UNIVERSIDADE FEDERAL RURAL DE PERNAMBUCO
DEPARTAMENTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

LETÍCIA MENEZES CAMURÇA

INTERAÇÕES TRÓFICAS ENTRE PLANTAS, POLINIZADORES, FLORÍVOROS E ARANHAS: UMA META-ANÁLISE

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Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal Rural de Pernambuco como requisito para obtenção do título de Mestre em Botânica.

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“Foi o tempo que dedicaste à tua rosa que a fez tão importante.”

Antoine de Saint-Exupéry

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SUMÁRIO

RESUMO

As relações multitróficas entre plantas, polinizadores, florívoros e aranhas que predam visitantes florais influenciam o sucesso reprodutivo das plantas, e algumas características das plantas influenciam as escolhas desses animais pelos sítios de forrageamento. Apesar dessas relações multitróficas serem bastante conhecidas em diversos biomas, não há estudos que integrem os dados obtidos, apontem tendências de resultados e lacunas do conhecimento. Este estudo teve como objetivo integrar os dados globais das relações multitróficas supracitadas, e responder às seguintes perguntas: 1) Como os estudos estão distribuídos no tempo e nos biomas? 2) Quais os tópicos estudados? 3) Quais os grupos de plantas, polinizadores, florívoros e aranhas registrados? 3) Quais os polinizadores e florívoros predados? 4) Características das plantas explicam a escolha por florívoros e aranhas? 5) As aranhas têm efeito positivo, negativo ou neutro na produção de frutos? Os dados foram obtidos por meio de uma revisão bibliográfica sistemática nas principais bases de dados científicos, e usando combinações das palavras florivoria, aranha, polinizador, polinização, risco de predação e reprodução de plantas. Dos artigos retornados foram extraídos ano de publicação, bioma, espécies de plantas, aranhas, polinizadores, florívoros e grupos predados. A relação entre as características das plantas e a presença de florívoros e aranhas, bem como o efeito da presença de aranhas na produção de frutos foram testados por meio de uma metanálise, O número de estudos cresceu desde 2000 e os estudos foram conduzidos principalmente em ambientes tropicais. Espécies herbáceas de Asteraceae, Hymenoptera, Coleoptera e Thomisidae foram, respectivamente, os grupos de plantas, polinizadores, florívoros e aranhas mais estudados. Os dípteros foram o principal grupo de presas. Os resultados mostram que a escolha das flores pelos florívoros e aranhas não ocorre de forma aleatória, uma vez que algumas características explicam sua presença nas plantas (longevidade floral e unidade de polinização para florívoros e hábito, simetria, forma, unidade de polinização e recurso floral para aranhas). Em relação às interações polinizador-aranha, os dípteros foram as principais presas, embora as abelhas sejam comumente os polinizadores mais frequentes nas comunidades de plantas. Uma importante lacuna de conhecimento foi identificada: estudos incluindo florívoros. Não foi demonstrado um efeito significativo da presença de aranhas na produção de frutos, indicando que, em um contexto geral, as aranhas têm um efeito neutro sobre o sucesso reprodutivo das plantas. A maioria dos estudos não fornece informações compatíveis e / ou adequadas para a aplicação de uma meta-análise. Portanto, novos esforços de pesquisa seguindo metodologias padronizadas são necessários.

Palavras-chave: abelhas, atributos florais, florivoria, predação, sucesso reprodutivo, Thomisidae.

ABSTRACT

The multitrophic relationships between plants, pollinators, florivores and spiders that prey on floral visitors influence the reproductive success of the plants, and some characteristics of the plants influence the choices of these animals for foraging sites. Although these multitrophic relationships are well known in several biomes, there are no studies that integrate the data obtained, point to trends in results and knowledge gaps. This study aimed to integrate the global data of the aforementioned multitrophic relationships, and to answer the following questions: 1) How are the studies distributed over time and biomes? 2) What topics are studied? 3) Which groups of plants, pollinators, florivores and spiders are registered? 3) What are the pollinators and florivores preyed? 4) Do plant traits explain the presence of florivores and spiders? 5) Do spiders have a positive, negative or neutral effect on fruit production? Data were obtained through a systematic literature review in the main scholarly databases, using combinations of the words florivory, spider, pollinator, pollination, risk of predation and plant reproduction. From the returned studies, it was extracted year of publication, biome, plant species, spiders, pollinators, florivores and predated groups. The relation between plant features and the presence of florivores and spiders, as well as the effect of the presence of spiders on fruit production were tested through a meta-analysis. The number of studies has grown since 2000 and the studies were conducted mainly in environments tropical. Herbaceous species of Asteraceae, Hymenoptera, Coleoptera and Thomisidae were, respectively, the most studied groups of plants, pollinators, florivores and spiders. Diptera were the main group of prey. It was clear that the choice of flowers by florivores and spiders does not occur randomly, since some characteristics explained their presence in the flowers (floral longevity and pollination unit for florivores and habit, symmetry, shape, pollination unit and resource floral for spiders). In relation to pollinator-spider interactions, dipterans were the main prey, although bees are commonly the most frequent pollinators in plant communities. An important gap of knowledge was identified: studies including florivores. It was not demonstrated a significant effect of the presence of spiders on fruit production, indicating that, in a general context, spiders have a neutral effect on the reproductive success of plants. Most studies do not provide compatible and / or appropriate information for the application of a meta-analysis. Therefore, new research efforts following standardized methodologies are necessary.

Keywords: bees, floral attributes, florivory, plant reproductive success, predation, Thomisidae.

1. INTRODUÇÃO GERAL

As interações planta-animal constituem um importante componente para a manutenção da biodiversidade em todos os biomas. Dentre essas interações, a polinização por insetos é altamente relevante, pois permite a reprodução da maioria das espécies de plantas (CRUPINSKI; SILVEIRA; LIMBERGER, 2017). A polinização pode ser influenciada negativamente por florívoros e / ou predadores de polinizadores, especialmente aranhas da família Thomisidae (UETZ, 1992). Florívoros e aranhas, por influenciarem a polinização, podem afetar direta ou indiretamente a frutificação e, consequentemente, reduzir o sucesso reprodutivo das plantas (GONÇALVES-SOUZA *et al*., 2008). Dada a sua importância ecológica, relações multitróficas envolvendo plantas, polinizadores, florívoros e aranhas têm sido embasadas na literatura, com grandes avanços nas últimas décadas (LIMA *et al*., 2013). Tais estudos indicam que a evolução dessas interações multitróficas vem de adaptações dos organismos (LEROY *et al*., 2019).

