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THE POTENTIAL OF PLANTS TO MEDIATE THE INTERACTION BETWEEN HERBIVORY AND POLLINATION

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Abstract: Herbivory may affect important plant traits that mediate the interaction with floral visitors and potential pollinators with consequences to fruit and seed production. These may occur through varied mechanisms, ranging from a trade-off in resource allocation for defense and reproduction, to pleiotropic effects in the biosynthesis of secondary compounds for plant defense and floral attractiveness. The subject has been receiving attention and is leading to new perspectives in the study of ecology and evolution of insect-plant interactions. Here our main goal is to briefly review the scientific literature and discuss theoretical aspects of plant mediation of interactions between herbivores and pollinators. We conducted an extensive but non-systematic search for literature on the main theme “effects of herbivory on floral visitors and pollination”. We found experimental studies and reviews reporting that foliar and floral herbivory usually change floral traits that mediate plant-pollinator interactions. The effect of herbivores on floral visitation tend to be neutral or negative, and does not always lead to negative impacts on seed production. These results open a path for new hypotheses on how plants may avoid or compensate for possible ecological costs of herbivory. We suggest that future studies should explore finer mechanisms through which herbivory affects pollination by considering natural history, pollination effectiveness, and the chemical background upon which flowers are presented to pollinators. Such studies will improve our understanding of how indirect effects structure ecological communities and their role in the evolution of plant-animal interactions.

Keywords: floral traits; herbivory costs; induced responses; pollinator attraction; trait-mediated indirect interactions.

INTRODUCTION

An intuitive way of understanding how organisms impact each other is to reduce them to pairs of individuals in direct interaction. The focus on direct interactions had a huge influence on the construction of ecological theory and fostered a trophic bias in how we understand the relationships between organisms (Hairston *et al.* 1960, Paine 1980, Crawley 1993). However, over the last two decades, it has become clear that exclusively considering direct interactions to assess the dynamics and structure of communities is too simplistic (Strauss 1991, Wootton 1994a, Utsumi *et al.* 2010a). Each direct interaction, whether trophic or not, has the potential to indirectly affect other organisms in the community, as well as the interactions they also establish (Stanton 2003, Schmitz 2009, Terry *et al.* 2017). Therefore, indirect ecological effects play an important role as an emergent property of natural communities that connect organisms by non-trophic links (Wootton 1994b).

An indirect ecological effect occurs when the impact of a first organism on a second one is mediated by a third organism or intermediate environmental factor, which transmits the effect (Strauss 1991, Wootton 1994a, Abrams *et al.* 1996). The theoretical construction of this definition is still controversial, as there is no explicit consensus in the literature about the nature of intermediate agents (whether they are only other organisms, or environmental factors should be considered as well), and whether reciprocity is necessary for considering the effect of an ecological interaction (Wootton 1994a, Abrams *et al.* 1996, Schmitz 2009). Faced with such inconsistencies, there is a risk of overestimating the strength of indirect links between organisms, since an effect may flow in only one direction (Werner & Peacor 2003, Terry *et al.* 2017). Therefore, from now on we use the term "indirect effect" and not "indirect interaction".

Mediation is a fundamental process for interpreting the dynamics of indirect ecological effects, because through it we can recognize the mechanisms responsible for the transfer of effects (Wootton 1994a). When the mediator is an abiotic factor (*e.g.*, water), the indirect effect is usually simple and requires changes in environment (*e.g.*, increased water turbidity by the foraging activity of predatory fish, which affects other organisms that are not its prey; Wootton 1994a). On the other hand, when the mediator is another organism, the indirect effects are more complex and require changes either in density (density-mediated indirect effects - DMIE) or in the phenotypic traits of the mediator (trait-mediated indirect effects - TMIE). Considering TMIEs, changes occurs in traits of mediator may be physiological, morphological or behavioral which may have an impact on other organisms with the mediator interacts (Werner & Peacor 2003, Utsumi *et al.* 2010b). An example of TMIE is when herbivore damage changes a plant trait (*e.g.*, leaf chemistry, floral abundance or fruit set) which may affect other herbivores and also pollinators (Lehtilä & Strauss 1997, Utsumi & Ohgushi 2008, Cozzolino *et al.* 2015). These changes themselves and their ecological effects will depend on plant response time and inducibility (*i.e.*, its ability to induce responses to herbivory), which are traits that vary among individuals in the population (Karban & Baldwin 1997, Howe & Jander 2008).

