making flowers less conspicuous. Flower size, longevity and arrangement (single *vs.* inflorescences) are linked with flower appearance and hence may drive florivory levels. In deciduous plant systems, leaf herbivores are expected to act as florivores when leaves are absent or *vice-versa* (Boaventura *et al.,* under review). For instance, in tropical deciduous species (where dry-season blooming occurs in leafless trees) or in temperate ecosystems (where leaves and flowers are often flushed at different times throughout spring and summer), natural selection may favor phytophagous animals capable of using both resources (leaves and flowers), and extend their foraging opportunities and timings (Boaventura *et al.,* under review). In turn, the optimal defense theory (ODT, McKey, 1974) is also evoked as a mechanistic explanation for the variation in the distribution of chemical defenses across plant tissues and organs depending on their vulnerability to attack and fitness value. The ODT is based on two fundamental assumptions: defenses enhance plant fitness when enemies are present and they are costly, decreasing plant fitness when enemies are absent. Natural selection is therefore expected to enhance defense systems with positive benefit-cost ratios, predicting that the most valuable plant organs should be constitutively defended, as is the case of young leaves and flowers or flower parts (McCall & Fordyce, 2010). In contrast, the plant apparency hypothesis (PAH, Feeny, 1976) suggests variation in secondary chemistry investment between and within plants based on the chance of encounter by generalist and specialist herbivores. Because flowers are ephemeral resources and attack levels might be unpredictable and linked to flower longevity, they might be less apparent and also less defended than their counterparts (leaves) within given individuals or species (e.g., McCall & Fordyce, 2010). Both theories – ODT and the PAH – may explain why strict florivores are rare in nature, as coevolution mediated by secondary chemistry might not be the case in florivore-flower systems as commonly reported in herbivore-leaf systems (e.g., Keith & Mitchell-Olds, 2017).

Here, we explore overlooked aspects of florivory by using a global, continuously-updated, open-access database to address some issues at the macroevolutionary scale. In particular, we 1) reviewed the evidence for florivory occurrence and addressed its sources of variation using data published in the literature over the past decades; and 2) collected field data with a standardized protocol to a) compare floral damage between tropical and temperate plants; b) examine the effects of plant traits on floral damage, and c) explore the eco-evolutionary dynamics of flower-florivore interactions. Finally, we propose a standardized protocol for florivory measurements that would provide support to macroecological, biogeographic and evolutionary approaches in complex plant-animal interactions.

Material and methods

Global trends of naturally occurring florivory

Published data was systematically sampled by searching the keywords (Florivor* OR Florivore* OR "Flower enemy" OR "Flower antagonis*" OR "Floral damage" OR "Flower damage") in the title, abstract and keywords of papers published between 1945 and 2020 in the Web of Science and Scopus. Studies found were individually examined following the PRISMA guidelines (Page *et al.,* 2021) for database construction and transparency. We also surveyed the references from recent reviews (González-Browne *et al.,* 2016; Caruso *et al.,* 2019; Moreira *et al.,* 2019) and extracted data on floral damage, defined as any kind of damage to any floral part, including petals, sepals and sexual organs. It was not always possible to separate damage within the reproductive structures, so the damage to stamens, pistils and ovules was collectively labelled as reproductive parts.

We classified studies according to 1) region (temperate or tropical), 2) country, 3) season of the year in which data were collected), and 4) plant family, and 5) species. We retrieved the following floral traits: 1) symmetry (zygomorphic or actinomorphic), 2) corolla size, 3) color, and 4) flower number and arrangement (single or multiple/inflorescence). In our database flower color is reported as perceived by human eyes but we acknowledge that ideally color categories should be addressed from the perspective of animals that use flowers as resources, as has been done for honey bees (Waser *et al.,* 1996). Florivores were classified according to their 1) Order, 2) guild (chewers, suckers, parasites and pollen feeders) and 3) broad taxonomic group (birds, mammals, insects, other invertebrates, and several groups). Lastly, floral damage was classified according to the response variable used as a *proxy* for florivory: 1) frequency of attacked flower or flower parts and 2) percentage of floral area removed [(corolla damage divided by total corolla area) *100]. Data recorded as presence or absence of florivory were not included in our dataset as our main goal was to provide quantitative estimates of florivory levels in natural plant populations. When published studies recorded different florivory measurements, different plant species and/or different locations, each record was considered as an outcome (Supporting information, Table S1). Database is available at datadryad.org (https://doi.org/10.6084/m9.figshare.15106230).

Florivory levels from published studies are reported separately in the database for each response variable (frequency of attacked flowers and percentage of flower area removed by florivores), but only frequency of attacked flowers had enough replicates to allow statistical analysis using phylogenetically least square models (PGLS). We tested for differences in florivory between regions, florivore guilds and floral traits accounting for phylogenetic relatedness among species, adjusting the expected covariance under a multivariate Brownian motion model (Felsenstein, 1985; Martins & Hansen, 1997). In this model we fitted frequency of flower attack as the response variable, and as fixed effects we included region, flower symmetry, number, and color, florivore broad taxonomic group and florivore guilds. Plant species was included as a random effect to account for non-independence among data. The phylogeny tree for the 98 plant species (Supporting information, Fig S1) was constructed using the package *phytools* (Revell, 2012) in R studio (R Core Team, 2019) and analyses were done using *nlme* (Pinheiro *et al.*, 2018), *lme* and *lme4* packages (Bates *et al.*, 2015).

Field data - florivory levels and trait-mediated florivory

To supplement the database using standardized data on florivory levels under natural conditions, we sampled flower damage from 36 plant in Mexico, Brazil, and Scotland using a standardized protocol for data sampling and flower measurements. Given that field data on florivory levels (percentage of corolla damage) is yet rare, we included as many species as possible to increase our generalization capacity. Up to 20 adult individuals of each plant species were randomly selected, marked, and georeferenced in the field. The canopy of every selected individual was sampled in order to haphazardly collect approximately 25 flowers, regardless of signs of damage by florivores (Supporting information, Fig. S2). For plant species with inflorescences, five inflorescences were sampled per individual and all flowers were examined for petal or sepal damage in the laboratory. Due to the ephemeral nature of flowers and to the logistics of digitizing fresh flowers in the field, we focused our study in floral damage on petals and sepals (or tepals) and direct damage to sexual organs was not evaluated in these sampled flowers.

Flower petals and or sepals were digitized for the 36 plant species sampled (Supporting information, Table S2) and florivory was estimated according to damage classes by a single researcher using digital images, a method commonly used for herbivory studies (Dirzo & Dominguez, 1995). Classes of removed floral area were assigned as: (0)- intact flower, (1) 0.01 to 1%, of floral area removed by florivores, (2) between 1 and 5%, (3) between 5 and 25%, (4) between 25 and 50%, (5) between 50 and 75% and (6) between 75 and 100% of flower area removed. A damage index was calculated for each individual, as IFD = Σ ni (i)/N, where IFD is the index of flower damage, “ni” is the number of flowers in category “i" and “N” is the total number of flowers collected per individual. For 14 of those species (Supporting information, Table S3), florivory levels were also precisely measured evaluating the ratio of petal area removed by florivores divided by the total corolla or calix area. Each flower (n=3,025) was digitized with a numeric scale and images were processed using the ImageJ® software after calibrating each image to 0.01 mm.

We used phylogenetically-adjusted least square models (PGLS) to evaluate the effects of region, floral and plant traits on the variation of florivory levels among related plant species. First, we fitted phylogenetically-adjusted regressions mixed models, where the response variable was the mean level of floral damage, whereas region, flower traits, and plant growth form were considered as explanatory factors. We assumed a Brownian motion model of trait evolution, and all analyses were conducted following the details mentioned above (Supporting information, Figure S3).

Eco-evolutionary dynamics of herbivory and florivory

To illustrate the spatio-temporal complexity of florivory, we used standardized data from four sympatric, congeneric trees with leafless-blooming during the dry season (Bignoniaceae). Four deciduous species with different blooming lengths (*Handroanthus heptaphyllus*, *H. crysotrichus*, *H. ochraceus* and *Tabebuia roseo-alba*) were examined to evaluate florivory and herbivory levels, and the community of insects associated to flowers or to leaves. Deciduousness promotes spatio-temporal separation of the type of resource available to insects, as either leaves (during summer and spring) or flowers (during fall and winter). In 2017, we monitored flower phenology from beginning to end of by recording the number of days individual plants had open flowers in 60 individual trees [*H. heptaphyllus* (n=17), *H. chrysotrichus,* (n=15), *H. ochraceus* (n=15), *T. roseoalba* (n=13)] in southeastern Brazil (21° 08' 09" S 44° 15' 43" W). We also collected insects associated to either leaves (in the wet season of 2017) or flowers (in the dry season of 2017) using an entomological umbrella (Gullan & Craston, 2017) and a trimmer with a telescopic handle attached to an entomological net. We carried out five beats in the canopy of each individual tree with the entomological umbrella and all the insects that fell into the trap were collected. We also inspected each plant for 10 minutes, collecting insects on it with tweezers. All captured insects were identified to the lowest possible taxonomic group and the resource used (leaves or flowers) was recorded. Simultaneously, twenty leaves and five inflorescences were collected from each plant. Herbivory and florivory levels were calculated for each individual plant as mean percentage of floral or leaf area removed, using leaves or flowers as replicates per individual plant, and correcting for leaf or flower size. Leaf or flower area removed was calculated using digital images processed on ImageJ® after calibrating each image to 0.01 mm (Mendes *et al.,* 2021).

Because these four plant species are phylogenetically related, we also applied PGLS models to test for differences in insect communities, herbivory and florivory levels among species. The response variables were the level of floral damage, the level of leaf damage and species richness of florivores or herbivores, whereas plant species and number of days plants were blooming were included as explanatory factors. Phylogenetic relatedness was calculated using *phytools* package (Revell, 2012) and included in the model as a random variable assuming Brownian covariance correlation. All analyses were conducted using the *nmle* and *lme4* packages on R software. Goodness of model fit was tested using a maximum likelihood (ML) with link and variance functions.

A standardized protocol for measuring florivory

Standardized measures of florivory are needed to allow us to address and discuss the effects of florivory on plant fitness and to test predictions on flower-florivore interactions at the macroevolutionary scale, as has been lengthily done for herbivores (Dyer *et al.*, 2007; Turcotte *et al.*, 2014; Kozlov *et al.,* 2015a,b; Zhang *et al.,* 2016; Galmán *et al.,* 2018). The available data are yet insufficient to rigorously test predictions at large scales and to be included into meta-analytic frameworks. Having standardized measurements of florivory and flower traits will allow us to run analyses at the macroecological scale and to further identify, for example, the functional significance of flower defensive traits. The results of our review of published data (see below) indicated that frequency of attacked flowers is the most common variable used to quantity florivory. The results of our field data (see below) showed that it is not always possible to assess the levels of florivory using the same methods used to evaluate leaf herbivory, such as categorical measurements of floral area removed. Therefore, we propose a standardized protocol that includes easy-to-measure steps that can be applied to species with different floral traits (Supporting information, Methods S1), and a method to precisely quantify the amount of corolla area removed due to florivore damage.

Results

Global trends of naturally occurring florivory

Eighty studies on florivory were published between 1976 and 2019, generating 458 independent comparisons regarding flower damage for 144 plant species from 47 families, in both temperate and tropical areas (Supporting Information, Fig. S4). Flower damage was inflicted by animals from different lineages (Supporting Information, Fig. S5, Fig. S6).

Florivory was widespread among plant lineages (Fig. 1) and levels of attack are variable at both plant and flower scales. Frequency of attacked flowers was the most common response variable used to estimate florivory (85% of cases), with values ranging from 0.2 to 97%. Frequency of attacked flowers was significantly higher in the tropics ($F_{1,293}$=8.35, P=0.004), in single flowers compared to inflorescences ($F_{1,294}$=4.076, P=0.007), and higher for flowers attacked by chewers compared to other guilds and for mammals or birds compared to insects and other invertebrates ($F_{7,293}$=9.371, P<0.0001) (Fig. 2). Neither flower color nor flower symmetry influenced levels of florivore attack. We did not detect a phylogenetical significant signal in any of the variables evaluated to modulate florivore attack (Supporting information, Table S4).

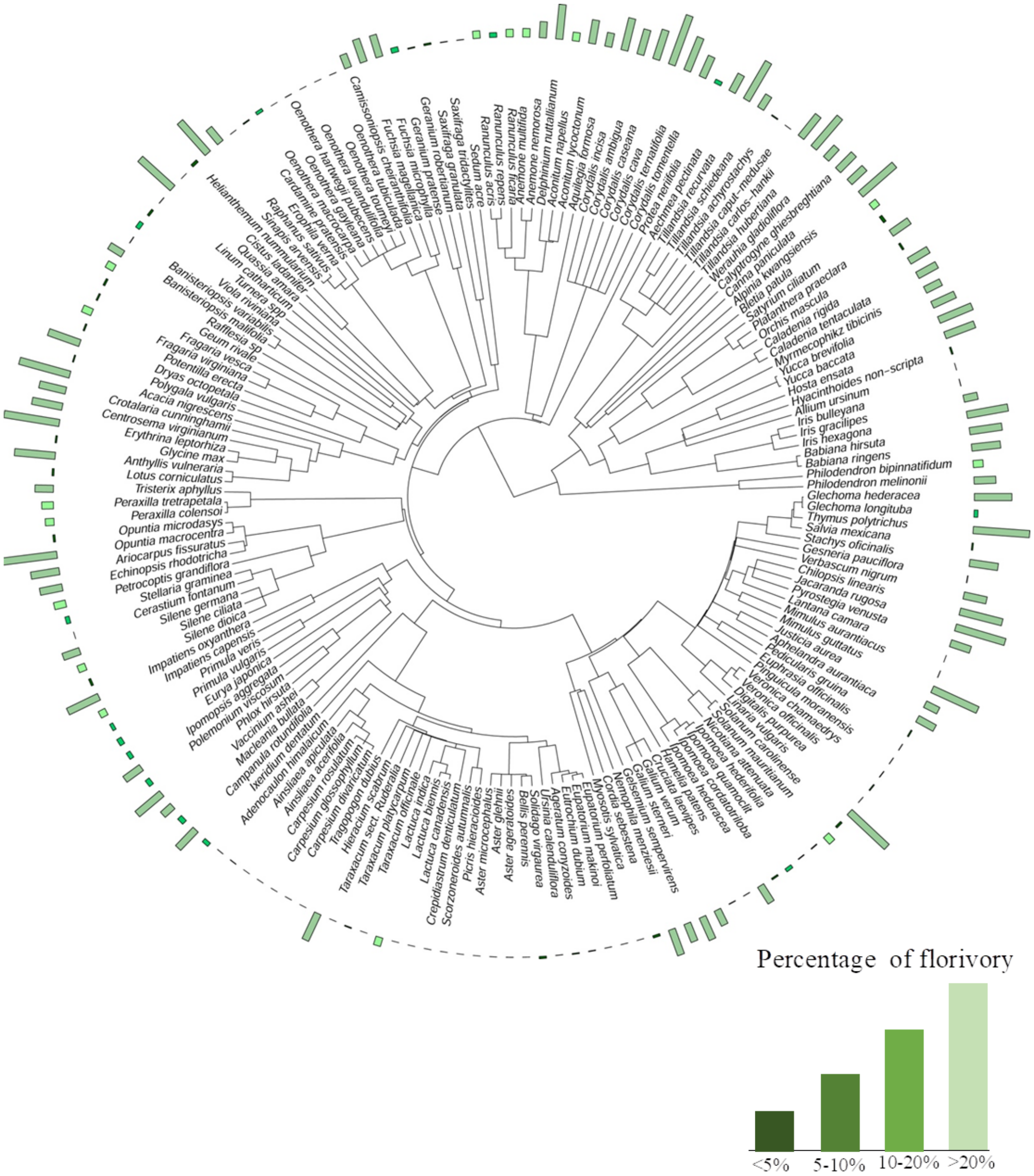

Figure 1. The phylogenetic distribution of floral damage in the global florivory database mapped onto the phylogeny of 144 angiosperms. The phylogeny was reconstructed using Qian & Jin (2016) database. See Supporting Information Table S3 for detailed species name, family and florivory levels.

The percentage of floral area removed was measured in 15% of florivory studies. Average floral area removed by florivores in attacked flowers was 7.21% (±1.53 SE, n=66). The phylogenetic distribution of florivory indicates that flower damage is widespread and variable across angiosperm lineages (Fig. 1), but two times higher in the tropics than in temperate regions (10.1 % ±2.3 SE for tropical flowers vs. 4.56% ±0.97 SE for temperate flowers; $F_{1,18}$=4.71, P=0.003). Neither flower symmetry, flower number or florivore guild had a significant effect on levels of damage on flowers. Our assessment on the distribution of floral damage clearly indicates that florivory is not homogeneously distributed across lineages, ecosystems or functional groups despite the phylogenetic and biogeographic biases (Supporting information, Fig. S4), opening new research avenues on the evolutionary ecology of florivory.

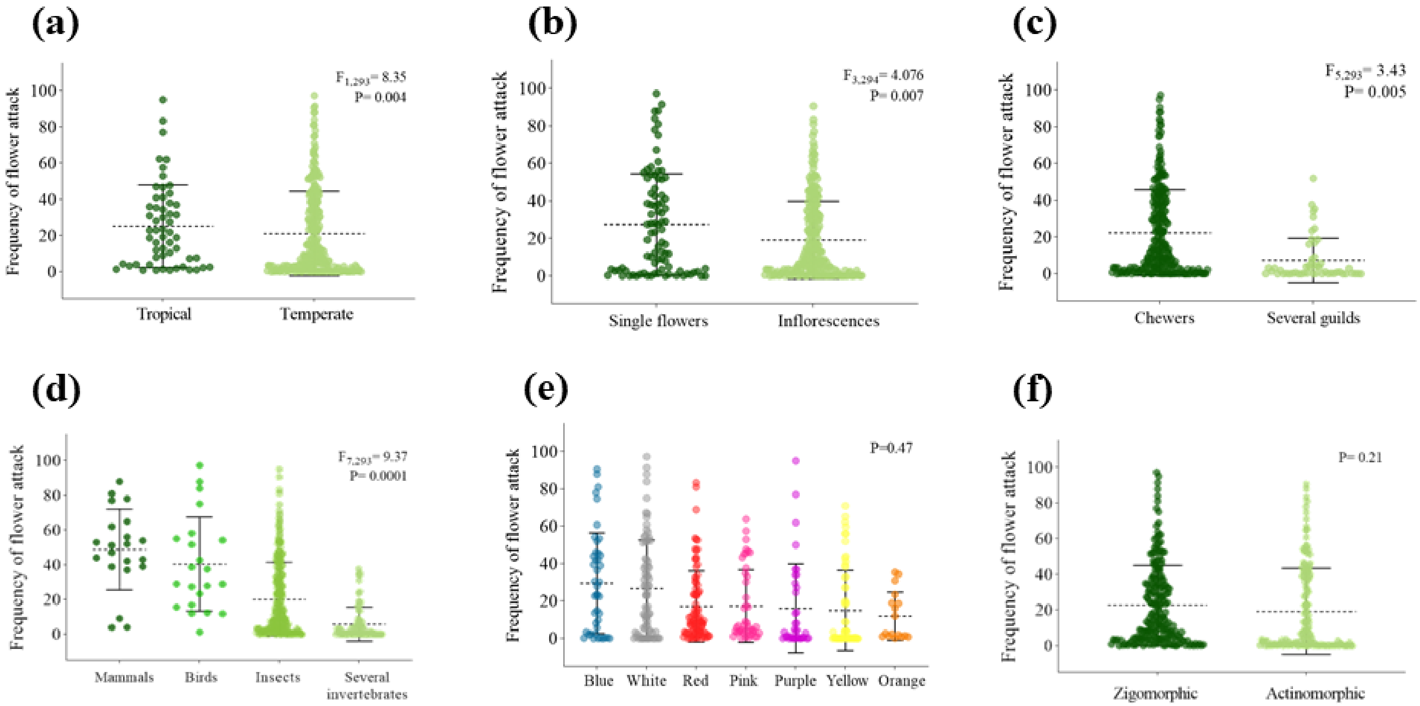

Figure 2. Comparison of florivory levels (measured as frequency of attacked flowers) according to a) region, b) flower color, c) florivore guild, d) flower arrangement, e) florivore group, and f) flower symmetry for 98 plant species. Data were extracted from previously published studies between 1945-2020. The line indicates the mean, and the error bars denote SD. For more details see Supporting Information Table S1.