Características florais como exibição floral (por exemplo, BRODY; MITCHELL, 1997; RUANE; ROTZIN; CONGLETON, 2014), forma (GALEN; CUBA 2001), longevidade (TEIXIDO; MÉNDEZ; VALLADARES, 2011) e recursos (ADLER; BRONSTEIN, 2004) são resultados de pressões seletivas que favorecem a atração de polinizadores (KNAUER; BAKHTIARI; SCHIESTL, 2018), mas também podem atrair florívoros (LIM; RAGUSO, 2017). Os danos causados pela florivoria podem impactar diretamente na reprodução das plantas pelo consumo do gineceu e androceu, ou indiretamente, pelo consumo de partes e / ou recursos florais, que diminuem a atração e recompensa oferecida aos polinizadores (GORDEN; ADLER 2016). Por um lado, se há uma seleção de componentes físicos e químicos nas plantas que repelem ou diminuem o desempenho dos florívoros (COUTURE; SERVI; LINDROTH, 2010), por outro lado há uma seleção de características dos florívoros que podem ajudar a superar essas dificuldades impostas, como desenvolver resistência aos metabólitos secundários (HARTMANN; OBER, 2000) ou armazená-los para autodefesa (STÄDLER; REIFENRATH 2009).

No caso das aranhas-caranguejo, a escolha dos locais de predação parece ser influenciada por características que também influenciam a escolha dos polinizadores e florívoros, como hábito (LOUDA, 1982), exposição floral (THÉRY; CASAS, 2002), cor e odor das flores (HEILING; CHENG; HERBERSTEIN, 2004). Além disso, as aranhas se camuflam em plantas escolhendo locais de forrageamento com cores semelhantes a seus corpos (THÉRY; CASAS, 2002), ou mesmo mudando suas cores de uma forma que melhor se camufle em flores e inflorescências (OXFORD; GILLESPIE, 1998). As aranhas também podem refletir a luz ultravioleta, ajustando suas propriedades de refletância para atrair presas específicas (LLANDRES *et al*., 2011). Finalmente, as aranhas Thomisidae escolhem flores cujo odor também atrai polinizadores (HEILING; CHENG; HERBERSTEIN, 2004).

A presença de aranhas pode beneficiar a planta ao se alimentar de florívoros e, consequentemente, reduzir os danos às flores (GAVINI; QUINTERO; TADEY, 2019). Por outro lado, as aranhas têm um efeito negativo nas plantas quando se alimentam de polinizadores ou quando os polinizadores evitam visitar flores com aranhas (comportamento antipredatório, DUKAS, 2001). Em ambos os casos, haverá uma redução na frequência de visitas dos polinizadores, o que pode reduzir a produção de frutos e / ou sementes (COUTINHO; STABILE; VIANA, 2012). Por fim, as aranhas podem ter efeito neutro, ou seja, não interferem no desempenho reprodutivo das plantas. O efeito das aranhas na reprodução das plantas (positivo, negativo ou neutro) depende principalmente da densidade das aranhas nas populações de plantas (COUTINHO; STABILE; VIANA, 2012).

Embora existam muitos estudos que abordam as relações multitróficas entre flores, polinizadores, florívoros e aranhas em diversos biomas, não há estudos que integrem esses dados, apontando os principais resultados e lacunas de conhecimento. Este estudo teve como objetivo integrar os dados globais publicados em revistas científicas e testar algumas hipóteses ecológicas sobre as complexas relações entre esses organismos. Primeiramente, testamos as hipóteses de que o número de estudos aumentou ao longo do tempo e de que existe uma diferença na frequência dos hábitos das plantas nos estudos. Também relatamos a porcentagem de estudos referentes aos biomas, os escopos dos artigos e os grupos de plantas, polinizadores, florívoros e aranhas estudados. Então, considerando que a evolução das interações multitróficas vem de adaptações dos organismos interagentes (LEROY *et al*., 2019), testamos as hipóteses de que o hábito da planta e os atributos florais explicam a presença de florívoros e a presença de aranhas. Como os principais polinizadores das angiospermas são as abelhas (CRUPINSKI; SILVEIRA; LIMBERGER, 2017), também testamos a hipótese de que as abelhas são os polinizadores mais predados. Por fim, testamos a hipótese de que a presença de aranhas nas flores afeta a produção de frutos.

2. REVISÃO DE LITERATURA

As interações ecológicas interespecíficas são caracterizadas por ocorrerem entre indivíduos de espécies distintas. Ricklefs e Relyea (2016) classificaram as interações interespecíficas em competição, mutualismo, comensalismo, amensalismo e interação consumidor-recurso, que compreende predador-presa, herbívoro-planta e parasita-hospedeiro.

O mutualismo é uma interação ecológica caracterizada pelo benefício mútuo entre as espécies envolvidas (BRONSTEIN, 2015). As mais conhecidas interações mutualísticas incluem as associações entre fungos e algas (líquens) e entre fungos e raízes de plantas (micorriza), além de polinização e dispersão (RAVEN; EVERT; EICHHORN, 2014). As interações consumidor-recurso, por outro lado, são caracterizadas pelo benefício do consumidor em detrimento do prejuízo do organismo consumido (RICKLEFS; RELYEA, 2016).

Interações planta-animal

Interações planta-animal são amplamente estudadas (e.g. RIBEIRO; FERNANDES, 2000; GONÇALVES, 2015; PEREIRA; CAZASSA; SILVA, 2016; DEPRÁ; GAGLIANONE, 2018; KLOC *et al*., 2019) uma vez que são umas das mais frequentes, podendo ser positivas mutuamente, como é o caso da polinização, ou prejudiciais para pelo menos um dos lados implicados, como no caso da herbivoria (SOUZA *et al*., 2013). Essas interações refletem em ambos os envolvidos, onde geram respostas um em função do outro (AOYAMA; LABINAS, 2012). Os compostos químicos são os principais mediadores dessas interações, uma vez que a planta pode emitir substâncias que influenciam o comportamento do inseto, atraindo ou repelindo, ou ainda atraindo os predadores naturais de seus algozes (SILVA *et al*., 2012). As interações animal-planta são as principais responsáveis pela estruturação da comunidade e manutenção das cadeias tróficas (DEL-CLARO *et al*., 2013).

a) Polinização vs. florivoria

Devido a importância de se entender as interações planta-animal e seus efeitos na estrutura da comunidade, a polinização (e.g. VOSGUERITCHIAN; BUZATO, 2006; OBERMULLER *et al*., 2008; BARÔNIO *et* al., 2016; DEPRÁ; GAGLIANONE, 2018; QUEIROZ *et al*., 2018) e a florivoria (herbivoria) (e.g. NETO; TEIXEIRA, 2006; FERREIRA; TOREZAN-SILINGARDI, 2013; COTARELLI; ALMEIDA, 2015; PALACIOS-MOSQUERA; MONDRAGÓN; SANTOS-MORENO, 2019; MARTINS *et al*., 2020) têm sido amplamente estudadas.