Plant-herbivore interactions represent a suitable system for indirect ecological effects to occur, since herbivory may induce changes in plant traits relevant to their interaction with other organisms (Agrawal & Rutter 1998, Heil 2011, Fatouros *et al.* 2012, Karban 2015, Dicke 2016). Throughout their life, plants interact with a myriad of organisms, both antagonistic and mutualistic, above and below ground (Poveda *et al.* 2005, Del-Claro & Torezan-Silingardi 2009). Which of these interactions will be indirectly affected by herbivory is in part a matter of how plants respond to damage: whether locally or systemically and in a specific or generalized manner (Karban & Baldwin 1997, Boege & Marquis 2005, Karban 2011). In plants whose responses tend to be systemic, generalized, and long-term, indirect effects tend to have a great influence on a wide range of interactions. In some cases, new interactions may be established such as those developed between damaged plants and natural enemies of its herbivores (Price *et al.* 1980, Agrawal & Rutter 1998, Dicke & Baldwin 2010).

Although frequent, most plant-mediated indirect effects on mutualisms are relatively unexplored in the literature, despite the attention given to tritrophic interactions and indirect defenses requiring parasitoids and predators of the herbivores (Dicke & Baldwin 2010, Kessler & Heil 2011, Torezan-Silingardi 2011). An exception are studies addressing the effects of herbivory on pollination, in which herbivores are shown to affect plant reproduction (Strauss *et al.* 1996, Bronstein *et al.* 2007, Adler 2008). This may happen directly through the consumption of flowers, and indirectly through changes in the number, identity and behavior of pollinators in response to effects on floral production and attractiveness (Mothershead & Marquis 2000, Adler & Irwin 2005, Lucas-Barbosa *et al.* 2011, Ferreira & Torezan-Silingardi 2013). There are methodological limitations for exploring such effects, mainly concerning approaches and techniques for detecting its mechanisms. In fact, it may involve trade-offs caused by a conflicting demand of resources for plant growth, defense and reproduction (Herms & Mattson 1992, Kessler

& Halitschke 2009), besides the pleotropic effects of herbivory on plant physiology and gene expression (Johnson *et al.* 2015).

In this paper, the main goal is to synthesize our understanding of the effects of herbivory on pollination and to discuss directions for future research. We specifically address how plants are able to mediate direct and indirect effects between these interactions and highlight some of the mechanisms by which this could happen. We then conclude by identifying gaps in our knowledge, which could contribute towards future research on the ecology and evolution of insect-plant interactions.

MATERIAL AND METHODS

We conducted a search in the scientific literature guided by the broad theme: effects of herbivory on floral visitors and pollination. We selected experimental and theoretical articles, as well as textbooks and did not establish a time-cut for the date of publication, although we have directed the research to include the first studies about the theme. All research was done in a non-systematic way between February 2015 and June 2017. Online databases such as Web of Science, Scopus, and Google Scholar were consulted.

THE POTENTIAL OF PLANTS TO MEDIATE INDIRECT EFFECTS

Any organism that is part of a community has the potential to initiate, mediate or be affected by indirect ecological effects. For plants, this potential, in particular to mediate TMIEs, is most evident because they (1) form the base of most ecosystems and thus connect many interactions throughout their life time; (2) usually they are not entirely consumed by herbivores; and (3) many plants are more long-lived than many of their herbivores. From the first point above, it is implicit that plants develop several ecological interactions with different organisms. These interactions are, upon first inspection, isolated in space when occurring in different plant organs above and below ground (Krupnick *et al.* 1999, Poveda *et al.* 2003, Heil 2011), and time, when they occur at different stages throughout plant ontogeny (Boege & Marquis 2005, Buchanan & Underwood 2013). Changes in plant traits caused by each interaction generate a potential for such interactions to be connected by indirect effects (Denno *et al.* 1995, Denno & Kaplan 2007). The consequences of such indirect effects will be subject to how plants respond to herbivory, which leads to the second point highlighted above.