Field data - Florivory levels and trait-mediated florivory

Most of our field sampling was conducted for species blooming in spring (28.9%) and summer (31.4%), with actinomorphic flowers (59.4%), arranged into inflorescences (87%). Almost one third of the species evaluated had yellow flowers (31.1%), followed by purple (25.6%) and white flowers (15.7%; Supporting information, Table S2).

Our field data showed that, on average, a quarter of all flowers per individual experience florivory (frequency of occurrence of damaged flowers: 24.3 ± 1.1% SE). Consistently two-times higher florivory levels were reported in tropical plants (Fig. 3). Flower symmetry, color and growth form did not significantly influence the levels of floral damage on these 36 plant species. Florivory levels estimated via the IFD showed an average of 1.65 (±0.05 SE) of flower area removal, which is equivalent to having up to 5% of petal area consumed by florivores (Supporting information, Methods S1). Based on precise estimates of the floral area removed by florivores using digital images of each flower (n= 14 woody species, 3,025 flowers measured), the floral area lost was 7.6% (± 0.21SE) and this pattern was not influenced by plant phylogeny (Supporting information, Table S5).

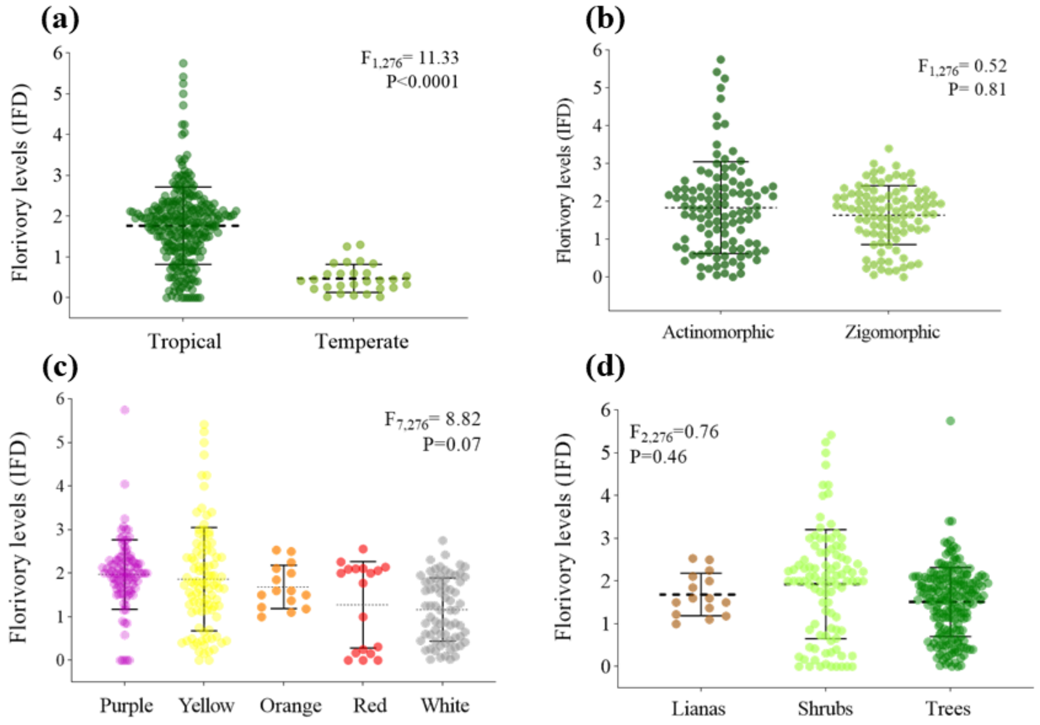

Figure 3. Florivory levels (percentage of floral area removed) measured by the Index of Floral Damage (IFD) for the 36 sampled plant species according to a) region, b) growth form, c) flower color and d) flower symmetry. Plants and flowers were sampled in the field using a standardized protocol (detailed in Supporting Information). Classes of removed floral area were assigned as: (0)- intact flower, (1) 0.01 to 1% of floral area damage, (2) between 1 and 5%, (3) between 5 and 25%, (4) between 25 and 50%, (5) between 50 and 75% and (6) between 75 and 100% of flower area damage. The line indicates the mean and the error bars denote SD.

Eco-evolutionary dynamics of herbivory and florivory

Florivory levels did not significantly vary among the four species of Bignoniaceae (Supporting information, Fig. S7), but herbivory and florivory were positively correlated within each species, indicating that plants that were more attacked by herbivores were also more attacked by florivores. Interspecific levels of herbivory varied between 2.6% (± 0.2) to 5.95% (± 1.02; Supporting information, Fig. S7), and flower area removed ranged from 4.29% (± 1.13) to 7.3% (± 1.87). A total of 78 species of florivores and 99 species of herbivores were sampled in these host plants and similarity between herbivore and florivore communities was low (Supporting information, Fig. S8). However, there was no relationship between richness of florivores or herbivores and damage level on flowers ($F_{1,58}$=1.76, P=0.190) or leaves ($F_{1,58}$=2.206, P=0.143). Longer blooming periods of flowers, however, were positively correlated (r=0.543) to a greater diversity of florivores ($F_{1,58}$=24.29, P<0.001; Supporting information, Fig. S8).

A standardized protocol for measuring florivory

In brief, our protocol called for field sampling of 20 fresh flowers from at least five individuals of five different species from natural areas. Flowers should be digitized with a scale for reference, measured on image processing software to precisely measure floral area removed (ratio between flower tissue removed and total flower tissue area). Flower traits should be registered along with data from each location. This protocol is already in use (Mendes *et al.,* 2021) and is intended to facilitate sampling of florivory measures across biogeographic regions and plant lineages, which will improve representativeness in our continuously-updated database. We provide data for more than 13,500 flowers in 36 plant species from 17 families across sites spanning over 38 degrees of latitude.

Discussion

Biogeography of flower-florivore interactions

Our global survey using both published and standardized field data collection suggests florivory is more common than previously conceived (see also Xiao *et al.,* 2021), and provides novel insights about the biogeographical, phylogenetic and ecological distribution of floral tissue consumption by florivores both at the plant and flower scales. Our results for published data show that patterns of damage to flowers were influenced by the florivore guild, flower arrangement and florivory metric accounted for. We found higher levels of florivory on tropical plants caused mainly by petal-chewing caterpillars, but higher frequency of attack on flowers when florivores were birds and mammals and flowers were singly arranged. The higher intensity of florivory in tropical plants - observed in the published data and also in our field sampled species - suggests a potential higher impact of floral damage on plant performance in the tropics and sheds light into the long-standing discussion on latitudinal gradients in insect-plant interactions (Forister *et al*., 2015; Roslin *et al*., 2017). Surprisingly, data gathered from the published literature and our field sampling both show that global florivory levels are almost twice as high as global herbivory levels reported (Kozlov *et al.,* 2015a), with higher impact on tropical plants compared to temperate ones. Tropical species might accumulate more specialized communities of herbivores, florivores and also natural enemies of both guilds (Basset *et al.,* 2012), and higher levels of florivory on tropical plants might indicate higher specialization of, for example, Lepidoptera larvae on this particular resource. Caterpillars are amongst the most common chewing herbivores in the tropics (Rinker & Lowman, 2004), and we suggest some species might be specialized in flowers as is the case of several species occurring in Asteraceae flower heads (Oguro & Sakai, 2014; Nobre *et al.,* 2016).

Florivory is inconsistently reported in the literature, but frequency of damaged flowers in plants or plant populations was the most commonly used metric, followed by the level of florivory on flowers or flower parts, measured as percentage of area removed by florivores. Each metric provides different information on florivory levels, including either prevalence of damage or damage level, and therefore are non-comparable measurements of florivory. In contrast, sophisticated and widely-accepted methods and metrics are used to estimate herbivory levels on plants (e.g., Machado *et al*., 2016; Getman-Pickering *et al.,* 2020). The IFD (Index of Floral Damage) analogous to the IHD (index of herbivory damage – the most widespread method to quickly evaluate levels of leaf herbivory in the field) – seems to flatten and obscure the estimates of flower area removed by florivores. Data from our field sampling provides empirical evidence of this, showing that flowers classed in the same IFD category in reality had very different levels of damage when measured quantitatively through image processing (Supporting information, Figure S9). This result strongly suggests the need for switching from semi-quantitative to quantitative measures to allow the identification of thresholds of tissue loss that can be tolerated without hindering plant fitness, as done in parallel of studies on leaf-herbivore interactions (Kozlov & Zvereva, 2017). Flower morphology and structure strongly differ from the usually flat-shaped leaves, posing additional challenges to estimate florivory levels, and impairing quick assessment of florivory in the field as proposed by the IFD. Our results indicate that the quantification of floral area removed with the aid of digital images and precise measurements of petal loss, corrected by flower size, will contribute to a deeper understanding of the effects of flower antagonists on plants and will fill this gap we identified in the published literature.

Trait-based flower-florivore interactions

Besides regional and latitudinal variation in florivory levels, another promising research avenue is the examination of flower functional traits that influence flower damage, either via attraction or repellence of florivores (Table 2). Species floral traits and time of flowering have been suggested as major drivers of pollinator attraction (Albor *et al.*, 2020) but, despite some recent efforts (e.g., Paterno *et al.,* 2020) flower traits are rarely sampled in global plant trait databases and have rarely been linked to florivory levels experienced by plants. Our results showed that some flower and plant traits influenced the frequency of attack on flowers but also the levels of florivory experienced by plants.

Table 2 - Floral traits suggested to have effects on florivory levels on plants.

Flower trait	Putative effects on florivory
Flower colour	Floral pigments are often linked to biosynthetic pathways of metabolites that can have defensive properties and also support the idea that florivores, just like pollinators, can use flower colour as cues for locating resources.
Flower longevity	Longer-lived flowers often sustain higher levels of florivory, except when they are better protected by either constitutive or induced defenses. The relationships between defenses and flower longevity in terms of costs and resource allocation remain poorly explored.
Flower size	Smaller flowers might escape florivory due to lower apparency compared to larger flowers, which are conspicuous and attractive to both pollinators and florivores. Although some data support a negative relationship between flower size and floral damage, data from tropical plants are still lacking.
Flower arrangement /number	The number of open flowers and the arrangement of flowers (single flowers or inflorescences) can potentially make flowers more or less conspicuous for florivores and levels of florivory may increase with the increase of the floral display.
Floral symmetry	Floral symmetry has been widely studied in terms of pollinator attraction or repulsion, but is still unclear whether floral symmetry (actinomorphic or zygomorphic) influences levels of damage by floral enemies.
Floral phenology	Plants can delay or advance flowering phenology to reduce overlapping with abundance of florivores. It is not clear, however, whether this strategy would be effective against generalist florivores.
Floral scent	Flowers that produce volatile organic compounds used as cues by florivores for oviposition and/or feeding might suffer higher floral

	damage. On the other hand, floral scents might be used by natural enemies of florivores, thereby reducing florivory levels.
Plant growth form	Plant growth form can make flowers more or less apparent to florivores, so that herbs, shrubs or lianas may experience lower levels of florivory compared to trees, where flowers might be less accessible. This functional trait has already been extensively studied for leaf herbivory, but studies that have investigated its relationship with florivory are still scarce.

Flowers tend to be the most diversely pigmented plant structures, displaying a wide range and combination of colors often both between and within species (Willmer, 2011). Although plant pigments have been generally interpreted as means to attract mutualists, they are often linked to biosynthetic pathways of metabolites that can have defensive properties and support the idea that florivores, similarly to pollinators, can use flower color as a cue for either locating resources or for flower consumption. Surprisingly, in our current analyses flower color did not influence the levels of petal damage, both for the published and sampled field data, even though floral color has been shown to drive the foraging decisions of several pollinators (Reverté *et al.,* 2016), and florivores have been flagged as potential drivers influencing flower color polymorphisms (McCall *et al.,* 2013). In species with flower color polymorphism where florivory has been assessed, florivores prefer certain color morphs over others (McCall *et al.,* 2013). However, the evidence is still scarce and based on single study cases in experimental settings. We do wonder to what extent this lack of effect in our database is reflecting a general biological pattern or is the result of lack of power to describe a highly variable and complex process, given the limited data on both florivory levels and floral traits. Documenting flower color and florivory levels in wider censuses, along with experiments testing florivore preferences in controlled experimental settings would help fill building a broader picture on the role of florivores in shaping flower color.

Flowers arranged into inflorescences experienced overall lower florivory than single flowers and these results are consistent with the hypothesis that escape may be a mechanism to reduce florivory levels, as documented for herbivory. This underscores similar patterns in resource usage by herbivores and florivores. The plant apparency hypothesis (PAH; Feeny, 1976) suggests that conspicuous plants, such as trees, are 'bound to be found' (Smilanich *et al.,* 2016) and have evolved higher concentrations of chemical and/or physical defenses against herbivores due to greater tissue longevity and exposure. We suggest that the PAH might also apply to flowers that are less conspicuous when singly arranged and therefore less 'bound to be found' by florivores, compared to those bundled in dense resource patches as is the case for inflorescences. The evaluation of the frequency of attack in flowers arranged into inflorescences and the levels of florivory experienced by single flowers within an inflorescence will help to understand how flower arrangement, time of blooming, and longevity influence florivore choice.

Flower size is another floral trait that influences mutualistic and antagonistic interactions. Larger-flowered species (or populations within species) may be more attacked following the PAH (Feeny, 1976), although this is contingent upon particular ecological and/or phylogenetic contexts. Thus, if populations with larger flowers suffer greater florivory levels, florivores may ultimately act as a selective pressure to reduce flower size (McCall & Irwin, 2006; Teixido *et al.,* 2011). Flower size, however, was not commonly or precisely reported in the published studies compiled in our database, appearing in less than a quarter of the studies that described flowers consumed by florivores.

The understanding of flower color, arrangement, size, and flower secondary compounds and their effects on both herbivores and florivores is crucial to evaluate the role of generalist plant consumers and their effects as drivers of selection and flower evolution. We here provide a first list of general florivore-related flower traits (Table 2) hoping it will inspire the collection and inclusion of such data in global databases in order to facilitate florivory research in the near future. Overall, if one wishes to understand the effects of multiple and simultaneous forces on floral attraction to both florivores and pollinators, then floral traits should also be included in such studies. Moreover, patterns of co-variance between floral traits and florivory across multiple species using phylogenetic comparative approaches – as done here – are required for a better understanding of the evolution of plant-florivore interactions.

Eco-evolutionary dynamics of flower-florivore interactions

For almost 90% of the animal-pollinated flowering plants (Ollerton *et al.,* 2011), complex, multispecies interactions with floral enemies and herbivores often result in conflicting selection on plant traits (Jacobsen & Raguso, 2018) including floral display, phenology, flower size, color, morphology, nectar quality and fragrance (Galen, 1999b; Caruso *et al.*, 2010; Agren *et al.*, 2013; Ramos & Schiestl, 2019). Our empirical data is in line with previous studies indicating that leaf herbivores might feed on flowers of the same plant species (e.g., McCall, 2008; McCall *et al.,* 2018). Our field data using four related Bignoniaceae species as a study system showed correlated levels of florivory and herbivory within species, but low similarity in the communities of insect florivores and herbivores (Fig. S8). Ants were important components of both communities, acting as florivores in leafless plants, and as predators of herbivores when plants were flushing new leaves and associated herbivores were abundant. Although greater florivore richness did not translate into greater florivory levels for these plant species, florivores were more diverse and abundant in plants with longer blooming periods. Florivory was 2-fold higher than to herbivory for species with the shortest blooming periods (5-7 days). The highest similarity between florivore and herbivore communities was also found for the species that had the longest blooming (~30 days), indicating that plant phenology, flower apparency and phenophase duration may also modulate the levels of flower damage (Albor *et al.,* 2020). Temporal segregation of flowers and leaves in these deciduous-blooming species might be driving the dissimilarity of insects based upon different resources, but we suggest that the determination of insect identity as well as resource use over time are crucial for future studies of florivore-plant interactions.

Florivory impacts on plants have to be addressed beyond the effects of floral damage on pollinator attraction and we suggest florivory should be considered as a 'stand-alone' interaction in studies involving flowers and animals. It has the potential to directly and indirectly influence plant fitness via the direct consumption of costly tissues and through impacts on plant attractiveness to pollinators (e.g., abundance, number and duration of visits), and jointly altering fruit and seed production (Moreira *et al.,* 2019). As most research has focused on the positive (mutualistic) animal-flower interactions, negative interactions between animals and flowers, like florivory, have been overlooked or evaluated out of the context of antagonistic interactions. This knowledge gap prevents a better understanding of the multi-layered interaction networks (Genini *et al.,* 2010;

Pilosof *et al.,* 2017), hinders its applied facets for mitigating economic losses associated with flower destruction by animals (Kelley *et al.*, 2001), and, because of the inherent importance of flowers in plant fitness, hampers a comprehensive understanding of plant evolution (Chalker-Scott, 1999; Tanaka & Brugliera, 2007).

We revisited florivory indicating global levels of floral damage, the identity of florivores and a first list of pivotal florivore-related flower traits that influenced floral damage, hoping it will inspire the sampling and incorporation of these key elements into global databases. We hope that our protocol for standardized measurements of florivory, coupled with the examination of flower traits that mediate damage incidence and level would allow the generation of robust, realistic and comparable estimates on the amount of floral tissue removed by to florivores and its impacts on plant fitness.