A polinização é a transferência de grãos de pólen para o estigma da flor (FAEGRI; VAN DER PIJL, 1979), podendo ocorrer na mesma flor (autopolinização), entre flores do mesmo indivíduo (geitonogamia) ou em flores de indivíduos distintos (xenogamia) (ALVES-DOS-SANTOS *et al*., 2016). É considerada um serviço ecossistêmico fundamental por sustentar outros serviços ecossistêmicos, sendo em grande parte dependente de vetores bióticos ou abióticos para ser realizada (RECH et al., 2014). Estima-se que entre 75% (CGEE, 2017) e 87,5% das espécies de angiospermas do mundo sejam polinizadas por animais (OLLERTON; WINFREE; TARRANT, 2011), sendo as abelhas o grupo com maior representatividade (CRUPINSKI; SILVEIRA; LIMBERGER, 2017). Embora essa interação planta-animal seja mutuamente benéfica (KROHLING; EUTRÓPIO; SILVA, 2010), a polinização não ocorre de forma altruísta. As plantas são responsáveis por uma série de mecanismos para atração dos polinizadores e culminância do processo de transferência do pólen para o estigma (SOUZA *et al*., 2013). As plantas liberam substâncias (cairomônios) que instigam a visita de animais polinizadores (SILVA *et al*., 2012), além de ofertar recursos, tais quais néctar, pólen, óleos, perfumes, resinas, dentre outros, que também servem para atração (MALERBO-SOUZA; TOLEDO; PINTO, 2008). Essa interação é responsável por conservar a biodiversidade (RECH et al., 2014), uma vez que dá suporte ao funcionamento das cadeias tróficas (DEL-CLARO *et al*., 2013), sendo responsável pela sobrevivência das espécies e pela promoção da robustez da comunidade (VANBERGEN *et al*., 2017). Em um outro extremo temos a herbivoria, que é uma interação consumidor-recurso, onde o herbívoro pode ser considerado um predador, se consome a planta, ou um parasita, se apenas alimenta-se sem ocasionar morte (RICKLEFS; RELYEA, 2016). A florivoria é um tipo de herbivoria na qual o animal alimenta-se das partes florais (GORDEN; ADLER, 2016), influenciando na reprodução das plantas envolvidas (ROCHA *et al*., 2006). Do ponto de vista da comunidade, essas interações se sobrepõem, uma vez que a florivoria é responsável por uma série de efeitos nos polinizadores (KESSLER; HALITSCHKE; POVEDA, 2011) e nas plantas (e.g. RUANE; ROTZIN; CONGLETON, 2014; GORDEN; ADLER, 2016), seja no ponto de vista das respostas florais aos danos causados (SILVA *et al*., 2012), ou pelo ponto de vista dos danos indiretos causados pelos florívoros às flores (ROCHA *et al*., 2006).

Alusivo à florivoria, os principais efeitos são referentes ao desenvolvimento reprodutivo da planta. Isso ocorre pois a florivoria é responsável por desde as influências diretas (quando o dano floral é causado nas estruturas reprodutivas), quanto pelas indiretas (quando há diminuição no número de visitas, uma vez que o florívoro pode provocar alterações no tamanho do dislpay e na simetria floral, assim como na produção de néctar) (MCCALL; IRWIN, 2006). O dano floral causado diretamente tem os efeitos mais óbvios, uma vez que os florívoros podem consumir os grãos de pólen e os óvulos, impedindo a reprodução (CARDEL; KOPTUR, 2010); por outro lado, os efeitos indiretos são equivalentemente danosos, uma vez que as alterações no display floral causada pelos florívoros têm diversos efeitos na reprodução da planta. Esses efeitos podem ocorrer de forma imediata, quando o dano floral ou a presença do florívoro faz com que o polinizador evite a flor, ou mais tardiamente, quando os florívoros induzem as flores às respostas bioquímicas de defesa (KESSLER; HALITSCHKE; POVEDA, 2011). Essa defesa pode ser física, como a presença de espinhos ou tricomas (KROHLING; EUTRÓPIO; SILVA, 2010), ou química, seja na produção de substâncias que repelem insetos (SILVA et al., 2012), como na produção de antocianinas e taninos (WINK, 2003), além de compostos antidigestivos e antinutritivos (KESSLER; HALITSCHKE; POVEDA, 2011) que repelem os florívoros.

Em um estudo recente, Martins *et al*. (2020) constataram que os florívoros foram responsáveis pela perda de importantes atributos florais, além de alteração no display floral de *Ipomoea carnea* subs. *fistulosa* (Martius & Choise) (Convolvulaceae), concomitante com a redução do número de visitas, o que é extremamente prejudicial para essa espécie, uma vez que esta é autoincompatível, sendo totalmente dependente de visitantes florais para polinização e formação de frutos. Em um experimento realizado com *Centrosema virginianum* (L.) Benth, uma espécie autocompatível, mas dependente de polinizadores, Cardel e Koptur (2010) verificaram que a florivoria era um grande obstáculo para o sucesso reprodutivo da espécie, uma vez que os danos florais interferiram na atração e sistema de recompensa da flor, reduzindo significativamente o número de visitas e, consequentemente, o número de frutos formados. Porém, em um estudo com uma espécie autocompatível, Gorden e Adler (2016) observaram que *Impatiens capensis* Meerb. (Balsaminaceae) aumentou sua autopolinização devido à escassez de polinizadores após a florivoria. Além disso, a espécie aumentou a produção de compostos secundários nas folhas e de taninos nas flores, o que reduziu não só a florivoria, mas o roubo de néctar por parte do pilhadores.

Em um experimento realizado com *Phlox hirsuta* E. E. Nelson (Polemoniaceae) foi verificado que à medida que o display floral aumentava, maior era a florivoria e, consequentemente, menor era a visita de polinizadores, devido às alterações no tamanho e na cor da corola. Vale salientar que o tamanho da corola não era influenciado pela florivoria, mas pela densidade floral de outras espécies na área estudada (RUANE; ROTZIN; CONGLETON, 2014). Experimentos com a espécie *Solanum peruvianum* L. (Solanaceae) demonstraram que a herbivoria real e simulada (aplicação de metil jasmonato) reduziu a atratividade floral, reduzindo o número de visitas de polinizadores. Foi verificado que a diminuição da polinização não ocorreu devido aos danos florais, mas devido ao fato de que as abelhas solitárias que polinizam essas flores utilizavam esse volátil floral como indicativo para evitar inflorescências danificadas, demonstrando o custo ecológico causado pela herbivoria (KESSLER; HALITSCHKE; POVEDA, 2011).