Grazers, particularly insects, represent a great part of organisms that consume plants (Schoonhoven *et al.* 2005). According to the definition proposed by Crawley (1993) and Begon *et al.* (2007), grazers are all herbivores that damage plant tissues without consuming the plant entirely. Therefore, even after herbivory, damaged plants remain in the community and interact with other organisms. These interactions, simultaneous or subsequent to herbivory, tend to be affected if damage changes population density or plant traits. Density changes should be analyzed from a different perspective, since it is not trivial to determine what constitutes an individual in different plant species. One alternative is to use biomass as a proxy for density. In such cases, herbivores are able to drastically change plant biomass and thus trigger indirect effects to other herbivores and organisms that interact with them (Denno & Kaplan 2007, Ohgushi *et al.* 2007). On the other hand, trait changes may happen due to induced effects in plant morphology or its profile of primary (*i.e.*, plant nutritional status) and secondary (*i.e.*, its palatability, digestibility, toxicity) metabolites. Such changes may hinder or facilitate the damage by other herbivores (Utsumi & Ohgushi 2008, Ramirez & Eubanks 2016) and also affect plant mutualistic interactions, such as pollination (Strauss *et al.* 1999, Johnson *et al.* 2015).

In the specific context of pollination, the direct impact of herbivory on plant survival is added to the effect on their reproduction, meaning that both components of plant fitness will be affected (Bronstein *et al.* 2007, Adler 2008). The subject has received attention in the literature recently, probably due to the importance of pollination for reproduction of many angiosperms (Ollerton *et al.* 2011). This has led to ecological and evolutionary hypotheses on how herbivory and pollination evolved as opposing selective pressures on the same plant traits (Armbruster *et al.* 1997, Kessler &

Halitschke 2009, Lucas-Barbosa 2016). Nowadays, questions on this topic have been about which mechanisms explain the effect of herbivory on pollination, whether this effect is always negative as it appears to be, and whether there are cases in which it may be reciprocal (Bronstein *et al.* 2007, Willmer 2011).

LINKS BETWEEN HERBIVORY AND POLLINATION

When studying the effects of herbivory on pollination and vice versa, one should consider that both interactions are not mutually exclusive. Herbivory is a trophic interaction and pollination is a functional classification of an interaction. Therefore, many pollinators are herbivores as they consume plant tissue and products such as pollen and nectar (Willmer 2011, Rech *et al.* 2014). Thus, pollination may be considered a functional role of some herbivores, whose evolution as a mutualism occurred through mutual exploitation (Foster & Wenseleers 2006, Rech & Brito 2012, Althoff & Segraves 2016). This perspective brings together ecological and evolutionary links between herbivory and pollination that may not be evident. A broader approach indicates that pollinators are subject to plant responses to herbivory, and that herbivores may have an unconsidered effect on the evolution of floral traits (Pellmyr & Thien 1986, Armbruster 1997).

Herbivory negatively affect pollination either by florivory or leaf damage (Bronstein *et al.* 2007, Adler 2008). Florivory is characterized as the consumption of floral tissue, which may decrease the number, quality, and viability of the flowers (McCall & Irwin 2006). The negative impact of florivory on pollination is more intuitive than those caused by leaf consumption, which, among other effects, may redirect the allocation of plant resources towards defense that otherwise could be invested in floral production and attractiveness (Bertness *et al.* 1987, Strauss *et al.* 1996). One mechanism may lead to the other, and treating them separately is often difficult or artificial. Besides direct effects of florivory being the most commonly reported effects of herbivory on pollination (Bronstein *et al.* 2007), indirect effects may be just as relevant, especially for strictly self-incompatible and pollen-limited plants that depend on pollinators for pollen transfer.