Conclusion

Our study enhances the understanding of the role of floral antagonisms on plant fitness (McCall, 2008) and on flower form and function (Roddy *et al.*, 2021). Multiple ecological factors driving plant fitness and flower traits shape ecological communities and macroevolutionary patterns. A broad understanding of these factors should extend beyond the role of pollinators and include florivores as a major driver of the ecology and evolution of angiosperms. Insects are critical components of communities and ecosystems, providing important ecosystem services such as pollination and decomposition (Elizalde *et al.,* 2020). Many insect taxa act as both pollinators and florivores, but the consequences of their global population declines (van Klink *et al.,* 2020) in flower trait evolution remain largely unexplored. Incorporating florivores into complex multi-layered interactions networks on both natural and modified landscapes will provide a more realistic picture on their role in shaping plant traits, plant demography, community assembly and macroevolutionary patterns (see Burin *et al.,* 2021, Xiao *et al.*, 2021). We look forward to a time when knowledge on florivory is comparable to that of herbivory and pollination, so we can have a broader and realistic understanding of the relative role of phytophagous animals in shaping plant traits.

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Author contribution

Design of the research (TC, MGB, FAOS), performance of the research (all authors), data collection (all authors), data analysis and interpretation (led by MGB with contributions from all authors), manuscript writing and editing (MGB and TC with input from all authors).

Data availability statement

All data that support our findings are available as Supporting Information, and the database has been deposited in Figshare (https://doi.org/10.6084/m9.figshare.15106230).

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New Phytologist Supporting Information

Article title: **Revisiting florivory: an integrative review and global patterns of a neglected interaction**

Authors: Maria Gabriela Boaventura, Nora Villamil, Alberto L. Teixido, Richard Tito, Heraldo L. Vasconcelos, Fernando A. O. Silveira, Tatiana Cornelissen

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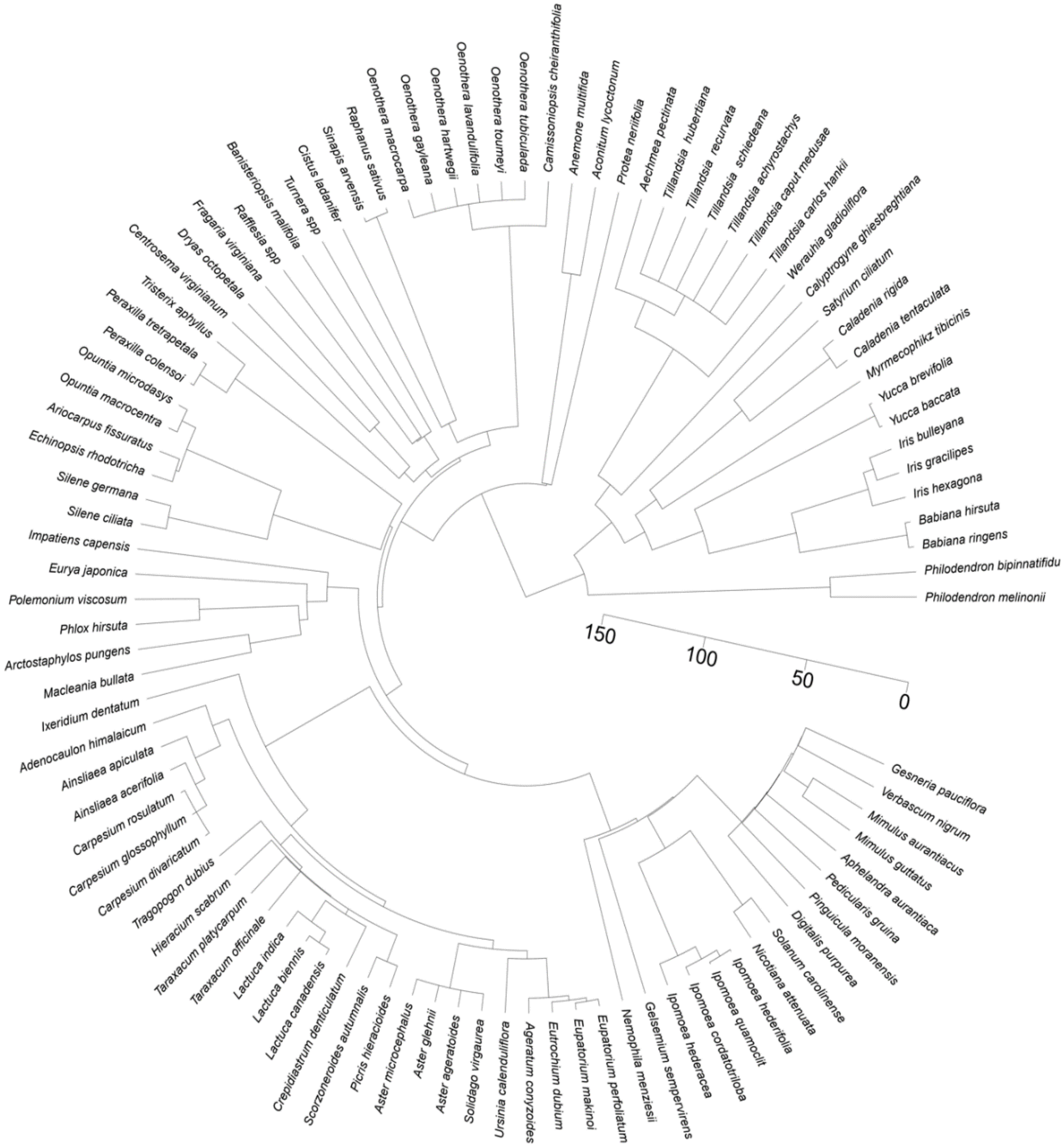

Fig. S1 - Phylogenetic tree of the plant species that had florivory reported as frequency of attacked flowers.

Florivory data of the 98 species were extracted from previously published studies (for more details see Supporting Information Table S1) and the phylogenetic tree was built using the Qian & Jin (2016) database.

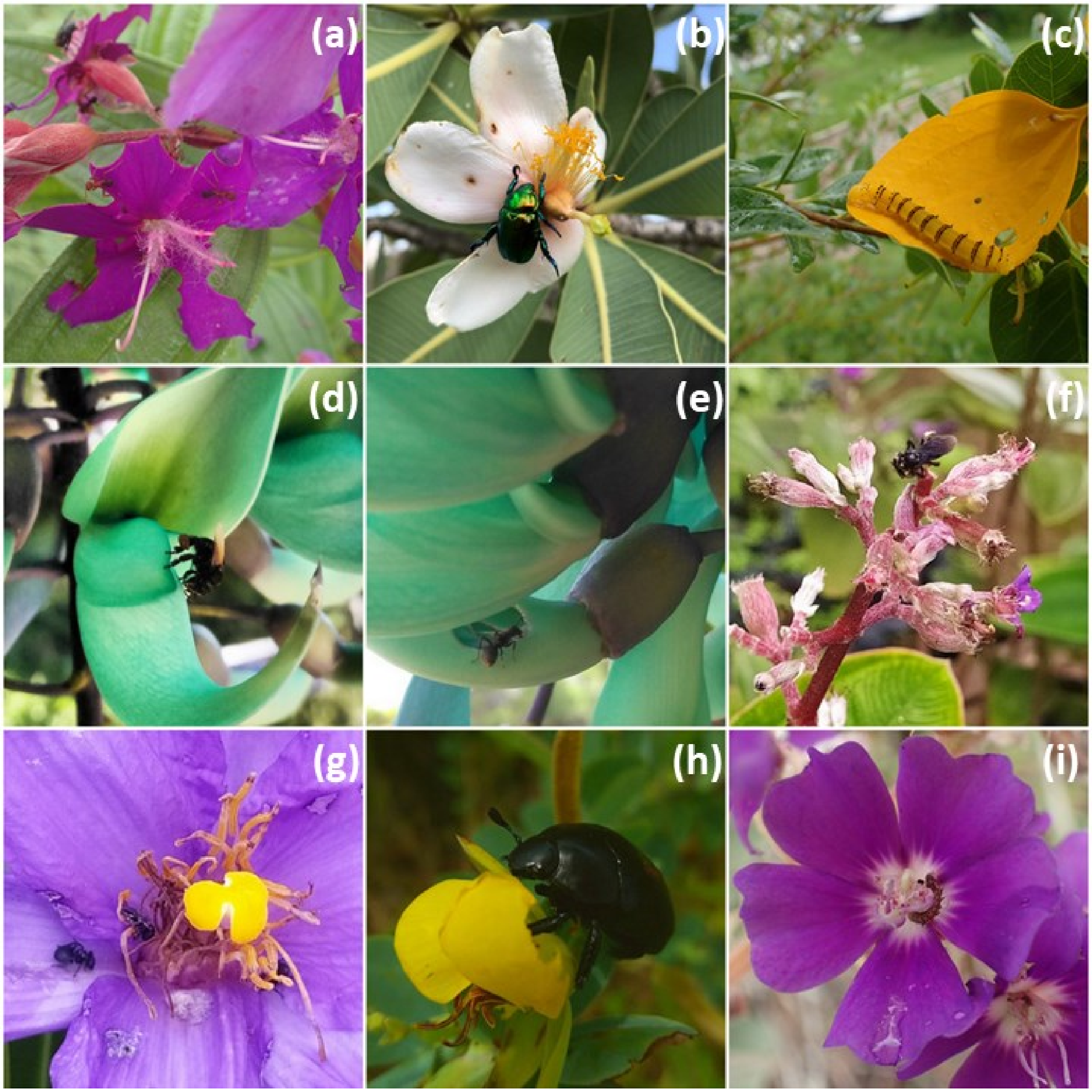

Fig. S2- Examples of floral enemies on tropical plant species. (a) Ants chewing on petals of *Pleroma* (Melastomataceae). (b) A beetle eating reproductive parts of a *Kielmeyera coriaceae* (Clusiaceae)flower (Photo by Cassio Cardoso). (c) A caterpillar, one of the most common florivores, chewing on flowers of *Senna spectabilis* (Fabaceae). (d) A *Trigona* bee, one the most common primary nectar robbers in the Neotropics, stealing nectar from *Strongylodon macrobotrys* (Fabaceae). (e) Secondary nectar robbing by ants on flowers of *Strongylodon macrobotrys* (Fabaceae). (f) A *Trigona* nectar robbing bee on flower buds of *Pleroma heteromallum* (Melastomataceae). (g) *Cephalotes* ants can act as florivores, nectar thieves or nectar robbers on a *Vellozia* flower (Velloziaceae). (h) A beetle thieving nectar from a flower of *Chamaecrista desvauxii* (Fabaceae) (Photo by Lorena Valadão-Mendes). (i) A tiny geometrid caterpillar feeding upon reproductive parts of *Pleroma heteromallum* flower (Melastomataceae).

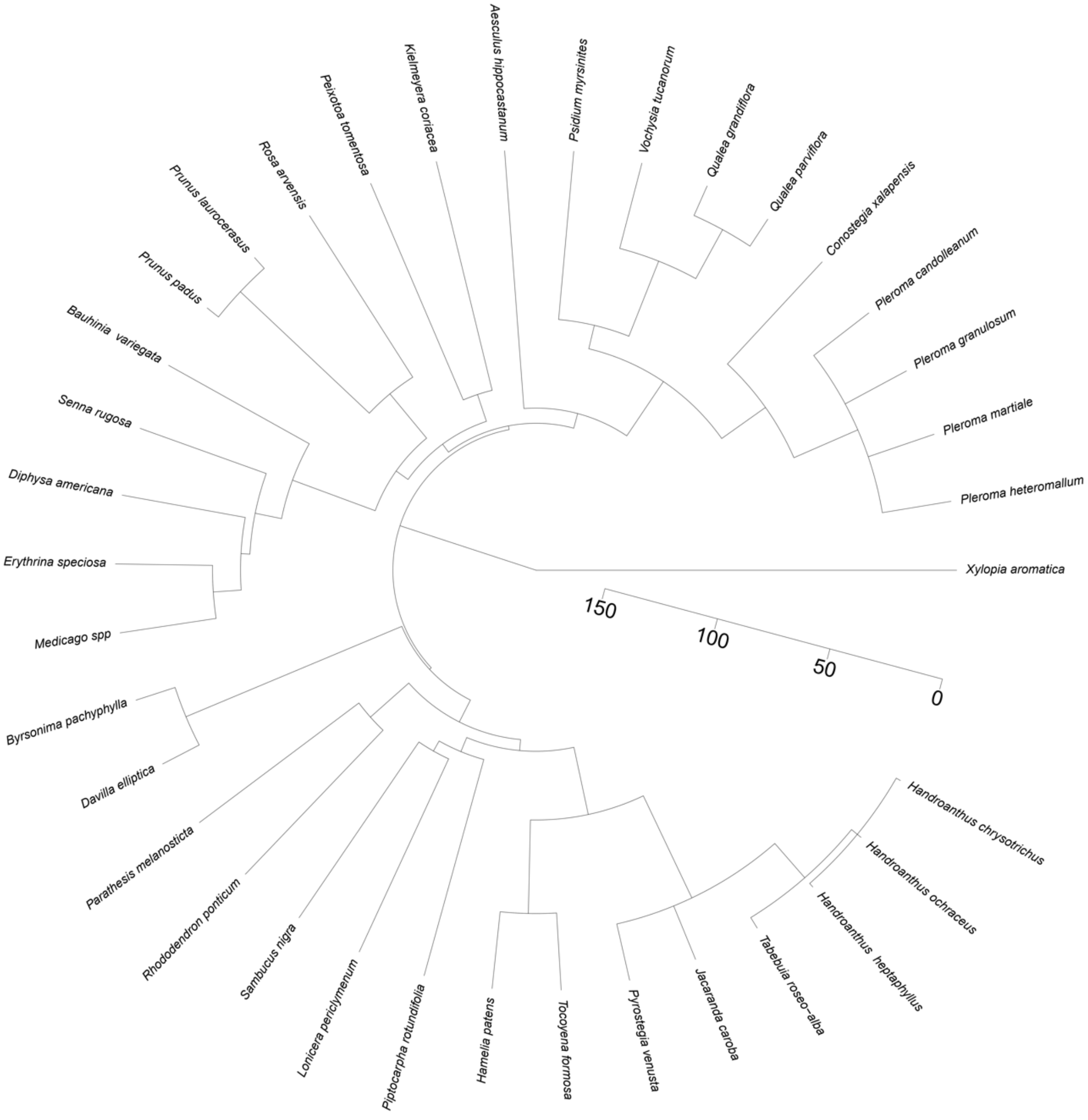

Fig S3 - Phylogenetic tree of the 36 plant species collected using a standardized protocol. The phylogenetic tree was built using the Qian & Jin (2016) database.

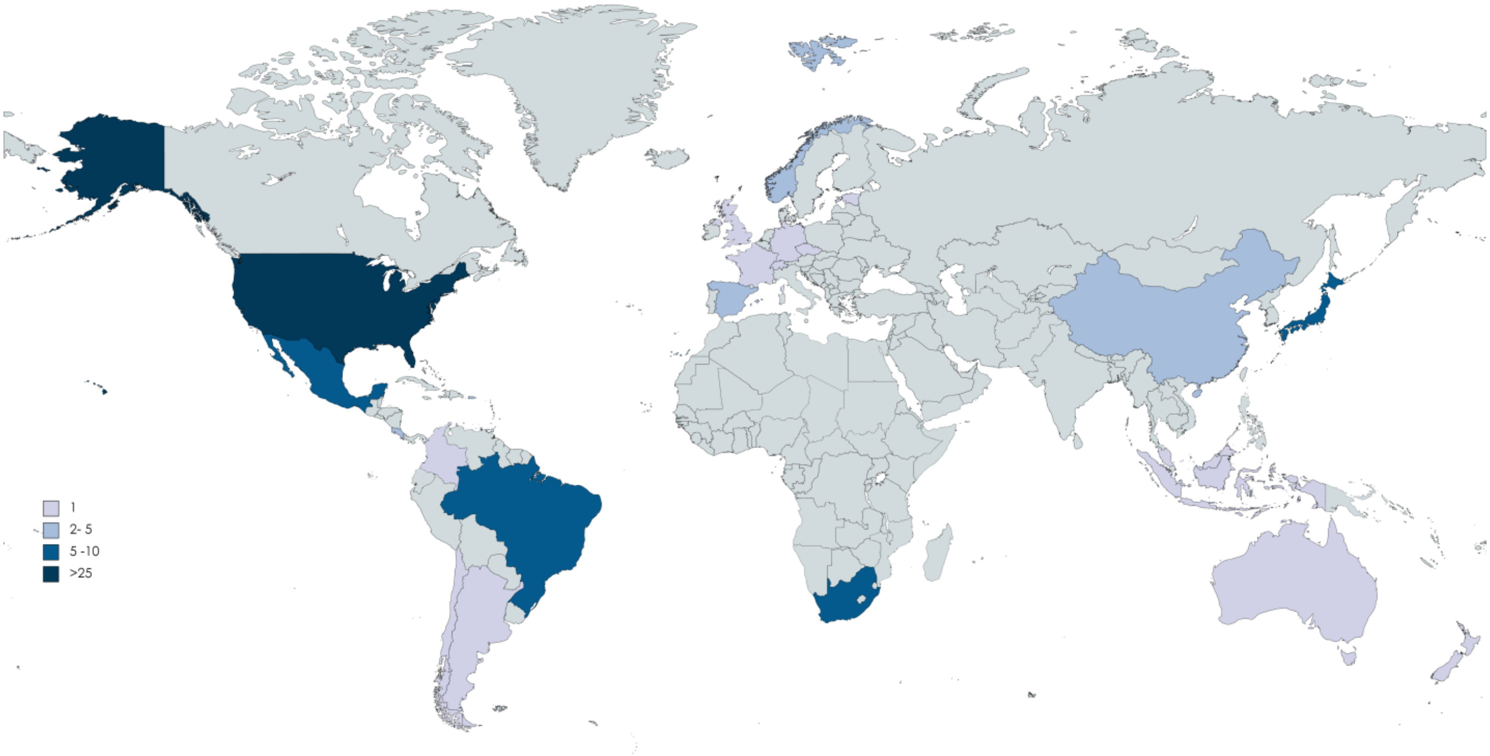

Fig. S4- Distribution and number of florivory studies in the florivory global database per country as a heat map in hues of blues. From the countries where studies are available, USA had the greatest number of studies and New Zealand had the least.