Um estudo com *Biscutella laevigata* L. (Brassicaceae) revelou que a florivoria induziu a planta a produzir β-Ocimeno, um volátil responsável por atrair insetos polinizadores, mas que também atraiu aranhas *Thomisus onustus* e estas apresentam comportamento de predar os florívoros (KNAUER; BAKHTIARI; SCHIESTL, 2018); eles também relataram que essa planta é adaptada a atrair essas aranhas predadoras quando são infestadas pelos florívoros. Mesmo que *T. onustus* também prede polinizadores, quase 90% dos insetos capturados eram florívoros, o que demonstrou a eficiência das aranhas em controlar a população de florívoros.

b) Planta-aranha

A interação planta-animal pode seguir um caminho diferente quando se inclui um terceiro nível trófico, que corresponde ao predador. A predação faz parte das interações consumidor-recurso, onde o predador retira a presa de sua população para nutrir-se e, assim, reproduzir-se (BEGON; TOWNSEND; HARPER, 2007). Diversos invertebrados predadores podem alimentar-se de insetos que visitam flores. Alguns desses invertebrados mais comuns são mantídeos e aracnídeos, os quais podem consumir fitófagos, parasitoides e polinizadores (HALAJ; WISE, 2001; GRISOLIA, 2014). As aranhas utilizam diferentes estratégias para a captura de suas presas e uma dessas estratégias é a do tipo senta-e-espera, comum entre espécies da família Thomisidae, as quais não produzem teias, mas ficam paradas à espera da presa e do momento de captura (UETZ, 1992). Essas espécies comumente forrageiam sob as flores, ficando posicionadas abaixo das pétalas e/ou camufladas sob as mesmas (GAVINI; QUINTERO; TADEY, 2019). A camuflagem constitui uma das diversas estratégias utilizadas por aranhas Thomisidae para atrair suas presas. Algumas espécies utilizam suas pernas para assemelhar-se a estruturas florais, posicionando seus membros anteriores perpendicularmente ao corpo, podendo ser confundidas com brotos ou flores; dessa forma, a maioria dos visitantes florais são incapazes de perceber a presença dessas aranhas (NOVO; SOUZA; CASTRO, 2010). Outras, utilizam as fragrâncias florais para atrair visitantes e predá-los, como o eugenol, um volátil floral com função de atrair visitantes florais; portanto as aranhas usam esse volátil para determinar seus locais de caça (KRELL; KRÄMER, 1998). Heiling *et al*. (2004)

observaram que as abelhas *Apis mellifera* usam o odor para eleger as flores de melhor qualidade, enquanto que as aranhas *Thomisus spectabilis* utilizam-se deste comportamento para selecionar essas flores e assim predar estas abelhas. Muitas aranhas são capazes de se camuflar pela cor, inclusive, aumentando o número de visitantes, polinizadores e florívoros, aumentando a polinização (WELTI; PUTNAM; JOERN, 2016). Um estudo com aranhas Thomisidae australianas relata que estes predadores são capazes de refletir em ultravioleta e variar suas cores para aumentar a atração de visitantes florais e, dessa forma, predá-los (LLANDRES *et al*., 2011).

A presença de aranhas em flores pode causar efeitos indiretos no sucesso reprodutivo da planta e, em decorrência da amplitude de presas as quais espécies de Thomisidae usam na sua alimentação, esses efeitos podem ser negativos (quando se alimentam de polinizadores) (DEL-CLARO *et al*., 2013), positivos (ao alimentar-se de florívoros e pilhadores) (ROMERO; VASCONCELLOS-NETO, 2003) ou apresentar um efeito neutro em relação à planta (GAVINI; QUINTERO; TADEY, 2019).

Há várias evidências dos efeitos negativos que as aranhas causam ao predar os visitantes florais. A presença de aranhas pode ocasionar comportamento de refugo e evitação por insetos menores, como moscas e pequenas abelhas, mas é indiferente para abelhas maiores, como as do gênero *Xylocopa* (BRECHBÜHL; KROPF; BACHER, 2010). Um experimento simulou tentativas de ataques de aranhas em abelhas que forrageavam flores de baixa e alta recompensa; as abelhas que visitavam flores de baixa recompensa, interrompiam o forrageamento após o ataque; entretanto, as abelhas que visitavam flores de alta recompensa, tendiam a mudar suas rotas e visitar flores de baixa recompensa, como uma estratégia de segurança; dessa forma, foi demonstrado que as abelhas podem mudar suas rotas de forrageamento para proteger-se, mesmo que isso implique na qualidade do recurso coletado (JONES; DORNHAUS, 2011). Um resultado semelhante a este foi encontrado por Dukas (2001) em um experimento com *Apis*, onde foi observado que, ao sofrer uma tentativa falha de predação (simulada pelos pesquisadores), essa abelha optava por flores livres de aranhas, porém com néctar de baixa qualidade, em vez de flores com recompensas de alta qualidade, porém com aranhas presentes, o que indica que essas abelhas possuem um comportamento “antipredador”. A presença de aranhas Thomisidae em flores de *Leucanthemum vulgare* (Vaill.) Lam. (Asteraceae) reduziu o número de visitas e o tempo que os polinizadores permaneciam nas flores, gerando um efeito em cascata que resultou na redução de 17% na formação de frutos e sementes (SUTTLE, 2003).

Quanto aos efeitos positivos, Romero e Vasconcellos-Neto (2003), em um experimento com flores de *Trichogoniopsis adenantha* (DC) (Asteraceae), observaram que, mesmo as aranhas *Misumenops argenteus* (Thomisidae) predando alguns polinizadores (8%), a maior parte de suas presas era composta de herbívoros (43,5%), o que demonstra o eficiente controle top-down realizado por estas aranhas, ocasionando a redução da herbivoria na população. De maneira ainda mais indireta, mas que pode interferir no sucesso do vegetal, Carter e Rypstra (1995) constataram que a presença de aranhas *Achaearanea tepidariorum* (Theridiidae) reduziu os danos causados pelos herbívoros às folhas de *Glycine max* (L.) Merrill (Fabaceae), aumentando a biomassa das plantas e, em contrapartida, em folhas cujas aranhas foram removidas, os danos foram elevados. Em relação às Thomisidae, algumas pesquisas demonstram que estas aranhas são capazes de selecionar suas presas, o que foi constatado no estudo de Marrero *et al*. (2013) ao estudarem essa interação em 28 plantas entomófilas perceberam que as aranhas predavam principalmente dípteros, considerados ineficientes polinizadores das plantas estudadas, mas predavam também himenópteros (principais polinizadores) em menor grau. No momento em que os dípteros foram removidos da rede de interação, as visitas de himenópteros aumentaram, o que beneficiou a produtividade das espécies vegetais, mesmo com o consumo dos polinizadores pelas aranhas, demonstrando que, além de afastar ou predar antagonistas, as aranhas Thomisidae podem aumentar a taxa de polinização. Welti *et al*. (2016) constataram que as aranhas Thomisidae serviam como atrativos para polinizadores, provavelmente devido à reflexão ultravioleta ou atração pelo odor, o que culminou em sementes com pesos maiores que as oriundas do grupo controle, evidenciando que a presença de aranhas aumenta o número de visitas e a polinização, favorecendo o sucesso reprodutivo.