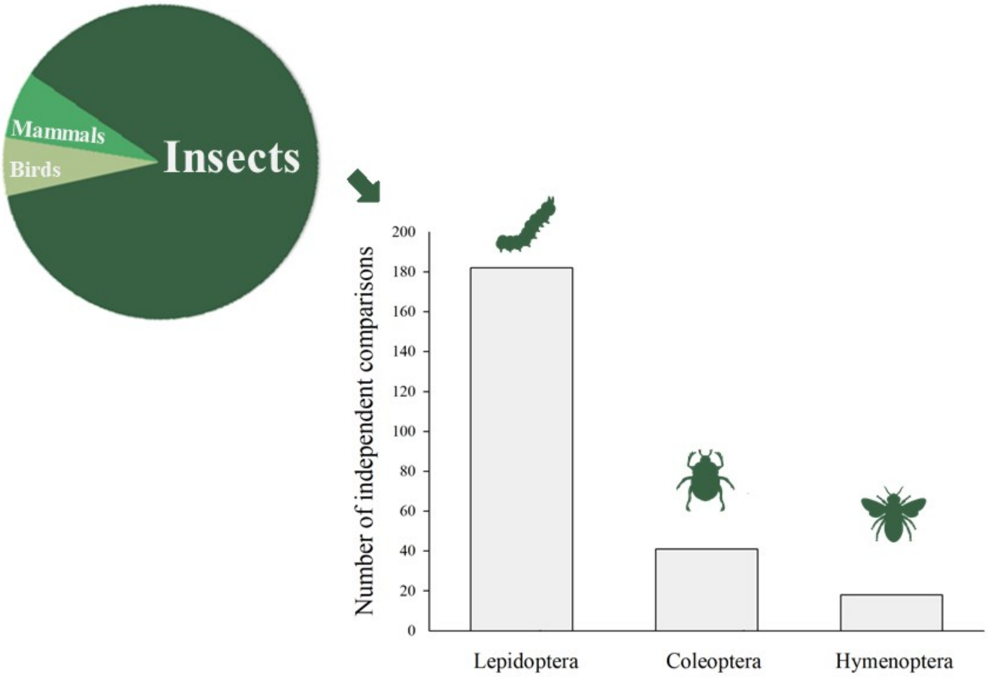

Fig S5 - Main florivore taxa according to broad taxonomic categories in the florivory global database. Insects were the most frequent taxa reported attacking flowers and chewing insects are responsible for inflicting the greatest amount of damage to the plants evaluated.

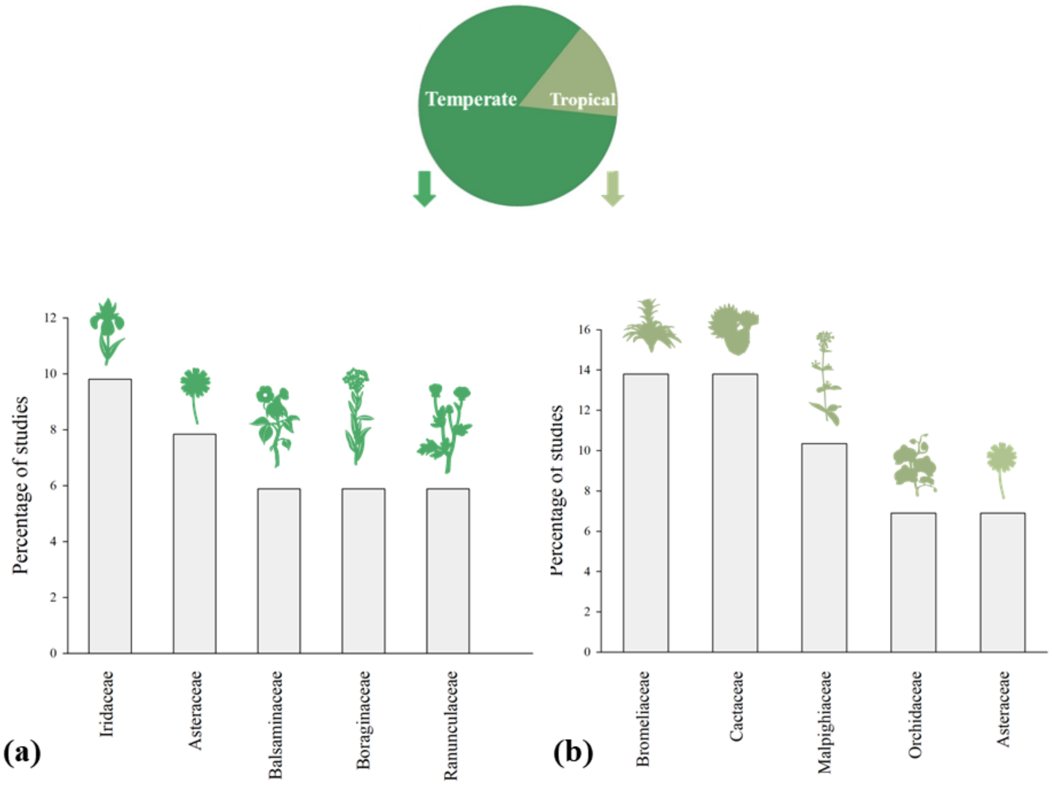

Fig. S6 - The distribution of florivory studies by region and by botanical families in (a) temperate regions and (b) tropical regions. Data come from published studies included in our global database.

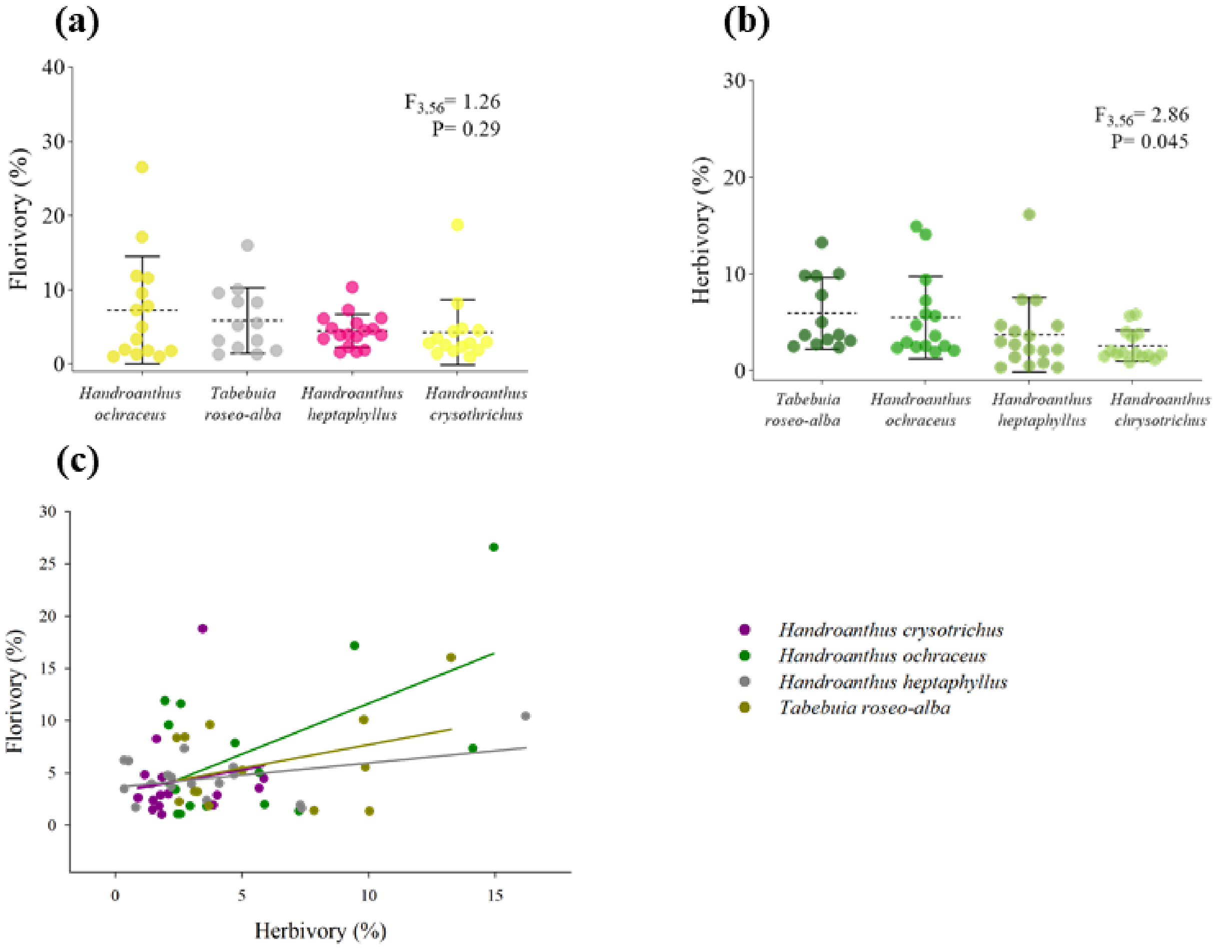

Fig. S7 - Levels of a) florivory and b) leaf herbivory, measured by the percentage of average damage, for four plant species of the Bignoniaceae family and c) relationship between florivory and herbivory for each species of Bignoniaceae. Each point represents individual replicated trees. The line indicates the mean and the error bars denote SD.

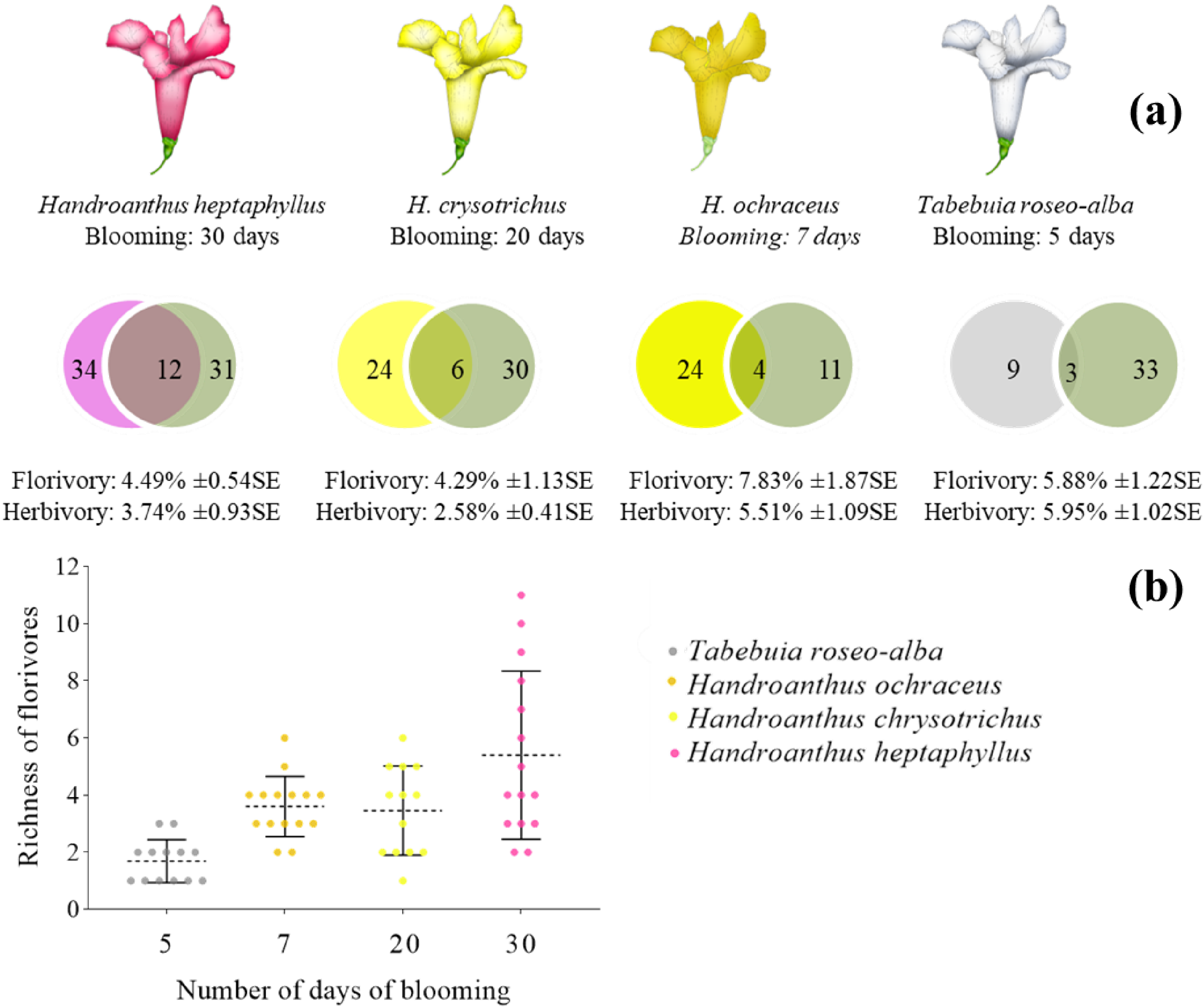
(a)
Handroanthus heptaphyllus
Blooming: 30 days
H. crysotrichus
Blooming: 20 days
H. ochraceus
Blooming: 7 days
Tabebuia roseo-alba
Blooming: 5 days
34
12
31
24
6
30
24
4
11
9
3
33
Florivory: 4.49% ±0.54SE
Herbivory: 3.74% ±0.93SE
Florivory: 4.29% ±1.13SE
Herbivory: 2.58% ±0.41SE
Florivory: 7.83% ±1.87SE
Herbivory: 5.51% ±1.09SE
Florivory: 5.88% ±1.22SE
Herbivory: 5.95% ±1.02SE
(b)
Richness of florivores
0
2
4
6
8
10
12
5
7
20
30
Number of days of blooming
● *Tabebuia roseo-alba*
● *Handroanthus ochraceus*
● *Handroanthus chrysotrichus*
● *Handroanthus heptaphyllus*

Fig S8 - a) Species richness of florivores and herbivores in four species of Bignoniaceae with corresponding levels of florivory and herbivory and b) the relationship between number of days plants were blooming and richness of florivores. Each dot on panel represents an individual plant sampled and colors represent the colors of the flowers from each species. The line indicates the mean and the error bars denote SD.

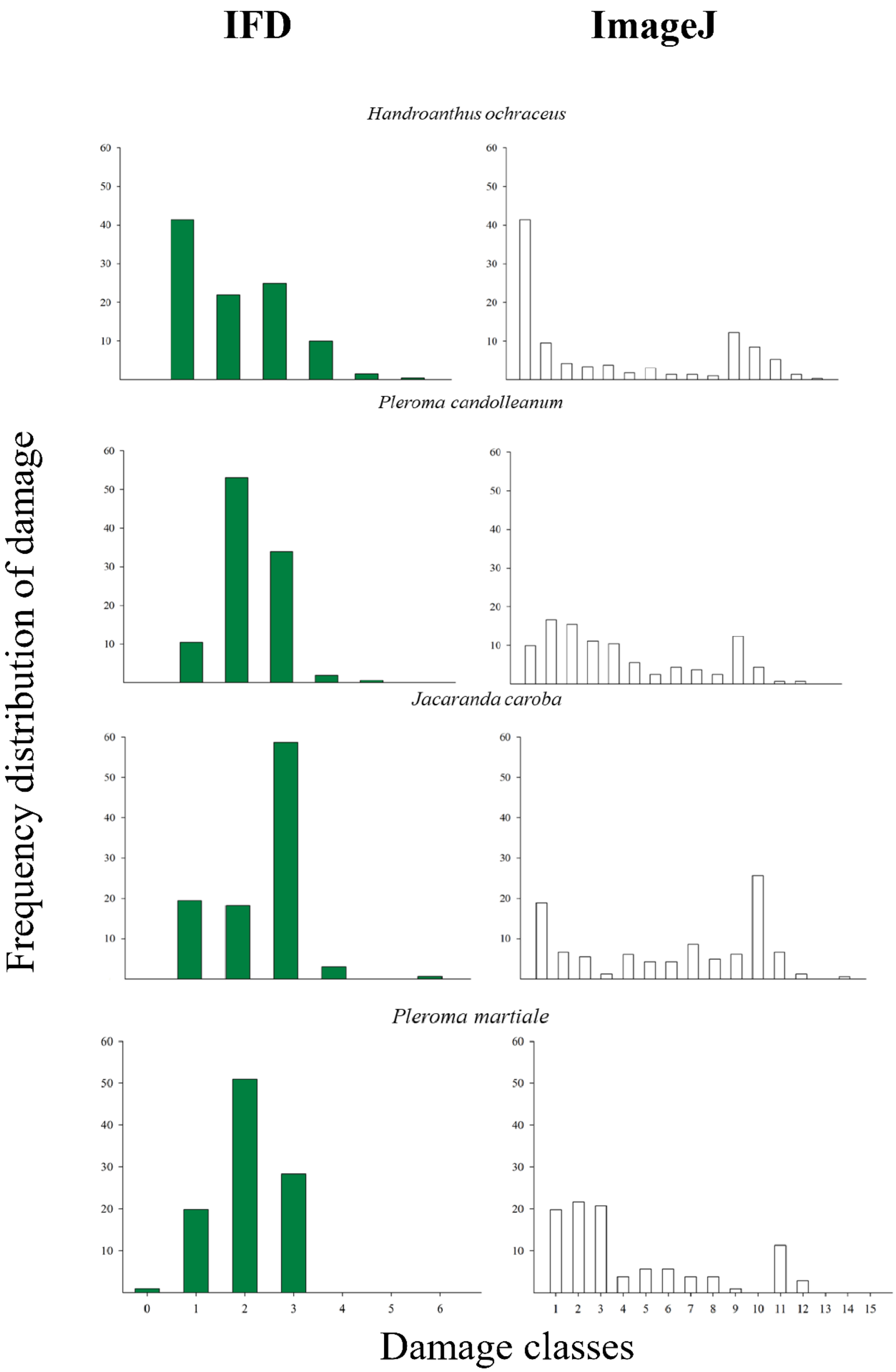
IFD
ImageJ
Handroanthus ochraceus
Pleroma candolleanum
Jacaranda caroba
Pleroma martiale
60
50
40
30
20
10
Frequency distribution of damage
0
1
2
3
4
5
6
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Damage classes

Fig S9. Distribution of flower damage into damage classes according to the IFD (left panels) and digital measurements of the same flowers using ImageJ software. The x-axis on both groups of panels indicate the classes of damage in percentage of floral area removed.

Methods S1 – A protocol for florivory evaluation (sampling, measuring damage and general guidelines).

1) Samples should be conducted in natural areas, protected areas or in modified areas, which should be described in the appropriate column.

2) Get GPS data (exact latitude and longitude), as well as altitude for the selected locality.

3) Select at least 5 leaf-bearing plant species that are flowering (preferably during the flowering peak) in the period you will sample. Record Latin name, the geographic coordinates, elevation, the biome where they were collected, growth form, flower color, and data of collection.

4) For each species, randomly choose 5 individual plants as replicates, at least 10m apart. From a distance of 5 m from you, choose up to 20 flowers to be sampled by plant, 5 from each corner around the canopy. Flowers should be fully developed and open. Researchers should record if anthers and/or stigma(s) are mature.

5) Store flowers in plastic bags (in the fridge) if you cannot examine the flowers immediately

6) Note that the flowers from the 5 individual replicates per species should be stored in plastic bags separately. You will end up with 25 samples per locality (5 species X 5 replicates, each replicate with 20 flowers).

7) For inflorescences/bouquets, collect 5 inflorescences/bouquets per replicate plant, but count and register all flowers in the bouquet.

8) The flowers must be digitized as soon as possible (n=500 per locality in the case of single flowers or 125 inflorescences per locality in case of bouquets). The flowers can be digitized through a scanner or digital camera, with a scale for measurements in millimeters and/or centimeters (e.g., a plastic or metal ruler). You must also identify which species, individual and flower each image belongs to.

10) If the flower has with tubular or buliform corolla, gently cut the corolla laterally so that the whole corolla area is digitized. You can use a double-sided tape so that the sides of the corolla are perfectly stretched or a piece of transparent glass can be placed over the flower.

11) If the flower has a radially symmetrical corolla, detach the petals carefully and use the double-sided tape to stretch them when necessary.