Os efeitos neutros da presença das aranhas Thomisidae foram relatados por alguns autores, como em um estudo sobre tripla interação entre flores de *Anemone multifida* Poir. S. Hoot (Ranunculaceae), seus visitantes florais e *Misumenops pallidus* (Thomisidae), onde foi observado que, mesmo as aranhas predando alguns polinizadores e florívoros, os efeitos top-down foram neutros, uma vez que a baixa densidade populacional das aranhas fez com que não causasse efeito significativo na população vegetal, já que não reduziu o número de visitas nem a quantidade e qualidade dos frutos e sementes formados (GAVINI; QUINTERO; TADEY, 2019). Coutinho *et al*. (2012) também constataram que a presença de aranhas Thomisidae em flores de *Byrsonima microphylla* A. Juss. (Malpighiaceae) reduziu o número de frutos formados por estas flores, mas a baixa densidade das aranhas não surtiu efeito significativo na população como um todo. Em experimento abordando a interação planta-visitantes florais-aranhas em flores de *Chamaecrista ramosa* (Vog.) H.S. Irwin e Barneby (Leguminosae), Telles *et al*. (2018) observaram que a presença de aranhas não impediu a visita das abelhas *Xylocopa* (polinizadores), porém, elas predavam e diminuíam a frequência de visitas das abelhas *Trigona* (pilhadores), o que diminuiu o número de anteras danificadas. Nesse estudo, os autores constataram que não houve diferença significativa no sucesso reprodutivo das flores com e sem aranhas. Importante salientar que o tamanho dos polinizadores, principalmente abelhas, influencia na tentativa de predação das aranhas Thomisidae, uma vez que abelhas de grande porte, como *Xylocopa* sp. e *Bombus* sp., sofrem menor predação que as abelhas menores (DUKAS; MORSE, 2003).

Contudo, é importante ressaltar que a maior parte dos estudos aborda apenas dupla ou tripla interação, seja esta aranhas-polinizadores, abordando como a presença das aranhas influencia no comportamento dos polinizadores (BRECHBÜHL; KROPF; BACHER, 2010); flores-polinizadores-aranhas, que além do efeito direto das aranhas sobre os visitantes florais, aborda o efeito indireto no sucesso reprodutivo da planta (HIGGINSON; RUXTON, 2010). Recentemente, Knauer *et al*. (2018) realizaram pesquisa que envolveu três níveis tróficos, porém, com polinizadores e florívoros no segundo nível. Os autores relataram que a presença de aranhas pode controlar a população de florívoros em flores de *Biscutella laevigata* L. (Brassicaceae). Indivíduos florivorados de *B. laevigata* produziam uma substância volátil que atraia as aranhas e estas consumiam ou afugentava os florívoros. Knauer *et al*. (2018), embora não tenham trazido informações mais aprofundadas em relação aos visitantes florais (se polinizadores ou pilhadores e como reagiam à presença dos predadores), informaram que as visitas foram reduzidas em flores com a presença de aranhas.

Por conseguinte, é possível perceber que mesmo com vários estudos realizados (citados acima), ainda há diversas lacunas a serem preenchidas, seja nas interações polinizador-florívoro (KESSLER; HALITSCHKE; POVEDA, 2011), como nas tripla-interações e seus impactos para a manutenção da comunidade (ROCHA *et al*., 2006), além de compreender melhor o efeito top-down de forma contínua, e não isolada, dando mais detalhes de como ocorre nas triplas-interações e dos impactos por este controle gerados (MORAN; SCHEIDLER, 2002).

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ARTIGO 1

TROPHIC INTERACTIONS BETWEEN PLANTS, POLLINATORS, FLORIVORES AND SPIDERS: A META-ANALYSIS

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Trophic interactions between plants, pollinators, florivores and spiders: a meta-analysis

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ABSTRACT

The multi-trophic relationships between plants, pollinators, florivores and spiders that predate floral visitors influence plant reproductive success, and some plant characteristics influence the choices of these animals. This study aimed to integrate the global data on that multi-trophic relationships, and answer the following questions: 1) How are the studies distributed over time and biomes? 2) Which are the groups of plants, pollinators, florivores, spiders and preyed groups recorded? 3) Plant features explain the presence of florivores and spiders? 5) What is the effect of spiders on fruit set? A systematic literature review was carried out in the main scholarly databases and, from the returned studies, it was extracted year of publication, biome, recorded organisms, and plant characteristics. The relationship between plant characteristics and the presence of florivores and spiders was statistically tested, as well as the effect of the presence of spiders on fruit production. The number of studies has grown since 2000 and were conducted mainly in tropical biomes. The most frequently observed groups of plants, pollinators, florivores, spiders and preys were herbaceous-Asteraceae, Hymenoptera, Coleoptera, Thomisidae and Diptera. The choice of flowers by florivores was explained by floral longevity and pollination unit, and spiders by habit, symmetry, shape, pollination unit and resource. Spiders had a neutral effect on fruit set, indicating the study scale influence the result. Spider choices enhance the possibility of predation. An

important gap of knowledge is the influence of florivores in fruit set. Studies that follow standardized methodologies are necessary.

1. INTRODUCTION

Plant-animal interactions constitute an important component for biodiversity maintenance in all biomes. Among those interactions, pollination by insets is highly relevant since it allows the reproduction of most plant species (Crupinski et al. 2017). Pollination may be negatively influenced by florivory and / or pollinator predators, especially spiders of the family Thomisidae (crab spiders, Uetz 1992). Florivores and spiders, by influencing pollination, can directly or indirectly affect fruit set and, consequently, reduce plant reproductive success (Gonçalves-Souza et al. 2008). Given their ecological importance, multitrophic relationships involving plants, pollinators, florivores and spiders have been ground the literature, with great advances in recent decades (Lima et al. 2013). Such studies indicate that the evolution of those multitrophic interactions comes from adaptations of the organisms (Leroy et al. 2019).

Floral characteristics such as floral display (e.g. Brody and Mitchell 1997; Ruane et al. 2014), shape (Galen and Cuba 2001), longevity (Teixido et al. 2011) and resources (Adler and Bronstein 2004) are resulted from selective pressures favoring the attraction of pollinators (Knauer et al. 2018), but may also attract florivores (Lim and Raguso 2017). The damage caused by florivory can directly impact plant reproduction because of gynoecium and androecium consumption, or indirectly, by the consumption of floral parts and / or resources, which decrease the attraction and reward offered to pollinators (Gorden and Adler 2016). On the one hand, if there is a selection of physical and chemical components in plants that repel or decrease the performance of florivores (Couture et al. 2010), on the other hand there is a selection of characteristics of florivores that can help to overcome these imposed difficulties, such as developing resistance to secondary metabolites (Hartmann and Ober 2000) or storing them for self-defense (Städler and Reifenrath 2009).