12) All flowers must be measured in the ImageJ® software. It is a free software and you can download it at https://imagej.nih.gov/ij/download.html.

13) In ImageJ®, open the image to be measured. Using the measuring line, carefully draw a 1 cm or 10mm line, using the ruler as scale. Click “Analyze” > “Set scale”. The program will open a box where you must standardize the scale at which your data will be measured. In the "known distance" box, add 1 cm or 10 mm and select the option "Global". All your measurements will be calibrated to this set line.

14) You must measure the original images of flowers. You will need to redraw the flower, contouring it with the pencil to account for flower areas lost to florivores. Use the zoom tool (Ctrl+) to precisely see the holes in the image.

15) Select the area icon on the top of the screen on ImageJ® and click on each area you have measured (total area of flower and "filled" lost area) and press the "M" key on the keyboard. This will return the value of the areas that you have measured. Record these values on a spreadsheet**.**

16) To account for intraspecific variation, data should be recorded for each plant species, each individual replicate and each individual flower in a spreadsheet.

Table S1 – Global database of florivory in plants.

Uploaded separately and deposited in figshare under d.o.i 10.6084/m9.figshare.15106230

Table S2 – Plant species collected for this study with a standardized protocol. Data indicates plant species collected in three countries for measurements of florivory, grouped by species, family, country, region, floral symmetry, inflorescence type, flower color and plant growth form. TROP= Tropical, TEMP= Temperate. Z= zygomorphic, A= actinomorphic. I= two or more flowers in an inflorescence, S= single flowers.

Plant species	**Plant Family**	**Country**	**Region**	**Flower symmetry**	**Flower number**	**Flower color**	**Growth form**
Pyrostegia venusta	Bignoniaceae	Brazil	TROP	Z	I	orange	liana
Jacaranda caroba	Bignoniaceae	Brazil	TROP	Z	I	purple	shrub
Handroanthus chrysotrichus	Bignoniaceae	Brazil	TROP	Z	I	yellow	Tree
Handroanthus ochraceus	Bignoniaceae	Brazil	TROP	Z	I	yellow	Tree
Handroanthus heptaphyllus	Bignoniaceae	Brazil	TROP	Z	I	purple	Tree
Tabebuia roseo-alba	Bignoniaceae	Brazil	TROP	Z	I	white	Tree
Bauhinia variegata	Fabaceae	Brazil	TROP	A	S	white	Tree
Senna Rugosa	Fabaceae	Brazil	TROP	A	I	yellow	Tree
Erythrina Speciosa	Fabaceae	Brazil	TROP	Z	I	red	Tree
Pleroma granulosum	Melastomataceae	Brazil	TROP	A	I	purple	Tree
Pleroma candolleanum	Melastomataceae	Brazil	TROP	A	I	purple	shrub
Pleroma martiale	Melastomataceae	Brazil	TROP	A	I	purple	shrub
Pleroma	Melastomataceae	Brazil	TROP	A	I	purple	shrub

heteromallum							
Peixotoa tomentosa	Malpighiaceae	Brazil	TROP	A	I	yellow	shrub
Piptocarpha rotundifolia	Asteraceae	Brazil	TROP	Z	I	yellowish	Tree
Kielmeyera coriácea	Calophyllaceae	Brazil	TROP	A	I	white	Tree
Davilla elliptica	Dilleniaceae	Brazil	TROP	A	I	yellow	Tree
Byrsonima pachyphylla	Malpighiaceae	Brazil	TROP	Z	I	yellow	Tree
Vochysia tucanorum	Vochysiaceae	Brazil	TROP	A	I	yellow	Tree
Xylopia aromática	Annonaceae	Brazil	TROP	A	I S	white	Tree
Psidium myrsinites	Myrtaceae	Brazil	TROP	Z	I	white	Tree
Tocoyena formosa	Rubiaceae	Brazil	TROP	Z	I	yellow	Tree
Qualea grandiflora	Vochysiaceae	Brazil	TROP	Z	S	yellow	Tree
Qualea parviflora	Vochysiaceae	Brazil	TROP	Z	S	purple	Tree
***Medicago* sp.**	Fabaceae	Mexico	TROP	A	I	violet	shrub
Hamelia patens	Rubiaceae	Mexico	TROP	Z	I	red	shrub
Diphysa americana	Fabaceae	Mexico	TROP	A	I	yellow	Tree
Parathesis melanosticta	Primulaceae	Mexico	TROP	A	I	pink	Tree
Conostegia xalapensis	Melastomataceae	Mexico	TROP	A	I	pink	tree

Prunus padus	Rosaceae	Scotland	TEMP	A	I	white	Tree
Aesculus Hippocastanum	Hippocastanaceae	Scotland	TEMP	A	I	white	Tree
Sambucus nigra	Adoxaceae	Scotland	TEMP	A	I	white	Tree
Rhododendron ponticum	Ericaceae	Scotland	TEMP	A	I	purple	Tree
Prunus laurocerasus	Rosaceae	Scotland	TEMP	A	I	white	Tree
Lonicera periclymenum	Caprifoliaceae	Scotland	TEMP	Z	I	white	shrub
Rosa arvensis	Rosaceae	Scotland	TEMP	A	S	white	shrub

Table S3- Plant species collected for this study with a standardized protocol which was measured using ImageJ. Data indicates plant species collected only in Brazil for measurements of florivory, grouped by species, family, floral symmetry, inflorescence type, flower color, plant growth type and florivory levels. Z= zygomorphic, A= actinomorphic. I= two or more flowers in an inflorescence, S= single flowers, SE = standard error.

Plant species	**Plant Family**	**Flower symmetry**	**Flower number**	**Flower color**	**Growth type**	**Florivory levels**
Pyrostegia venusta	Bignoniaceae	Z	I	orange	liana	3.9±0.98SE
Jacaranda caroba	Bignoniaceae	Z	I	purple	shrub	6.29±1.09SE
Handroanthus chrysotrichus	Bignoniaceae	Z	I	yellow	tree	4.29±1.13SE
Handroanthus ochraceus	Bignoniaceae	Z	I	yellow	tree	7.3±1.87SE
Handroanthus heptaphyllus	Bignoniaceae	Z	I	purple	tree	4.49±0.54SE
Tabebuia roseo-alba	Bignoniaceae	Z	I	white	tree	5.88±1.22SE
Bauhinia variegata	Fabaceae	A	S	white	tree	2.76±0.43SE
Senna Rugosa	Fabaceae	A	I	yellow	tree	7.21±1.3SE
Erythrina Speciosa	Fabaceae	Z	I	red	tree	3.51±0.6SE
Pleroma granulosum	Melastomataceae	A	I	purple	tree	8.79±5.45SE
Pleroma candolleanum	Melastomataceae	A	I	purple	shrub	5.48±0.81SE
Pleroma martiale	Melastomataceae	A	I	purple	shrub	4.08±0.87SE
Pleroma heteromallum	Melastomataceae	A	I	purple	shrub	9.65±2.83SE

Peixotoa tomentosa	Malpighiaceae	A	I	yellow	shrub	32.11±6.41SE

Table S4 - Results of the Phylogenetically Generalized Least Square (PGLS) models, used to evaluate the relationship between florivory (percentage of attacked flowers) and several factors in 98 plant species from published florivory studies in our database.

Response variable	Fixed factors (number of levels)	Random factors (number of levels)	F-value (d.f.)	P-value	r Brownian (P-value)	AIC value
Frequency of attacked flowers	Region (2)	Plant species (98)	8.35 (1,293)	0.004	-0.155 (0.2128)	3462.29
	Flower symmetry (3)	Plant species (98)	1.55 (2,294)	0.213	-0.08 (0.1230)	3460.06
	Flower number (3)	Plant species (98)	4.07 (2,294)	0.007	-0.071 (0.2285)	3444.98
	Florivore identity (8)	Plant species (98)	9.37 (7, 293)	0.0001	-0.082 (0.223)	3371.80
	Florivore guild (6)	Plant species (98)	3.43 (5,293)	0.005	-0.046 (0.127)	3378.90
	Flower color (7)	Plant species (98)	0.92 (6,293)	0.47	-0.267 (0.061)	3424.70

Table S5 - Results of Phylogenetically Generalized Least Square (PGLS) models, used to evaluate the relationship between florivory levels (Index of flower damage, IFD) and several factors in 36 plant species sampled in the field using a standardized protocol.

Response variable	**Fixed factors (number of levels)**	**Random factors (number of levels)**	**F-value (d.f.)**	**P-value**	**r (Brownian model)**	**AIC value**
Florivory (IFD)	Region (2)	Plant species (36)	11.33 (1,276)	0.001	-0.498 (0.605)	722.35
	Flower symmetry (2)	Plant species (36)	0.052 (1,276)	0.819	-0.104 (0.112)	732.68
	Flower color (7)	Plant species (36)	8.82 (6,276)	0.07	-0.43 (0.287)	729.57
	Growth form (3)	Plant species (36)	0.76 (2,276)	0.46	-0.158 (0.292)	729.61

Capítulo II:

Patterns of florivory vary with an urbanization degree in tropical cities

Patterns of florivory vary with an urbanization degree in tropical cities

Maria Gabriela Boaventura* and Tatiana Cornelissen

Center for Ecological Synthesis and Conservation, Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, CP 486, Belo Horizonte, MG, Brazil.

*Corresponding author:
Maria Gabriela Boaventura
Center for Ecological Synthesis and Conservation
Universidade Federal de Minas Gerais
Belo Horizonte - MG, Brazil
mgabiboaventura@ufmg.br

Suggested journals: Urban ecosystem, Ecological Indicators, Journal of urban ecology

Abstract

Florivory can impact plant reproduction both directly when florivores consume pistils, stamens, and/or ovules or indirectly, when florivores modify floral attributes related to attractiveness by consuming petals, sepals, and floral buds, interfering with plant-pollinator relationships. We still know little about how these direct and indirect impacts affect plants and about the mechanisms and processes that make certain species more susceptible to florivory. Urbanization has been identified as one of the main threats to biodiversity in the last few decades as the conversion of natural areas into urban areas produces significant changes in the biotic and abiotic environment, due to the replacement of native species by exotic ones, formation of heat islands and pollution. Recent studies have indicated that these changes negatively affect both the occurrence of insects in cities and cause changes in the composition and quality of host plants with potential consequences for insect-plant interactions. Here we evaluated if florivory patterns vary with an urbanization degree to examine whether environmental changes caused by urbanization influence florivory levels and, whether florivory levels are driven by plant attributes and functional and phylogenetic traits of flowers and plants. Percentage of attacked flowers (florivory incidence) and area removed from petals (florivory intensity) by florivores were examined in 61 species distributed into 20 botanical families, sampled in areas with different degrees urbanization considering the plant origin (native or exotic), plant function (ornamental or non-ornamental), and floral and vegetative attributes shared across plants lineages as potentially determining factors on florivory levels. Our results indicated that the intensity of florivory decreased with increased urbanization, due to the replacement of native species by exotic ones and the highest frequency of occurrence of ornamental plants for florivores, because of environmental stress in urban environments. On the other hand, urbanization did not modify patterns of florivory incidence. Florivory levels were also influenced by intraspecific variation in the functional traits of the plants in areas over different degrees of urbanization. We believe that the effect of urbanization and functional traits on levels of florivory are mediated mainly by changes in the nutritional quality of host plants for florivores, which varies depending on plant origin and the type of ecological function it performs. We suggest that the abundance and richness of florivores also contributed to our results, and we suggest that this should be better evaluated in future studies.

Keywords: florivory, floral damage, floral herbivory, urbanization, insects

Introduction

Antagonisms between animals and plants usually bring negative consequences for plant development, but in addition, they can also mediate negative effects to other ecological interactions, such as pollination (see McCall and Irwin, 2006), which is essential for reproduction of most angiosperms. The consequences of herbivory on plants have been well documented in the last decades (see Strauss 1996; McCall and Irwin 2006; Bronstein et al., 2007; Solga et al., 2014; Mendes et al., 2021), but florivory, on the other hand, has been much less evaluated in the ecological literature (Boaventura et al., 2022). Florivory is defined as any type of damage to flowers involving the consumption of floral tissues by vertebrate or invertebrate animals, but mainly insects (McCall and Irwin, 2006; Boaventura et al., 2022). Florivory can impact plant reproduction both directly when florivores consume floral structures effectively linked to this function - such as pistils, stamens, and ovules, reducing the number of gametes produced - or indirectly, when florivores modify floral attributes related to flower attractiveness by consuming petals, sepals, and floral buds, interfering therefore with plant-pollinator relationships (McCall and Irwin, 2006; Caruso et al., 2019; Rusman et al., 2019). Consequently, florivores cause negative selective pressures on the floral attributes associated with attraction to pollinators, which may result in a reduction in the ecological service provided by those animals (Caruso et al., 2019; Rusman et al., 2019; Boaventura et al., 2022).

Despite the potential negative impact of florivory, we still know little about how its direct and indirect effects affect plants and about the mechanisms and processes that make certain species more susceptible to this antagonism (Boaventura et al., 2022). It has been suggested, for example, that abiotic factors such as elevation (Gélvez-Zúñiga, 2021) and seasonal variations in environmental conditions (Ortiz et al., 2023), as well as functional traits of flowers and plants (Feeny, 1976; Boaventura et al., 2022) directly influence levels of florivory. Although the global levels of florivory are about twice as higher as the global levels reported for herbivory (see Kozlov et al., 2015 for herbivory and Boaventura et al., 2022 for florivory levels) it still unclear how and which environmental, phylogenetic, floral and vegetative attributes influence this interaction. Therefore, quantifying florivory and determining the patterns and processes related to it is an important aspect of ecology and is the first step towards improving our understanding of this interaction (Boaventura et al., 2022).

Current knowledge about how abiotic and biotic factors that influence plant distribution and development - such as climate and the richness and abundance of florivores (Fenoglio et al., 2020) - affect florivory levels is still quite narrow (Boaventura et al., 2022). Urbanization has been recently identified as one of the main threats to biodiversity (Johnson and Munshi-South, 2017). The conversion of natural habitats into urban areas produces significant changes in both the abiotic and biotic environment due to the reduction of native vegetation cover, increased surface impermeabilization, formation of heat islands, pollution, habitat fragmentation, and replacement of native species with exotic ones (Elmqvist et al., 2013; Wu, 2014; Johnson and Munshi-Shut, 2017; Kondratyeva et al., 2020; Fenoglio et al., 2021). Recent studies have also indicated that these changes negatively influence the occurrence of insects in cities (Fenoglio et al., 2020, 2021; Cornelissen et al., 2023) and cause changes in the composition and quality of host plants, with several consequences for insect-plant interactions (Fenoglio et al., 2020, 2021; Moreira et al., 2019a). Although some patterns of florivory in natural habitats have emerged lately, we still have limited information for a narrow number of plant species (e.g., Malo et al., 2001; Irwin et al., 2014; 2018) regarding the effects of changes in land use and plant-insect interactions. Although patterns of insect diversity in the cities have been summarized (see Cornelissen et al., 2023), effects of urbanization on ecological interactions have been largely unexplored, except for pollination (Teixido et al., 2022).

From the perspective of insect-flower antagonisms, urbanization could lead to an increase in levels of florivory if, for example, plants in cities are more susceptible to florivory compared to plants in natural areas, if urbanization represent a source of abiotic stress which increases plant susceptibility to antagonisms (Cuevas-Reyes et al., 2013), as proposed by the Plant Stress Hypothesis (PSH, White, 1969;1984), and/or because plant species are exotic and have not yet developed adequate anti-florivory defenses (Raupp et al., 2010, Stemmelen et al., 2020). On the other hand, urbanization could also lead to a decrease in florivory levels due to the decrease in the abundance and diversity of florivores in these areas (Fenoglio et al., 2020), or even if exotic/ornamental plants represent a low-quality food resource for these insects (Fenoglio et al., 2021). Studies on *Gelsemium sempervirens* in rural and urban environments indicated that levels of florivory increased with urbanization, due to a decrease in corolla tube length and greater floral apparency (i.e., larger number of flowers produced per day) in an urban environment (Irwin et al., 2014; 2018). However, most of these studies only estimated florivory as a binary variable (presence or not of florivory in flowers in a population), and/or performed only visual estimates of the extent of floral damage, which may not be an adequate measurement of the extent of florivory levels and its impacts on plant populations (Boaventura et al., 2022). To date, we are not aware of any study that has evaluated the effects of urbanization on florivory at the plant community level, or of studies that have evaluated how floral traits influence levels of flower damage in the cities. If florivory really does increase with urbanization, we can expect that urban plants will have an amplified fitness loss due to the combination of high levels of florivory and scarcity of pollinating insects (Fenoglio et al., 2020), which could ultimately lead to a collapse in the urban plant community due to a decrease in the ecological service of pollination.

To advance our understanding of impacts of florivory in plants, it is necessary to take into account the biotic and abiotic factors that influence damage levels in different plant lineages and in different environmental contexts. Although urbanization represents one of the most dramatic environmental changes on Earth and although it is expected that urban expansion will continue to occur rapidly in the upcoming decades (Fenoglio et al., 2020;2021), its effect on insect-flower antagonisms are still poorly understood. Even less is known about how floral and vegetative attributes influence levels of florivory in the urban context.

In this study we assessed florivory patterns in several plant species sampled in areas within different degrees of urbanization to understand the dynamics of plant-florivore interactions, considering i) environmental and plant attributes related to urbanization (level of urbanization of the collection site, origin and type of plant function), ii) taxonomic relatedness (phylogenetic relationship between species) and iii) biological variation among species and individuals (functional traits of plants and flowers). As the methods for collecting and evaluating florivory have been recently standardized (see Boaventura et al., 2022), damage levels were evaluated both as the percentage of attacked flowers (florivory incidence) and as the percentage of floral area removed (florivory intensity). Following the arguments that florivory can be influenced by urbanization, we hypothesized that: 1) environmental changes caused by urbanization modify patterns of plant-florivore interaction and directly influence florivory levels; 2) levels of florivory will be related to plant attributes related to urbanization, such as plant origin (exotic or native) and its ecological function (ornamental vs. non-ornamental plants); 3) florivory levels will be related to functional and phylogenetic traits of flowers and plants. We also assessed whether incidence and intensity of florivory are related within individual plants and species, and we assessed the identity of the florivores responsible for the damage.

Material and Methods

Field sampling

Between February 2021 to June 2022, we performed periodic collections campaigns of data collection (every 2-3 months) in several locations in the central region of Minas Gerais state and 61 plant species (n= 305 individuals) were evaluated during its flowering period. The plant species were collected in areas under different degrees of human disturbance and the main land use impact evaluated in our study was the degree of urbanization of each collection site. Here we classified as 1) natural areas those under environmental protection, such as Federal and State Parks, away from urban centers; 2) rural or periurban areas were those where we detected dirt roads, farms, small towns with less than 5,000 inhabitants and areas in the boundaries between cities and environmental protected areas in which most of the soil coverage was permeable; and 3) urban areas were those composed of cities under stronger human influence, with more than 5,000 inhabitants and where most native vegetation cover was replaced by impervious surface cover.

All plant species studied here were selected considering taxonomic identity in a way to sample the largest possible number of genera and/or families (Fig.S1). The plant species were chosen and collected according with the protocol for sampling and measurements of florivory proposed for Boaventura et al. (2022) and plants were sampled according to its flowering phenology (i.e., whether they were flowering during the collection period). At least five synchronous individuals with flowers were sampled per plant species and individuals were spaced at least 10m apart. In the case of climbing plants or herbs arranged in intermittent patches, all branches or patches within a radius of 2 m from the main distinguishable branch or patch were considered as a single individual. For herbs arranged in continuous patches, individual flowers spaced at least 3 m apart were collected. We collected 20 flowers for individual and 100 flowers per plant species, totaling 6,100 flowers evaluated in this study. Whenever possible, we also collected and/or identified the florivore insects that were responsible for flower damage at the moment of sampling. Plant species were identified consulting specialists, taxonomic keys and, using an online herbarium (http://reflora.jbrj.gov.br/reflora/PrincipalUC/PrincipalUC.do).

Florivory levels

As proposed by Boaventura et al. (2022) ontogenetic traits intrinsic to plant species and lineages and also attributes related to the site where plant species were collected can potentially influence levels of florivory. We firstly categorized the sampled sites according to the degree of urbanization (preserved areas: n=24, periurban/rural areas: n=19 and urban areas: n=18). For each plant species sampled, we also categorized species according to plant attributes related to urbanization, such as plant origin in the site where it was collected (native or exotic) and type of plant function in each site (ornamental or non-ornamental). Finally, plants were categorized by type of floral arrangement (single flower or inflorescences), flower symmetry (actinomorphic or zygomorphic), flower color (the predominant color of the corolla as perceived by the human eyes), flower size (corolla area in cm^2), and plant growth forms (lianas, herbs, shrubs, or trees).

Because florivory can be evaluated as both the frequency with which flowers of a plant or a population are attacked by florivores and also by the amount of floral tissue removed from the petals or corolla (see Boaventura, et al., 2022), here we measured and categorized levels of florivory as two distinct metrics: 1) florivory incidence is the percentage of flower attack and 2) florivory intensity is the percentage of floral area removed. To assess the incidence of florivory we counted the number of flowers collected from each species (n=100) with any signs of florivory and the number of intact flowers. If, for example, a species had 45 damaged flowers and 55 intact flowers, we consider florivory incidence as 45%. To evaluate the intensity of florivory, all flowers with some signs of florivory, of all studied species, were laminated with the aid of a laminator or transparent adhesive tape and digitized through a digital camera, using a ruler as a default scale for all images. After being digitized, the flowers were measured using ImageJ® software, where all digital images were calibrated to 1.0 cm and the percentage of floral area removed was determined by adding the areas removed from each flower divided by the total area of the flower. Florivory intensity was multiplied by 100 to express florivory as a percentage of floral tissue lost due to florivory (Boaventura et al., 2022).

Flower size was determined by measuring at least 20 intact flowers of each plant species (following the same procedures above for measurements of lost floral area) and the floral size per plant species was determined as the average of the total areas of all the flowers measured (cm²).

Data analysis

Using generalized linear models (GLMs) we evaluated how site, plant and flower functional floral traits affected florivory. We tested whether the degree of urbanization of the collection area (preserved, rural/periurban and urbanized), plant origin at the collection site (native or exotic), plant function type at the collection site (ornamental vs. non-ornamental) flower size, flower color , floral arrangement (flowers in inflorescences vs. individual), floral symmetry (actinomorphic or zygomorphic), and plant growth type (vine, herbaceous, shrub or tree) were factors that could predict and influence florivory levels. Two distinct models were built for each predictor variable for each of the analyzed florivory metrics (florivory incidence and florivory intensity). Additionally, because florivory incidence and intensity are distinct measurements of florivory that can be taken for the same species at the same time, we evaluated whether they could be related in some way. In this last model, florivory incidence was used as the explanatory variable and florivory intensity as the response variable. All models were run considering the negative binomial error distribution due to overdispersion of data and using R packages "MASS" (Venables and Ripley, 2002) and "vegan" (Oksanen et al., 2022).

We use phylogenetic generalized least square (PGLS) to tested differences in florivory levels among collection sites, plant origin and function and plant and flower traits to account for phylogenetic relatedness between species and adjusted for expected covariance under a multivariate model of Brownian motion (Felsenstein, 1985; Martins and Hansen, 1997, Symonds and Blomberg, 2014). In these models we adjusted florivory incidence or florivory intensity as response variables and built two distinct models to separately evaluate these two evaluated florivory metrics. We included as fixed effects the type of collection site (rural, urban, natural), the origin of the plant, function of the plant, flower color, flower symmetry, flower arrangement, flower size and plant growth form. Plant species were included as a random effect to account for non-independence among data. The phylogeny of the 61 plant species was reconstructed using the “V.PhyloMaker” (Jin and Qian, 2019), "ape" (Paridis and Schliep, 2019), "nlme" (Pinheiro et al.,

2022) and, “phytools” (Revell, 2012). Analyses were done using the "picante" (Kembel et al., 2010) package. All analyzes were performed in the R 4.2.2 software (R Core Team, 2022).

Results

Patterns of florivory across urbanization degrees

We evaluated a total of 6,100 flowers from 61 plant species and 20 botanical families collected in areas under different levels of urbanization. Exotic and ornamental plant species were found only in urban or rural/periurban areas. According to the phylogenetic distribution of florivory levels on studied species, both incidence and intensity of floral damage is widespread and variable across plants lineages over different degrees of urbanization (Fig.1).

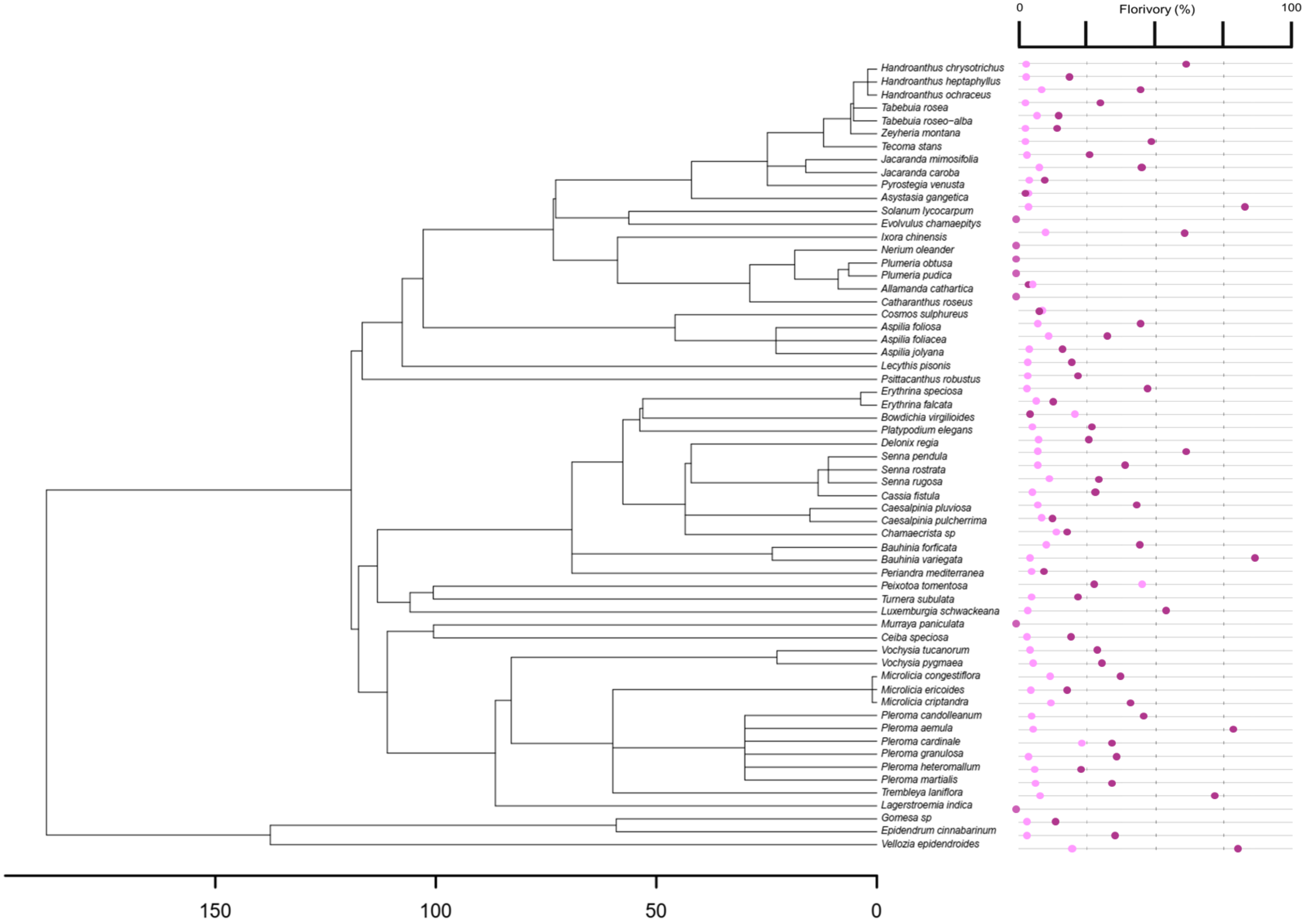
Florivory (%)
0
100
Handroanthus chrysotrichus
Handroanthus heptaphyllus
Handroanthus ochraceus
Tabebuia rosea
Tabebuia roseo−alba
Zeyheria montana
Tecoma stans
Jacaranda mimosifolia
Jacaranda caroba
Pyrostegia venusta
Asystasia gangetica
Solanum lycocarpum
Evolvulus chamaepitys
Ixora chinensis
Nerium oleander
Plumeria obtusa
Plumeria pudica
Allamanda cathartica
Catharanthus roseus
Cosmos sulphureus
Aspilia foliosa
Aspilia foliacea
Aspilia jolyana
Lecythis pisonis
Psittacanthus robustus
Erythrina speciosa
Erythrina falcata
Bowdichia virgilioides
Platypodium elegans
Delonix regia
Senna pendula
Senna rostrata
Senna rugosa
Cassia fistula
Caesalpinia pluviosa
Caesalpinia pulcherrima
Chamaecrista sp
Bauhinia forficata
Bauhinia variegata
Periandra mediterranea
Peixotoa tomentosa
Turnera subulata
Luxemburgia schwackeana
Murraya paniculata
Ceiba speciosa
Vochysia tucanorum
Vochysia pygmaea
Microlicia congestiflora
Microlicia ericoides
Microlicia criptandra
Pleroma candolleanum
Pleroma aemula
Pleroma cardinale
Pleroma granulosa
Pleroma heteromallum
Pleroma martialis
Trembleya laniflora
Lagerstroemia indica
Gomesa sp
Epidendrum cinnabarinum
Vellozia epidendroides
150
100
50
0

Fig 1. Variation of the two estimates of florivory and the phylogenetic relationship of the 61 plant species evaluated in this study. The pink dots show florivory intensity (percentage of floral area removed) and the purple dots show florivory incidence (frequency of flower attack) for each sampled species. The phylogeny was reconstructed using the "V.PhyloMaker" package (Jin and Qian, 2019) in R software. The scale shown in the tree is thousands of years old.

Florivory was detected in 89% of the species evaluated here (Fig.1). The seven plant species (11%) that did not show any sign of florivory were collected in urban or periurban sites and most of them were exotic and belonged to the Apocynaceae family (n=4). The florivore insects responsible for floral damage were beetles (Coleoptera) (Fig. 2), mainly from the Chrysomelidae and Buprestidae families, followed by ants (Hymenoptera) from several tribes (not yet identified). We also found florivores of the orders Thysanoptera (Thrips), Hemiptera (bugs) and Lepidoptera (caterpillars) feeding on the floral tissue of the studied species.

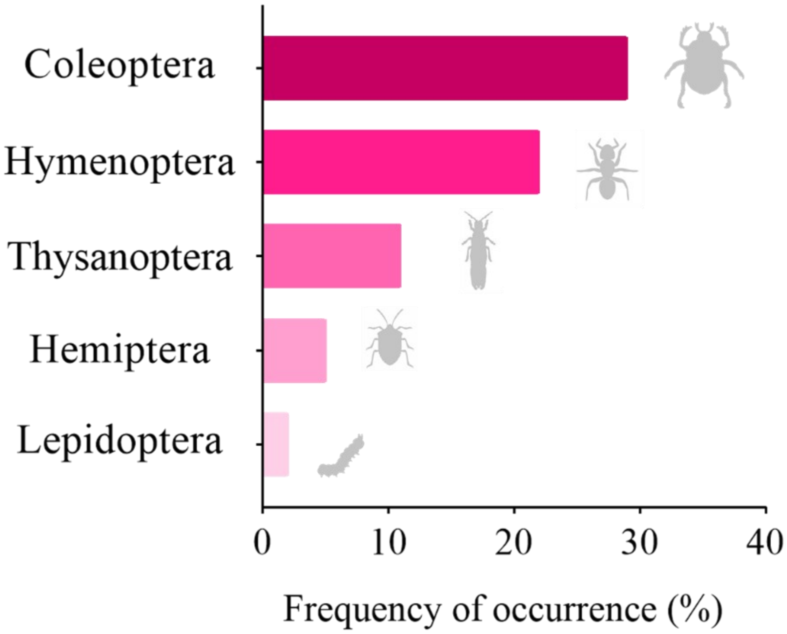

Fig 2. The main groups of florivores responsible for floral damage on the studied plant species in areas over different degrees of urbanization. Icons indicate each Order of insects.

About 30.1% (±2.94SE) of all evaluated flowers were attacked by florivores (Fig.1). *Solanum lycocarpum* (Solanaceae), a periurban species showed the highest percentage of flowers attacked, as 88% of all flowers (Fig.1) of this species showed some sign of florivory; *Bauhinia variegata* (Fabaceae), an urban species also had the second highest percentage of attacked flowers (87%, Fig.1), followed by *Vellozia epidendroides* (Velloziaceae) (78%, Fig.1), a wild species collected in a natural area. Florivores removed an average of 6.20% (±.9SE) of floral tissue (Fig.1) and all the three most intensely damaged species were collected in natural areas. *Peixotoa tomentosa* (Malpighiaceae) was the most consumed species, losing about 46% (Fig.1) of its floral area to florivores, followed by *Pleroma cardinale* (Melastomataceae) (24.5%, Fig.1), and by *Vellozia epidendroides*, (21.2%, Fig.1). Finally, a higher incidence of floral damage did not translate into increased intensity of florivory, and our results showed that these two florivory metrics occurred independently in the studied plants (rd= 1.3, df=59, p=0.25, Fig.3).

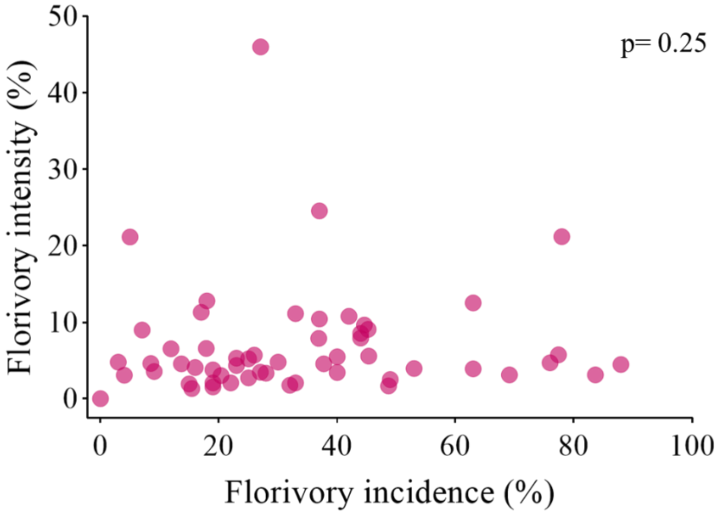

Fig 3. Relationship between the incidence and the intensity of florivory for 61 plant species sampled in areas over different degrees of urbanization. Dots indicate the average values of each plant sampled.

Forivory levels and trait-mediated florivory across urbanization degrees

Our results showed that the level of urbanization of the sampling site influenced the intensity of florivory (rd= 21.726, df=58, p<0.0001) and the levels of floral damage decreased with the increase of urbanization (Fig.4a). Plants from natural areas showed floral damage intensity three times higher compared to plants collected in urbanized sites (9.9% ± 2SE, 3.1% ± 0.55SE, respectively) (Fig.4b). The incidence of florivory, despite being higher in plants from preserved sites (36.1%±3.9SE) and lower in plants from periurban/rural (22.9% ±4.4SE) and urban (25.7%± 5.4SE) sites, was not statistically different among these three groups (rd=3.75, df=58, p=0.15) (Fig.4b), indicating that urbanization does not influence the frequency of floral damage in the studied system.

Plant origin (exotic or native) and the type of plant function in the collection site (ornamental or non-ornamental) influenced the intensity of floral damage (origin: rd=7.8, df, 59, p=0.005; function: rd= 13.2, df=59, p= 0.0002, Fig 4c-e) and flowers from native and non-ornamental plants were twice as consumed (7.2% ±1.5SE and 8.68% ±1.7SE, respectively) compared to flowers from exotic and ornamental plants (3.14% ±0.97SE and 3.81% ±0.56SE, respectively). Although native and non-ornamental plants showed a higher incidence of floral damage (33.33% ±3SE and 34.9% ±4.2SE, respectively) compared to exotic and ornamental plants (20.17% ±6.8SE and 25.4% ±4SE, respectively), these differences were not statistically significant (origin: rd= 2.69, df=59,p=0.10; Function: rd= 1.57, df=59, p=0.20; Fig 4d-f).