In the case of crab spiders, the choice of predation sites seems to be influenced by characteristics that also influence the choice of pollinators and florivores, such as habit (Louda 1982), floral display (Théry and Casas 2002), color and flower odor (Heiling et al. 2004). In addition, spiders camouflage in plants by choosing foraging sites with similar colors to their bodies (Théry and Casas 2002), or even by changing their colors in a way that best camouflage in flowers and inflorescences (Oxford and Gillespie 1998). Spiders can also reflect UV light, adjusting their reflectance properties that attract specific preys (Llandres et al. 2011). Finally, Thomisidae spiders choose flowers whose odor also attract pollinators (Heiling et al. 2004).

The presence of spiders can benefit the plant when they feed on florivores and, consequently, reduce the damage on flowers (Gavini et al. 2019). On the other hand, spiders have a negative effect on plants when they feed on pollinators, or when pollinators avoid visiting flowers with spiders (anti-predatory behavior, Dukas 2001). In both cases, there will be a reduction in the frequency of pollinators' visits, which may reduce fruit and/or seed set (Coutinho et al. 2012). Finally, spiders can have a neutral effect, that is, they do not interfere in plant reproductive performance. The effect of spiders on plant reproduction (positive, negative, or neutral) depends mainly on spiders' density in plant populations (Coutinho et al. 2012).

Although there are many studies that address the multitrophic relations between flowers, pollinators, florivorous and spiders in several biomes, there are no studies that integrate those data, pointing out the main results and knowledge gaps. This study aimed to integrate the global data published in scientific journals and to test some ecological hypotheses on the complex relationships between those organisms. First, we tested the hypotheses that the number of studies increased over time and that there is a difference in the frequency of plant habits in the studies. We also reported the percentage of studies regarding the biomes, the scopes of the articles and the groups of plants, pollinators, florivores and spiders studied. Then, considering that the evolution of multitrophic interactions comes from adaptations of the interacting organisms (Leroy et al. 2019), we tested the hypotheses that plant habit and floral attributes explain the presence of florivores and the presence of spiders. Because the main pollinators of Angiosperms are bees (Crupinski et al. 2017), we also tested the hypothesis that bees are the most predated pollinators. Finally, we tested the hypothesis that the presence of spiders in flowers affects fruit production.

2. MATERIALS AND METHODS

A systematic literature review was carried out (without year restrictions; last search in October 2020) at Web of ScienceTM (https://www.webofknowledge.com), Scopus (www.scopus.com), ScienceDirect® (https://www.sciencedirect.com) and SciELO (https://www.scielo.org/) scholarly databases. The following keyword combinations were used: "florivory AND spider", "pollination AND spider", "pollinator AND predation risk", "pollinator AND predation risk", "pollinator AND predation risk", "plant reproduction AND spider", " flower AND spider araneae", "plant fitness AND spider araneae". The following informations were extracted from each study: year of publication, biome (according to Raven et al. 2014), plants', spiders', pollinators' and florivores' species, groups of preyed animals, plant characteristics (habit, pollination unit, and floral symmetry, shape, color, odor, longevity), and fruit set in flowers with and without spiders.

To test the hypothesis that studies have been increasing through the years, a Spearman correlation was realized with the average number of articles for year. In addition, a test G was realized to test which is the most frequent habitat in the studies. To test the hypotheses that the occurrence of spiders and the occurrence of florivores (response variables) are associated with the predictor variables habit, pollination unit and floral attributes, we used a generalized linear model analysis with the glm function at R software (R Core Team 2019). As the response variables of the two generated models are binary (i.e., presence / absence), then the distribution of errors was modeled using the Binomial family with the logit link function. Two logistic regressions were run to estimate the probability of finding a spider (in one model) and a florivore (in other model) according to the predictor variables.

To define whether spiders have an influence on fruit set, it was used the *metabin* (Meta-Analysis of Binary Outcome Data) function of the *meta* package (Balduzzi et al. 2019) to perform a meta-analysis of randomic effect. The proportions of fruit set in the presence and absence of spiders were used to define the odds ratio as the effect size. Mantel-Haenszel estimator was used as a method to adjust the model, assuming a random effect because the environmental and biotic variations at each location where each study was conducted increase the variation in the effect size (Cooper et al. 2019). After running the initial model, the or2smd function of the meta package was used (Balduzzi et al. 2019) to convert the values of Odds ratios into Standadized Mean Difference (SMD). The odds ratio values were converted because the SMD produces more intuitive values, favoring the interpretation of the effect size, and allows comparisons with other studies that also used this effect size. The limit of the 95% confidence interval was used as a criterion to interpret significant differences of each species (see Hedges and Olkin 1985). Within the 50 plant species cited in the studies, there was information of fruit set with and without spiders only for eight species. In most cases, records of fruit production were discarded because the observation scales (i.e., flowers, inflorescences, or individuals) varied among studies.

3. RESULTS

A total of 38 studies had information of interest for this study. The studies started in 1970's decade and increased along the years (rs = 0.60, t = 3,381, p = 0.003). Most studies (81.57%) were published in the 2000 decade. Herbaceous plants were the most representative plant habit (herbaceous *vs.* subshrub: G = 16.37, g.l. = 1, p <0.0001; herbaceous *vs.* shrub: G = 16.37, g.l. = 1, p <0.0001 and herbaceous *vs.* tree: G = 38.11, g.l. = 1, p <0.001). Sub-shrubs and shrubs, in turn, were significantly more representative than trees (G = 6,197, g.l. = 1, p = 0.0128). Rainforests (n = 8; 22.23%) were the most studied biomes, followed by Temperate Mixed Forests (n = 7; 19.44%) and Arctic Tundra (n = 5; 13.89%). Few studies were performed in other biomes such as Scrub (n = 4; 11.12%), Taiga (n = 3; 8.33%), Temperate Deciduous Forests, Savannas and Grasslands (n = 2; 5.55% each); Deciduous Tropical Forests, Coniferous Forests, Alpine Tundra Forests and Mountain Forests (n = 1; 2.18% each). The revised studies addressed pollinator-spider interactions (n = 17; 44.74%), flower-pollinator-spider (n = 11; 28.95%), pollinator-florivorous-spider (n = 5; 13.16%), flower-spider (n = 3; 7.89%) and flower-pollinator-florivore-spider (n = 2; 5.26).