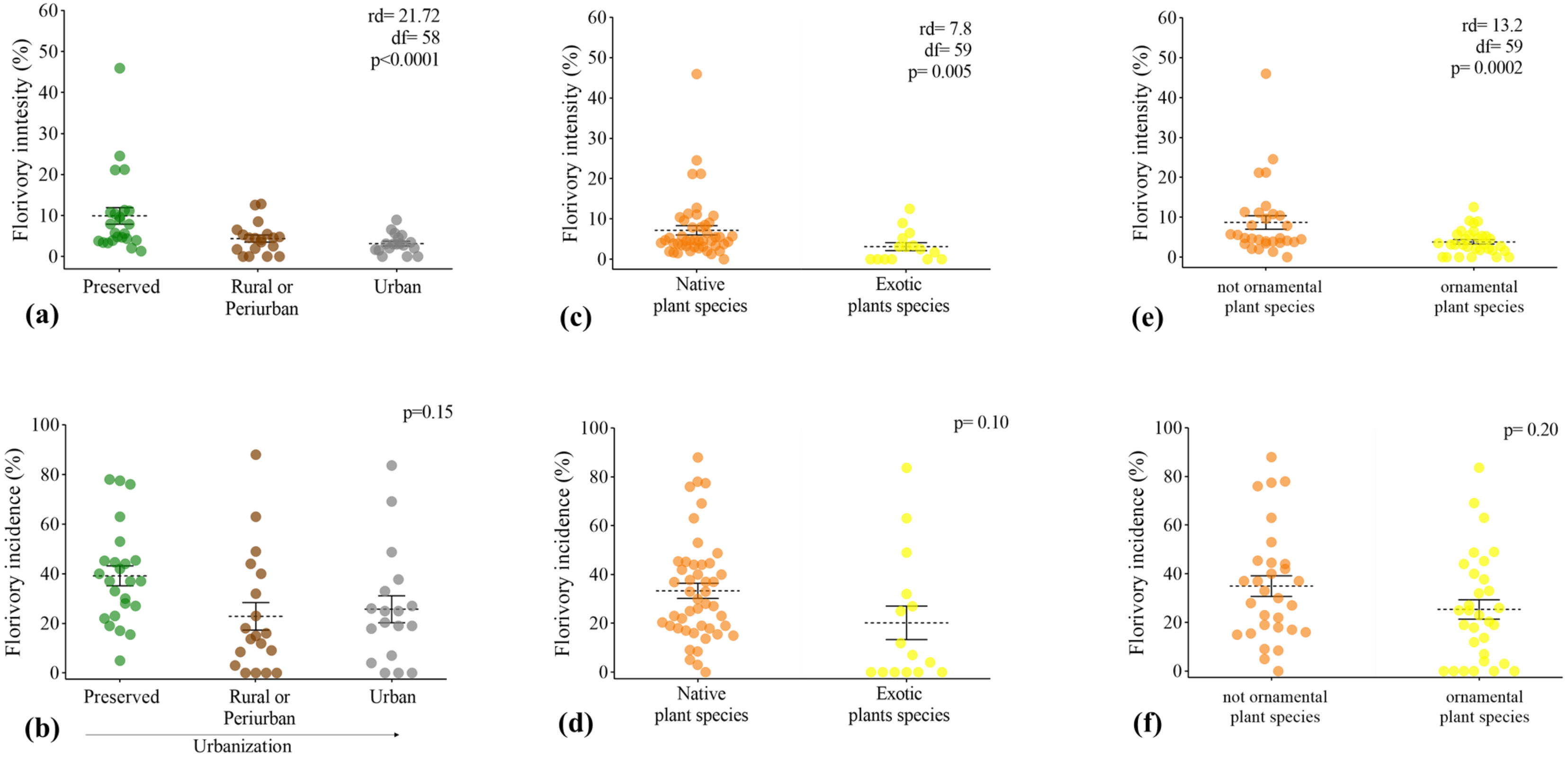

Fig 4. Effects of functional traits on florivory metrics (incidence and intensity) in n areas over different degrees of urbanization. Florivory levels were measured in two different metrics: florivory intensity (percentage of floral area removed) and florivory incidence (percentage of attacked flowers) for all 61 plant species sampled according to (a,b) degree of urbanization of their collection site, (c,d) plant origin in the site where it was collected and (e,f) type of plant function. Plants and flowers were sampled in the field using a standardized protocol (see Boaventura et al., 2022). The lines on each panel indicate the mean and the error bars denote SE.

Contrary to our expectations, our results showed that none of the functional traits of the flowers and plants evaluated here influenced florivory levels (Figs 5 and 6). Although floral damage levels varied across plant lineages and species functional traits, our results did not detect any signs that flower size (incidence: rd= 1.96, df=59, p=0.16, intensity: rd=0.75, df=59, p=0.38), flower color (incidence: rd= 2.73, df=55, p=0.74 , intensity: rd=5.63, df=55, p=0.34), floral symmetry (incidence: rd= 0.53, df=59, p= 0.46, intensity: rd=2.02, df=59, p=0.15), floral arrangement (incidence: rd=2, df=59 p=0.15 , intensity: rd= 0.72, df=59, p=0.39) and plant growth form (incidence: rd=4.56, df=57, p=0.20, intensity: rd=7.44, df=57, p=0.058) influenced the incidence or intensity of florivory.

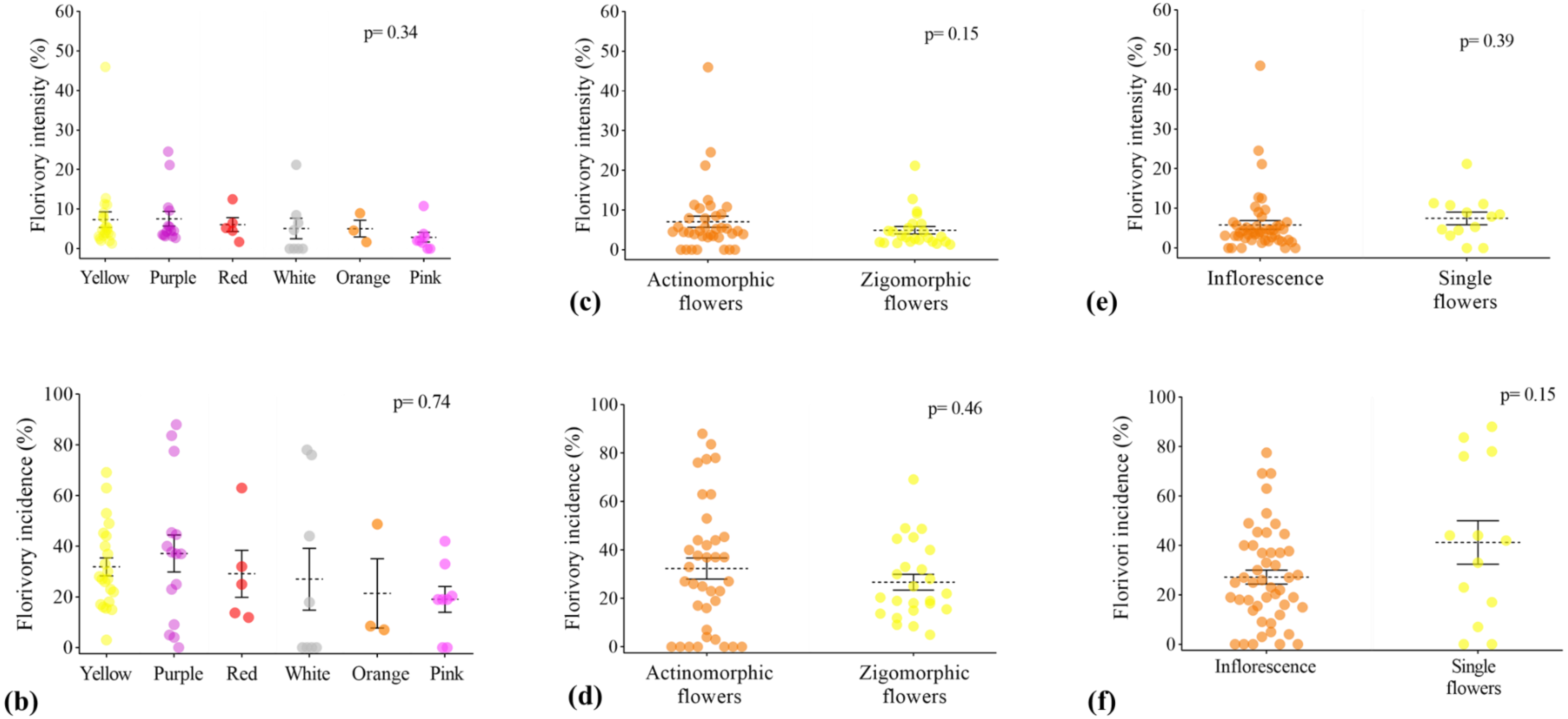

Fig 5. Functional traits that can influence florivory levels in n areas over different degrees of urbanization. Florivory levels were measured using two different metrics: florivory intensity (percentage of floral area removed) and florivory incidence (percentage of attacked flowers) for all 61 plant species sampled according to (a,b) flower color, (c,d) flower symmetry and, (e,f) flower arrangement. Plants and flowers were sampled in the field using a standardized protocol (see Boaventura et al., 2022). The line indicates the mean, and the error bars denote SE.

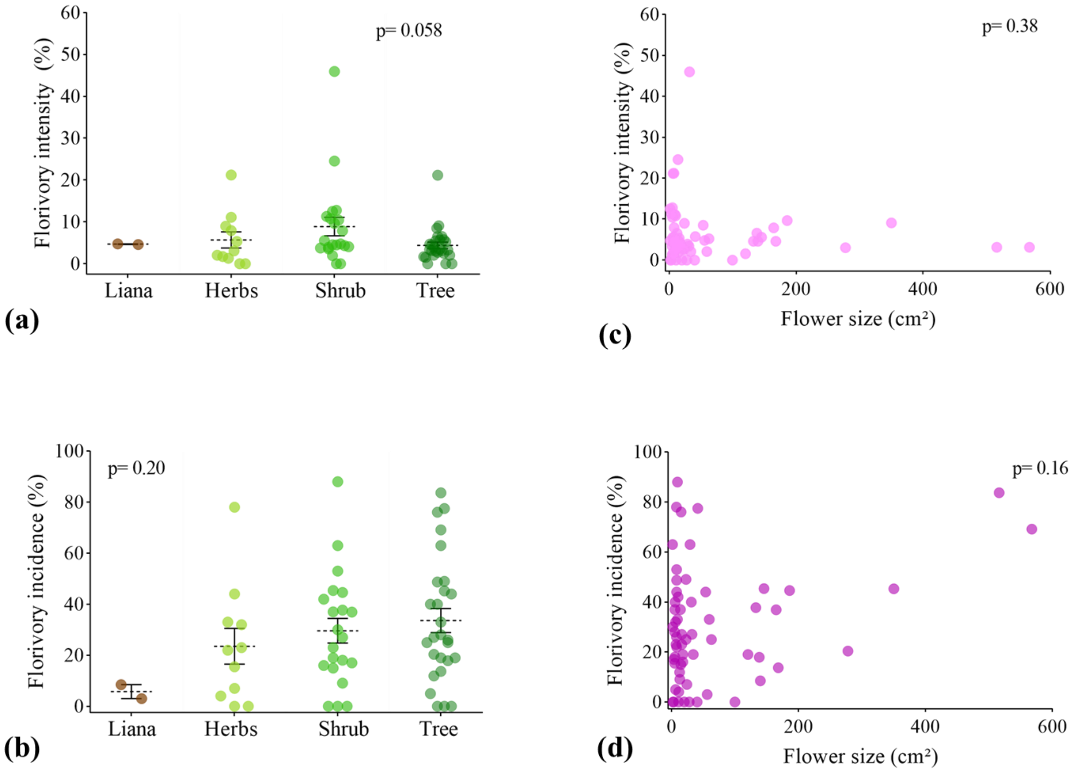

Fig 6. Functional traits that can influence florivory levels in n areas over different degrees of urbanization. Florivory levels were measured using two different metrics: florivory intensity (percentage of floral area removed) and florivory incidence (percentage of attacked flowers) for all 61 plant species sampled according to (a,b) plant growth form, (c,d) and flower size. Plants and flowers were sampled in the field using a standardized protocol (see Boaventura et al., 2022). The lines on each panel indicate the mean and the error bars denote SE.

Florivory patterns in a phylogenetic context

Our results showed that the relationship between levels of florivory and the functional traits of the species changed when we added the weight of phylogeny into our analyses (Fig.7, Tables S1, S2). Considering the phylogeny of the species evaluated here, florivory was positively influenced by plant growth form, flower color, and floral arrangement type and plant relatedness could explain the levels of damage experienced by these species (Fig.7, Tables S1, S2). Flower color and floral arrangement type also influenced the levels of florivory incidence ($F_{5,54}$= 3.30, p= 0.01; $F_{1,58}$= 6.0, p=0.01, respectively), and purple and yellow flowers were more frequently attacked by florivores (37.12% ±7.2SE and 31.85%±3.5SE, respectively), as well as single flowers (41.2%±8.8SE). Plant growth form, on the other hand, influenced the intensity of florivory ($F_{3,56}$= 3.68; p=0.01), (Tables S1 and S2), with shrubs experiencing the highest levels of floral tissue removal (8.9%±2.2SE), followed by herbaceous plants (5.7%±1.9SE). We found no evidence that phylogeny influenced the relationship between the other variables and levels of florivory.

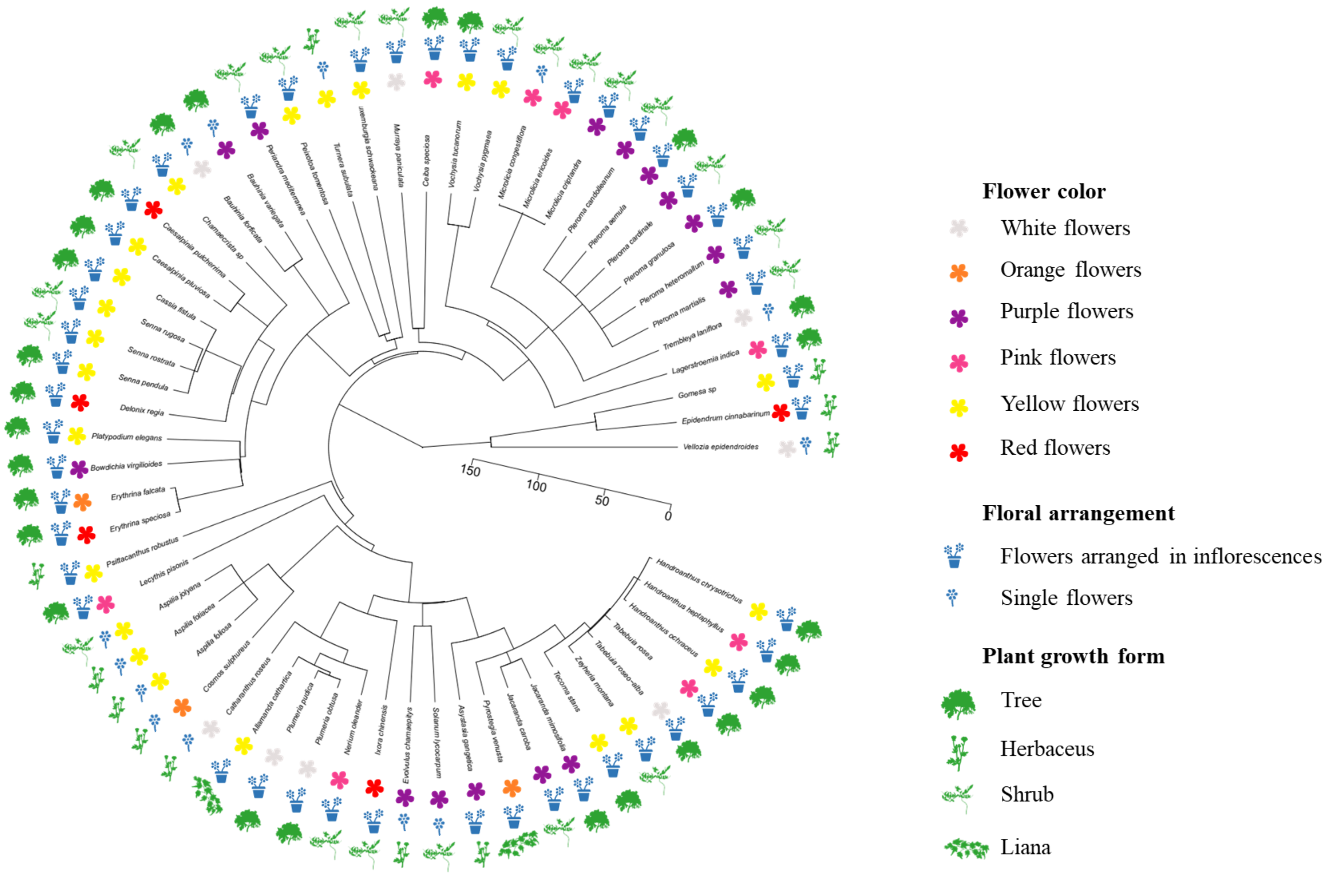

Fig 7. Functional traits of flowers and plants that influence florivory levels when we consider the evolutionary history shared by plant species. When adding the weight of the phylogeny of species in our analyses, flower color and floral arrangement directly influenced the incidence of florivory, while the plants growth form influenced the intensity of floral damage. The clipart's around the phylogenetic tree represent the functional traits that influence florivory levels.

Discussion

Patterns of florivory in areas under different degrees of urbanization

This was the first study to evaluate the variation of florivory levels over areas under different degrees of urbanization using multiple plant species sampled with a standardized protocol for collection and evaluation of florivory (Boaventura et al., 2022). We also measured floral damage using two distinct metrics simultaneously. Our results detected florivory in 89% (54 out of 61) of the plant species studied. About 30% of the flowers of these species suffered any kind of floral damage, and florivores, mainly beetles and ants, removed an average of 6.2% of the area of the petals. However, the two measurements of florivory are not related in the same plants nor are influenced by urbanization, as flowers in the cities experienced lower florivory intensity but no effect was detected in florivory incidence. The average of florivory levels found in our study are similar to those previously reported for flowers of several tropical and temperate plant species (24% and 7% for incidence and intensity of florivory, respectively; Boaventura et al., 2022), mainly regarding the intensity of floral damage, despite the florivore community in this study being predominantly composed by caterpillars. However, the average levels of florivory found in our study are about three times lower than those previously reported for *Gelsemium sempervirens* in urban and natural sites (52% and 20% for florivory incidence and intensity, respectively, Irwin et al., 2018). These results suggest that when studying the influence of environmental factors on florivory levels, it is necessary to consider the plant community and evaluate multiple plant species, in order to acquire a realistic picture of the direct and indirect impacts of florivory on plants. Evaluating florivory patterns only at the population level can bring a biased view regarding the magnitude of this interaction, simply because the observed result may come from intraspecific variation in attributes of species that occur naturally in nature and interfere with the interaction with floral enemies, which may or may not be influenced by the external environment. Thus, this study is pioneer in providing a more realistic estimate of the magnitude of the impacts of urbanization on insect-flower antagonisms, especially for tropical plant species, that have never been evaluated in this novel scenario of land use caused by urbanization. Our study has practical implications, as it has been previously shown that there is an indirect interaction between floral antagonists and floral mutualists (McCall and Irwin, 2006; Moreira et al., 2019b) and flowers attacked by insects tend to be less visited by pollinators (Krupnick et al., 1999; McCall, 2008; Liao et al., 2013), with potential negative effects of florivory on plant reproduction via reduced attraction to other beneficial insects such as bees and butterflies. Recent studies (e.g., Theodorou et al., 2020; Wenzel et al., 2020; Ayers and Rehan, 2021) have indicated that pollination is an ecosystem service that has been reduced in several cities around the world due to the negative impacts of urbanization in the populations of pollinators and our data shows lower levels of florivory intensity in the cities but also indicates that most plants studied have signs of florivore damage, which can translate into lowered fitness in urbanized areas where florivores - such as ants and beetles - are present.