Asteraceae was the most studied plant family, both in the number of species (15 or 30%) and number of studies (n = 12; 31.58%). Also, Asteraceae was the most representative group in studies regarding pollinator-spider (n = 6; 35.29%) as well as pollinator-florivore-spider interactions (n = 2; 40%).

Hymenoptera was the most frequent order of pollinators observed (n = 51; 50.49%), followed by Diptera (n = 29; 28.71%) and Lepidoptera (n = 17; 16.83%). Among the hymenopterans, bees were the most representative group (n = 38; 84.44%). Only 15 pollinators were identified until the species level, and, among them, *Apis mellifera* was the most representative (15.38%). Similarly, only eight dipteran species were identified, and belonged to the Syrphidae family (n = 8; 47.06%), followed by Drosophilidae and Chironomidae (n = 3; 17.65% each). Three Lepidoptera families were cited, and Nymphalidae was the most representative family (n = 8; 72.73%), followed by Erebidae (n = 2; 18.18%) and Pieridae (n = 1; 9.09%).

Seven studies (18.42%) addressed florivores in the tritrophic interaction. The most observed florivores were Coleoptera (n = 20; 38.46%), followed by Lepidoptera (n = 11; 21.15%) and Diptera (n = 7; 13.46%). The 16 identified beetles belong to four families, and Chrysomelidae was the most representative (n = 7; 43.75%), followed by Cantharidae, Curculionidae and Phalacridae (n = 3; 18.75% each). Lepidopteran florivores belong to four families, and Noctuidae was the most representative (n = 3; 37.5%), followed by Geometridae and Pieridae (n = 2; 25% each) and

Plutellidae (n = 1; 12.5 %). Dipterans florivorous belong to Tephritidae (n = 3; 42.86%), Cecidomyiidae and Agromyzidae (n = 2; 28.57% each). Among spiders, those from the family Thomisidae were the most studied (n = 16; 64%), followed by those species of Araneidae and Oxyopidae (n = 3; 12% each). The other families (Lycosidae, Philodromidae and Salticidae) were mentioned in one study each (4%).

Florivores were significantly more frequent in isolated flowers than in flowers arranged in inflorescences (LR X2 = 3,714, df = 1, P = 0.05), and in flowers that lasted between 1-5 days (LR X2 = 12.012, df = 2, P = 0.002464). The other plant characteristics were not significant, i.e., plant habit (LR X2 = 5.2256, df = 3, P = 0.156), flower symmetry (LR X2 = 0.26404, df = 1, P = 0.6074), shape (LR X2 = 1.6335, df = 2, P = 0.4419), color (LR X2 = 3.5058, df = 3, P = 0.32), odor (LR X2 = 0.085879, df = 1, P = 0.7695) and resources (LR X2 = 0.023385, df = 1 , P = 0.8785).

Spiders were significantly more commonly observed in shrubs than in other plant habits (LR X^2 = 9.717, *df* = 3, P = 0.02113), in actinomorphic than in zygomorphic flowers (LR X^2 = 5.2009, *df* = 1, P = 0.02257), and in disc-shaped flowers when compared to other flower shapes (LR X^2 = 11.275, *df* = 2, P = 0.003562). Although inflorescences were more commonly observed than isolated flowers, the probability of finding a spider in individual flowers was significantly higher (LR X2 = 4,972, df = 1, P = 0.02576). Spiders were significantly more often reported in nectariferous flowers that in flowers that offer only pollen (LR X2 = 6.6772, df = 1, P = 0.009766). Although there was a greater number of plants whose flowers last up to one day, flower longevity did not explain the presence of spiders (LR X2 = 0.45691, df = 2, P = 0.7958). Similarly, although there was a higher number of spiders in pink / lilac flowers, the color was not significant (LR X2 = 1.4382, df = 3, P = 0.6966), as well as the presence of odor (LR X2 = 2.8113, df = 1, P = 0.0936). The preys belong to the orders Diptera (52.71%) and Hymenoptera (18,85%), and the former was significantly more frequently cited (G = 140.86; g.l. = 1; p <0.001). The meta-analysis showed a significant heterogeneity in fruit set in flowers with and without spiders (I^2 = 75%, τ^2 = 0,154, p < 0,01). If on one hand Quintero et al. (2015) and Diniz et al. (2012) recorded a significant higher fruit set in flowers with spiders, on the other hand Ott et al. (1998) observed an inverse significant result. In the other studies of the meta-analysis, fruit set was slightly higher in flowers without spiders, but in none of them the difference was significant (p > 0,05) (Fig. 1). The overall mean fruit set in flowers without spiders was relatively higher, however, because of the divergent significant results of Ott et al. (1998), the difference was not significant (SMD = -0.13; $IC_{95\%}$ = -0.46-0.19; p < 0.05, Fig. 1).

4. DISCUSSION

In our systematic revision, it was found a significant increasing number of studies along years, indicating increased academic interest in studies concerning the interaction among plant-pollination-florivory-spiders in the last 50 years. Despite of that, it was observed that the researchers converged their effort to herbaceous species, once it was significantly the most plant group studied. The higher number of studies concerning herbaceous plant species is indeed expected, because of the friendly field procedures during the meticulous field observation, when compared to trees, for example. The revision also showed that the studies reported animal-plant interactions mainly in tropical forests, addressing the pollinator-spider interaction with high frequency of Asteraceae species. Hymenopterans (bees and wasps), dipterans (from Syrphidae family) and Thomisidae were, respectively, the most frequently recorded pollinators, florivorous and spiders. Concerning the ecological approach, the compiled data showed that a) habit and/or a floral attribute significantly explains the presence of florivores (explained by the floral longevity and pollination unit) and spiders (explained by habit, symmetry, floral shape, offered resource and pollination unit) in the plants, and b) the bees are not significatively the most predated pollinators. Finally, the meta-analysis showed that the presence of spiders does not affect the overall mean of fruit production.

Floral attributes that attract pollinators can also draw the attention of antagonists such as florivores (Harder and Johnson 2005; Sowell and Wolfe 2010; Alves-Silva et al. 2013; Eilers et al. 2021). In this study, the preference of these animals for flowers of greater longevity can be justified by the fact that they can explore the resource for a longer time. This condition can also be emphasized if we consider that the highest percentage of florivores observed were coleopterans, which can use various floral whorls as resources (MüllerSchärer and Brown 1995). Teixido et al. (2011) reported that the incidence of florivory in flowers lasting three or more days can be from 25% to 67% when compared to those of lesser longevity and these authors verified a higher frequency of ants and coleopterans among the flowers of *Cistus ladanifer* (Cistaceae). Regarding the preference for individual flowers, the present study does not allow an accurate interpretation, but the trophic relationship between individual flowers or inflorescences and animals will probably be related mainly to flower size, a topic that was already well documented (see references in Teixido et al. 2011; McCall and Barr 2012). However, the trophic relationship envolving pollination unit, floral size or flowering rate is still little known.