Processes that drive florivory levels in areas under different degrees of urbanization

The results of our study support the hypothesis that urbanization influences florivory levels, but only for florivory intensity. Consistent with our expectations, flowers collected from natural sites had a higher intensity of floral damage and were consumed up to three times more by florivores compared to flowers from urban sites. Our results do not support the findings of previous studies that reported an increase in florivory levels due to urbanization (see Irwin et al., 2014; 2018) and provide a new perspective on the influence of environmental changes on the dynamics of insect-flower antagonisms. The influence of urbanization on insect-plant antagonisms has been evaluated in previous studies (see Nuckols and Connor, 1995; Bode and Gilbert, 2016; Raupp et al., 2010; Cuevas-Reyes et al., 2013; Kozlov et al., 2017; Moreira et al., 2019a; Stemmelen et al., 2020). For foliar herbivory, for example, some of these studies have already pointed to a similar pattern to what was found here; a marked decrease in leaf damage levels due to urbanization (Nuckols and Connor, 1995; Bode and Gilbert, 2016; Kozlov et al., 2017; Moreira et al., 2019a). Explanations for these patterns found include both a decrease in the abundance and diversity of insects, as well as changes in the secondary chemistry composition of the plants and leaves (Nuckols and Connor, 1995; Kozlov et al., 2017; Moreira et al., 2019a).

For florivory, the results of our study indicated that the patterns of intensity of flower consumption found in areas under different degrees of urbanization are related to the host plants attributes associated with urbanization, corroborating our second prediction. Our results showed that the origin of the species is determinant for the levels of floral damage, and native plants experienced levels of florivory about twice as high than exotic plants, which would partially explain the patterns of damage found. One of the reasons exotic plants suffered lower levels of floral damage might be associated to the fact that these species sustain a lower abundance and diversity of insects because they provide a low-quality food resource, making flowers less attractive (Fenoglio et al., 2020;2021). In an experimental study that evaluated the herbivore community on native and exotic plant species, a decrease in the abundance of chewing insects (which were the main florivores) was reported in exotic plants, especially if those species were not phylogenetically close to local host species, which confirms our assumptions (Burghardt and Tallamy, 2013). In our study, six of the seven plant species in which we did not detect any signs of floral damage are exotic, and most of them (n=4) belong to the Apocynaceae family, which is widely known for its high toxicity due to the presence of glycosides and alkaloids in all parts of the plants, but mainly in the flowers (Larrea et al., 2014). Therefore, we believe that florivores neglected the flowers of exotic species because they offer low-quality food resources, that can often become toxic and unpalatable for them.

In addition to the origin of the species, another attribute related to urbanization that influenced the intensity of floral damage was the fact that the species were used for urban ornamentation. Ornamental species are those artificially planted in cities and rural gardens for urban afforestation and ornamentation and can be native or non-native to that region (Nuckols and Connor, 1995; Smith et al., 2006; Potgieter et al., 2017). In our study, ornamental species experienced levels of florivory about two times lower than non-ornamental species. Similar results have been reported by Nuckols and Connor (1995) when assessing levels of foliar herbivory for the same tree species in artificially planted gardens and natural environments. These findings contradict previous assumptions that plants in urban environments are more susceptible to attack by natural enemies (Dreistadt et al., 1990; Watson and Ware, 1994; Cuevas-Reys et al., 2013) and indicate that the environmental stress caused by increased temperature, decreased availability of water and nutrients, and increased CO_2 emissions in cities may mediate physiological changes in these plants, making them less attractive to florivores. Previous studies have shown, for example, that herbivores tend to avoid trees with water deficit (Hanks and Denno, 1993) and that host plants growing under high CO_2 conditions have low nutritional quality for antagonists due to a decrease in nitrogen concentration and an increase in tannin concentration in leaves (Stiling and Cornelissen, 2007). In fact, it has already been demonstrated that florivores preferentially consume flowers with higher concentrations of nitrogen and water (Ogura and Sakai, 2015). Although we have not yet evaluated physiological parameters of flowers, we believe that flowers may have decreased nitrogen concentrations and water in response to stress, as already demonstrated for leaves. Additionally, the identity and abundance of florivores may also influence the patterns of damage found in ornamental and exotic species, and this should be addressed in future studies.

Although the incidence of florivory was higher in flowers from natural sites, native and non-ornamental plants, we found that this florivory metric was not influenced by urbanization. Florivory incidence has been the most widely used measure to estimate floral damage (see Boaventura et al., 2022), and although it assesses the frequency with which flowers are attacked in populations and communities, this measure seems unable to represent the potential that environmental conditions must interfere with plant susceptibility to natural enemies. In contrast, the amount of floral tissue removed (florivory intensity) proved to be a much more effective measure for assessing levels of florivory, as in our study, because it indicates the degree of susceptibility to which plants are subjected to damage and varied consistently with different urbanization degrees. Thus, we believe that the evaluation of the magnitude of floral damage, represented by florivory intensity, is a much more reliable measure to estimate levels of florivory in flowers, and we recommend that future studies preferably use this measure to avoid bias and underrepresentation of floral herbivory.

Trait-mediated florivory in areas under different degrees of urbanization

In addition to plant attributes related to urbanization, our study has found that levels of florivory were also influenced by plant functional traits, although this influence was only detected when we added the weight of the phylogenetic relationship among the species, supporting our third hypothesis. As suggested by Boaventura et al. (2022), floral and vegetative traits inherited through plant lineages - which are often only studied in the lieu of pollinator attraction - can also attract florivores and consequently influence levels of florivory. Flower size (see Gallen, 1999; Oguro and Sakai, 2015; Gélvez-Zúñiga et al., 2018), corolla symmetry (McCall, 2008; Boaventura et al., 2022), flower color (Reverté et al., 2016; McCall et al., 2013), floral arrangement (Ortiz et al., 2023; Boaventura et al., 2022), and even plant growth form (Boaventura et al., 2018) have been reported in the literature as traits that can attract both pollinators and floral enemies and impact the dynamics of these interactions. According to the Plant Apparency Hypothesis (PAH, Feeny, 1976), when any plant trait makes both flowers and species more conspicuous, these attributes could contribute to an increase in florivory levels, and plants may adopt strategies to escape florivory by making flowers less visible and/or less attractive (Boaventura et al., 2022).

In our study we found that flower color influenced levels of florivory incidence, mainly because purple and yellow flowers that are phylogenetically closely showed similar levels of florivory incidence (see Fig.7). We now know that plant pigments, which give color to flowers, have the potential to influence florivory levels because, like pollinators, florivores can use the flower color as a cue to locate flowers and consume floral tissue, since these pigments are often related to biosynthetic and metabolic pathways that may have defensive properties (Boaventura et al., 2022). In plant species that have color polymorphism, for example, it has been demonstrated that florivores such as caterpillars, consume yellow and/or white flowers more intensely than pink and purple flowers because they have lower concentrations of anthocyanins, which are one of the main secondary defense compounds of flowers (Irwin et al., 2003; McCall et al., 2013). Here, the secondary chemistry related to flower color does not seem to have influenced the incidence of damage, as the most frequently attacked species have purple flowers, which theoretically would be better protected against natural enemies (Irwin et al., 2003). We suggest that the mechanisms that determine florivory incidence are different from those that determine the intensity of flower consumption and, florivores may use petal color as a cue to locate resources, making certain species more conspicuous and attractive to them (PAH, Feeny, 1976). In our study, the appearance of flowers may be related to their longevity, and purple flowers, for example, may have been more frequently attacked simply because they have a longer exposure time compared to flowers of other morphs. Many species of the genus *Pleroma* (synonymy: *Tibouchina*), which represent most of the purple flowers in our study, produce longer-lasting flowers and have a more prolonged flowering period (*personal observation*), which would increase the chances that these plants are found and attacked by natural enemies, which would help explain the results found here.

The type of floral arrangement influenced the incidence of florivory and flowers singly-arranged experienced higher levels of florivory compared to flowers arranged into inflorescences. These findings are consistent with the escape hypothesis proposed by the Plant Apparency Hypothesis (PAH, Feeny, 1976) and suggest that plants that are visually more conspicuous - such as those with flowers arranged in dense resources patches or in inflorescences - are "bound to be found" and therefore may escape florivory by presenting a higher concentration of physical and/or chemical defenses, making them less attractive to florivores, as happens with leaves (Smilanich et al., 2016, Boaventura et al., 2022). We believe that although single flowers are visually less conspicuous, in our study they were more frequently attacked because they have a lower investment in defenses against natural enemies, as previously suggested by Boaventura et al. (2022), and potentially present a better nutritional quality for florivores, since more than two-thirds of plants with solitary flowers were native species (78%) or non-ornamental (61%).

Plant growth form, which can also make plants conspicuous (PAH, Feeny, 1976) was the only functional trait that influenced the intensity of florivory considering species phylogeny. Shrubs and herbaceous plants, despite being visually less apparent, showed the highest levels of floral consumption compared to trees and lianas. The plant growth form has been widely evaluated as a functional trait capable of influencing herbivory levels in plants, and there is some consensus that trees suffer more intense levels of damage because they are apparent, compared to other life forms (see Feeny, 1976; Wright et al., 2004; Kozlov et al., 2015). For florivory, we found the opposite pattern, and we suggest that the intensity of consumption is related to some other process that is not the visual appearance itself, but that makes shrubs and herbaceous plants more attractive and apparent to florivores, such as the nutritional quality of flowers. The fact that most shrub and herbaceous species are not ornamental (81% and 54%, respectively) and are native (85% and 63%, respectively) would support our hypothesis that the nutritional quality in these plants would be superior and function as an attractive to florivores, more important than the physical appearance of the plant itself. Furthermore, the fact that most tree species were collected in urban and rural areas (74%) may also help explain our results because beetles, our main florivores, are one of the groups most affected by anthropization (see Fenoglio et al., 2020) and are experiencing a decline in abundance and diversity in urbanized areas. Therefore, lower levels of florivory may also have been detected in trees due to the decline in abundance and diversity of florivores and this point deserves further evaluation and the identification of flower consumers and diet breadth.

We did not find evidence that floral size or symmetry influence florivory levels in the evaluated plants, although these functional traits have recently been reported as potentially relevant for attracting florivores and influencing floral damage levels (see Boaventura et al., 2022). Several studies have even reported that large flowers are often more attacked and consumed by florivores (Ogura and Sakai, 2015, Ortiz et al.,2023), as well as flowers with radial symmetry (Boaventura, 2018), but in our study, attributes more related to floral attraction and flower quality were more relevant in determining florivory levels than floral size itself. We believe that the importance of functional traits for florivory levels may vary depending on environmental variables and the identity of the evaluated species. Therefore, we emphasize the importance of evaluating florivory for as many species and environmental contexts as possible.

Conclusion

Our study described how the patterns of florivory vary with an urbanization degree in tropical areas based on the functional and phylogenetic traits of the studied plant species. We provided one of the first assessments of florivory at the community level of species and through a new approach, to understand the combined effects of biotic and abiotic factors that influence the incidence and intensity of florivory, in the context of environmental changes that occur because of urbanization. We found that the florivory levels reported here are consistent with global estimates of floral damage for species collected around the world (Boaventura et al., 2022). We suggest that these findings are due to the use of standardized methods for collecting and evaluating levels of florivory in our study and therefore recommend the use of this standardized protocol in future studies. Our study demonstrated that florivory intensity decreased with increasing urbanization, due to the substitution of native species to exotic ones and because of the environmental stress experienced by ornamental plants in cities, which leads to a decrease in attractiveness of these species to florivores. Florivory incidence was not influenced by urbanization, and we emphasize that this method of evaluating floral damage is not as accurate as determining the amount of floral tissue removed (florivory intensity). We also found that functional traits of species and flowers, such as flower arrangement, flower color, and plant growth form, influenced levels of florivory, but this influence is only detectable when we added the weight of the evolutionary history shared by species in our analyses. Thus, we highlight the need to consider the phylogeny of species in future studies. Overall, our study demonstrated that the effect of urbanization and functional traits on florivory levels are mostly mediated by changes in the occurrence of host plants, which vary depending on the plant origin (native or exotic) and the type of ecological function it has (ornamental or non-ornamental). As most studies on antagonistic interactions in the context of urbanization have been about foliar herbivory, we still do not know which secondary compounds would lead to this observed reduction in flower quality, and we highlight the need for these mechanisms to be evaluated in the future. We believe that the identity, abundance, and richness of florivores in the collection areas may have also contributed to the results found here and suggest that future studies on insect-flower antagonisms in cities jointly evaluate the florivore community and levels of florivory. Finally, we emphasize the need for studies that evaluate the impact of florivory on plants reproductive success in areas under different degrees of urbanization because, even though floral damage levels in cities are lower than previously thought, they could still negatively impact plant fitness, especially in a scenario of pollinator scarcity.

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Supporting information

Fig S1. Florivory and florivores in some of the studied plant species. A- flowers and florivores of *Solanum lycocarpum*. B- Florivory in *Bauhinia variegata*. C- *Diabrotica speciosa* (Chrysomelidae), a florivore of *Turnera subulata*. D- Ant damaging *Periandra mediterranea* flowers. E- Chrysomelidae beetle feeding on the petals of *Chamaecrista* sp. F- Florivory in *Ceiba speciosa*. G- *Conognatha compta* beetle feeding on the petals of *Microliceae congestiflora*. H- Florivory in *Trembleya laniflora*. I- Florivory in *Aspilia* sp.

Table S1. Summary of phylogenetic generalized least squares (PGLS) models used to assess the weight of the phylogeny of 61 plant species on florivory incidence. The existence of a significant relation between the variables is indicated when the GLS does not show a relevant relationship, but the PGLS analysis does, which suggests that these relationships are relevant only when considering the impact of phylogeny. The (*) indicate fixed factors that may potentially have an influence the incidence of florivory independently of the influence of phylogeny.

Response variable	**Fixed factors (number of levels)**	**GLS**		**PGLS**	
		F-value	**p-Value**	F-value	p-Value
Florivory incidence **(Frequency of flower attack)**	Collected* Sitio (3)	$F_{2,57}$= 4.96	0.01	$F_{2,57}$= 4.73	0.01
	Flower* size (61)	$F_{1,58}$=4.12	0.04	$F_{1,58}$=9.29	0.003
	Flower Color (6)	$F_{5,54}$= 1.27	0.28	**$F_{5,54}$= 3.30**	**0.01**
	Flower arrangement (2)	$F_{1,58}$=1.51	0.22	**$F_{1,58}$= 6.1**	**0.01**
	Flower Symmetry (2)	$F_{1,58}$= 0.014	0.90	$F_{1,58}$= 0.005	0.94
	Plant Growthform (4)	$F_{3,56}$= 1.34	0.26	$F_{3,56}$= 0.46	0.70
	Plant Origin (2)	$F_{1,58}$= 10.53	0.001	$F_{1,58}$= 0.58	0.44
	Plant function (2)	$F_{1,58}$=4.002	0.05	$F_{1,58}$= 0.23	0.62
	Florivory Intensity (61)	$F_{1,58}$=16.99	0.0001	$F_{1,58}$=3.63	0.061

Table S3. Summary of phylogenetic generalized least squares (PGLS) models used to assess the weight of the phylogeny of 61 plant species on florivory intensity. The existence of a significant relation between the variables is indicated when the GLS does not show a relevant relationship, but the PGLS analysis does, which suggests that these relationships are relevant only when considering the impact of phylogeny. The (*) indicate fixed factors that may potentially have an influence the incidence of florivory independently of the influence of phylogeny.

Response variable	**Fixed factors (number of levels)**	**GLS**		**PGLS**	
		F-value	**p-Value**	**F-value**	**p-Value**
Florivory intensity **(Floral area removed)**	Collected* Sitio (3)	$F_{2,57}$= 8.49	0.0006	$F_{2,57}$= 11.43	0.001
	Flower size (61)	$F_{1,58}$=0.04	0.84	$F_{1,58}$=0.69	0.40
	Flower Color (6)	$F_{5,54}$= 1.41	0.23	$F_{5,54}$= 2.01	0.09
	Flower arrangement (2)	$F_{1,58}$=0.79	0.37	$F_{1,58}$= 1.95	0.16
	Flower Symmetry (2)	$F_{1,58}$= 0.22	0.63	$F_{1,58}$= 0.05	0.80
	Plant Growthform (4)	$F_{3,56}$= 1.44	0.24	**$F_{3,56}$= 3.68**	**0.01**
	Plant* Origin (2)	$F_{1,58}$= 10.33	0.002	$F_{1,58}$= 5.7	0.02
	Plant * function (2)	$F_{1,58}$=10.49	0.002	$F_{1,58}$= 4.52	0.03

Considerações Finais

Apesar do potencial impacto negativo da florívoria para as plantas, estudos sobre interações flor-florívoro permanecem amplamente negligenciados na literatura ecológica já que a maioria dos estudos com interações inseto-planta tende a se concentrar na herbívoria como relação antagonística e na polinização como relação mutualística. Aqui, nós fornecemos as primeiras informações sobre os padrões de florívoria a nível global, abordamos suas fontes de variação e identificamos os principais caminhos de pesquisa que ajudarão a preencher lacunas ainda persistentes no conhecimento acerca dessa interação. Ao dar os primeiros passos para avaliar a florívoria em ambientes naturais e modificados na região tropical, nós descobrimos que a ocorrência de dano floral é comum nas angiospermas, mas é amplamente variável entre as linhagens de plantas, apesar dos níveis de florívoria poderem ser até duas vezes maiores em flores de espécies tropicais comparado a espécies temperadas, sugerindo impactos potencialmente negativos ainda mais fortes na aptidão das plantas nos trópicos. Também descobrimos que tanto a identidade dos florívoros (classe e guilda alimentar), quanto o tipo de arranjo floral influenciam a frequência com que as flores são atacadas por inimigos florais. Descobrimos que os níveis de herbívoria e florívoria estão correlacionados dentro das mesmas espécies de plantas, embora as comunidades de florívoros e herbívoros sejam pouco similares, mas que as espécies plantas com períodos de floração mais longos formaram comunidades de florívoros mais similares, sugerindo que a fenologia das plantas, a aparição floral e a duração fenofásica também podem modular os níveis de dano floral em diversas espécies de plantas.

Ao avaliar a florívoria em ambientes modificados, como aqueles gerados pela urbanização, observamos que há um efeito das mudanças no uso da terra causadas pelo crescimento das cidades (e.g., aumento da cobertura de asfalto, diminuição das áreas verdes, avanço da ocorrência de espécies exóticas) no nível de florívoria, mas não na sua frequência de ocorrência, o que pode indicar que os insetos florívoros, ao encontrarem as plantas hospedeiras no ambiente urbano são capazes de infligir maior dano. Tal resultado tem aplicações para o plantio de espécies no ambiente urbano e no planejamento das cidades, uma vez que sabe-se que além dos efeitos negativos diretos da florívoria nas plantas, há também efeitos indiretos causados pela redução na atratividade das flores danificadas a insetos mutualistas, como polinizadores e dispersores. Assim, nossos resultados indicam que a florívoria pode impactar a aptidão de plantas urbanas - tanto nativas quanto exóticas - e maior número de estudos são necessários para testar a generalidade desse padrão em cidades que variam em termos de grau de urbanização e impactos de uso do solo na ocorrência de insetos florívoros.

Em conjunto, nossos resultados dos dois capítulos começaram a dar os primeiros passos para entender a importância da florívoria nas plantas, seu padrão de ocorrência e distribuição e guiam pesquisas futuras para avaliar como florívoros, herbívoros e mutualistas interagem com os recursos e como impactam a aptidão de plantas em ambientes naturais e modificados.

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