The trend of occurrence of Thomisidae spiders in shrub species was also found by Rocha-Filho and Rinaldi (2011). These authors found that at least two of the studied shrub species housed about 10-17% of the total species of Thomisidae spiders collected. Li et al. (2013), found a high significant difference of Thomisidae spiders in shrub species in relation to other habits, suggesting a positive response of these spiders to this habit. The results emphasize how much research involving plant-pollinator-spider may be underestimated, since the largest number of studies involved herbaceous to the detriment of other habits. Floral attributes have a strong influence on the choices spiders by foraging sites because they increase the potential for prey capture, especially pollinators (Heiling et al. 2004). Pollination unit, flower symmetry, shape, resource also contribute positively to the spiders' permanence in flowers. It is then possible to expect that actinomorphic, disc shaped, individual and nectariferous flowers may be the most attractive for pollinators and, consequently, for spiders. For example, bees have an innate preference for actinomorphic flowers, since associate them with better rewards (Wignall et al. 2006). Additionally, disc-shaped flowers attract a wide range of generalist insects, including several small species, since they have easy access to the nectar, which is a common reward of disc-shaped flowers (Arango et al. 2012; Moyroud and Glover 2017). Although isolated flowers are not the attribute that leads to a greater attraction of pollinators (see references in Teixido et al. 2011), it may be more associated with an important site for spiders, since it reduces the randomness in the choice of flowers by pollinators (Moyroud and Glover 2017), maximizing the predation success rate (Schmidt et al. 2014). Thus, the main prey of spiders consists of small-sized, generalist insects (Marrero et al. 2013).

Although the main preyed pollinators were dipterans, differently from what was expected in our hypothesis, it confirms the trend towards small-sized, generalist insects as the main preys of spiders. Marrero et al. (2013) found the dipterans constituted the main prey for Thomisidae spiders that in the studied community. When removing this group of insects from the community interaction network, there was a decrease in the richness of spider species. The authors reported that the choice of spiders was related to the most vulnerable floral visitors, that is, stingless, small-sized insects with delicate cuticles.

Although a negative relationship between the occurrence of spiders in flowers and the number of fruits produced was expected, it was demonstrated that, in the general average of the studies, this relationship was not significant. In general, some authors bring information that the presence of spiders in flowers can have negative, positive effects (Romero and Vasconcellos-Neto 2003) or neutral effects (Gavini et al. 2019) when related to fruit set. Gavini et al. (2019), in their study with *Anemone multifida* Poir (Ranunculaceae), pointed out that the neutral effect may be associated with a generalist feeding behavior (which was also evidenced in this survey), camouflage strategies and low population abundance. In addition, spiders may have a low rate of predation since they take a time consuming a single prey (Dukas and Morse 2005). Thus, it is possible to conclude that, even if there is a negative or positive effect of spiders upon fruit set locally, the effect may not be significant in a broad context. It is important to highlight the few amount of appropriate data for a meta-analysis, relating plant vs. plant reproductive success. presence of spiders in flowers. There is still a need for efforts in the collection and standardization of those information for a better and more accurate understanding of the ecological role of spiders in plants.

5. CONCLUSIONS

The study brings advances in the theoretical body of investigations regarding interactions between plants, pollinators, florivores and spiders, demonstrating how much these studies have grown over the years, especially with herbaceous species and in tropical forests. It was clear that the choice of flowers by florivores and spiders does not occur randomly, since some characteristics explained their presence in the flowers (floral longevity and pollination unit for florivores and habit, symmetry, shape, pollination unit and resource floral for spiders). In relation to pollinator-spider interactions, dipterans were the main prey, although bees are commonly the most frequent pollinators in plant communities. An important gap of knowledge was identified: studies including florivores. It was not demonstrated a significant effect of the presence of spiders on fruit production, indicating that, in a general context, spiders have a neutral effect on the reproductive success of plants. Most studies do not provide compatible and / or appropriate information for the application of a meta-analysis. Therefore, new research efforts following standardized methodologies are necessary.

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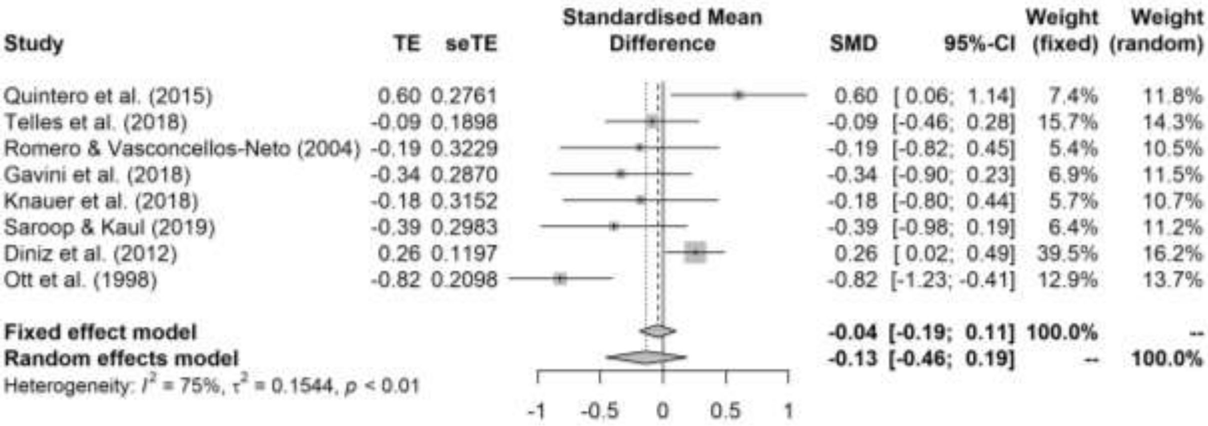

Fig. 1 Mean Standardized difference of fruit set in flowers with and without spiders recorded in studies returned from a global literature review.

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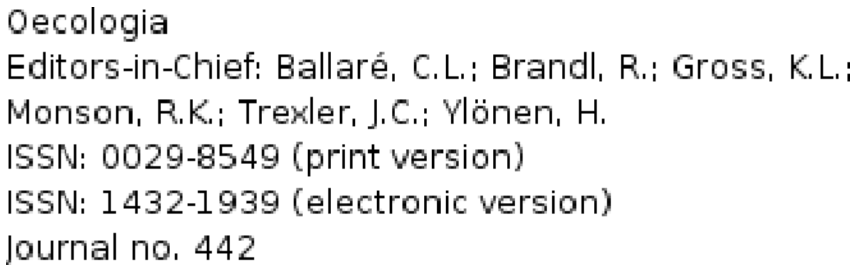

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