Among all the floral traits affected by herbivory, we can identify those specifically related to attractiveness to floral visitors, such as floral size, morphology, color, fragrance, as well as rewards such as nectar and pollen. Herbivory adversely affects floral display so that damaged plants tend to produce fewer and relatively smaller flowers (Karban & Strauss 1993, Lehtilä & Strauss 1997, Mothershead & Marquis 2000). Color, in turn, can be affected by biochemical crosstalk between the production of pigments and defense compounds (see below). Finally, floral fragrance is a blend of volatile organic compounds (VOCs), whose qualitative (compound identity) and quantitative (relative amount of each compound) profile can be affected by herbivory on flowers and leaves (Effmert *et al.* 2008, Kessler & Halitschke 2009, Theis *et al.* 2009, Pareja *et al.* 2012).

Regarding floral rewards, leaf herbivory leads to a decrease in both quantity and quality of nectar and pollen. In the case of nectar, leaf damage can lead to lower volume and lower sugar concentration when compared to plants without leaf damage (Strauss *et al.* 1996, Adler & Irwin 2005, Adler *et al.* 2006). It is important to note that the decrease in nectar quality may occur without any effect on volume (Aizen & Raffaele 1996). For pollen, the effect of leaf herbivory is less explored, though damaged plants can produce flowers with fewer pollen grains, or pollen with worse performance in pollen tube growth (Quesada *et al.* 1995, Mutikainen & Delph 1996).

If changes in floral signals and rewards are the result of lower investment of resources by plants due to the need for investment in defenses, these effects will represent allocation costs of herbivory for the plant. If they lead to a negative impact on the interaction with pollinators and plant reproduction, there would be also an ecological cost of herbivory (Agrawal & Karban 1999). There may be cases where the allocation costs never lead to an ecological cost, and cases where the ecological cost is not necessarily related to a resource allocation trade-off (see Kessler & Halitschke 2009). The latter case happens when nectar and pollen received induced secondary compounds that may be toxic, repellent or deterrent to herbivores, but also to pollinators (Strauss 1997, Adler *et al.* 2006).

MECHANISMS OF PLANT MEDIATED INDIRECT EFFECTS

Despite the evident impact of herbivory on several floral traits, the mechanisms by which herbivores may direct and indirectly affect pollinators are varied and usually complementary (Figure 1). Considering direct effects, the contact of pollinators with herbivores on flowers may decrease the number of approaches, landings, and time spent visiting flowers. The assumption is that floral visitors associate the presence of herbivores with either lower quality flower rewards or competition for resources (McCall & Irwin 2006, Cardel & Koptur 2010). All these possibilities are suggested based on the cognitive abilities of many pollinating insects, particularly bees, in associating floral signals with the presence and quality of rewards on flowers (Srinivasan 2010, Willmer 2011).

Competition for nectar, pollen and other floral rewards, such as essential oils, certainly is an important factor modulating the behavior of non-pollinating floral visitors and potential pollinators. The presence of visitors consuming floral rewards may decrease the chance of visit by others by obstructing access to the flower (interference competition), as well as affecting them indirectly by depleting resources (exploitation competition) (Lohman *et al.* 1996, McCall & Irwin 2006, Temeles *et al.* 2016). The result would be a decrease in the number of landings and less time spent per visit, which can potentially lead to lower pollination rate. There are several other cascading effects on plant reproduction that can be triggered by competition among pollinators, so that the net result should be considered in terms of a balance between pollinator competitive ability and its effectiveness in pollen transfer. The effects of the consumption of floral rewards tend to be worse for plants if they were caused by herbivores that do not pollinate, such as nectar thieves and robbers (Almeida-Soares *et al.* 2010; but see Richardson 2004).

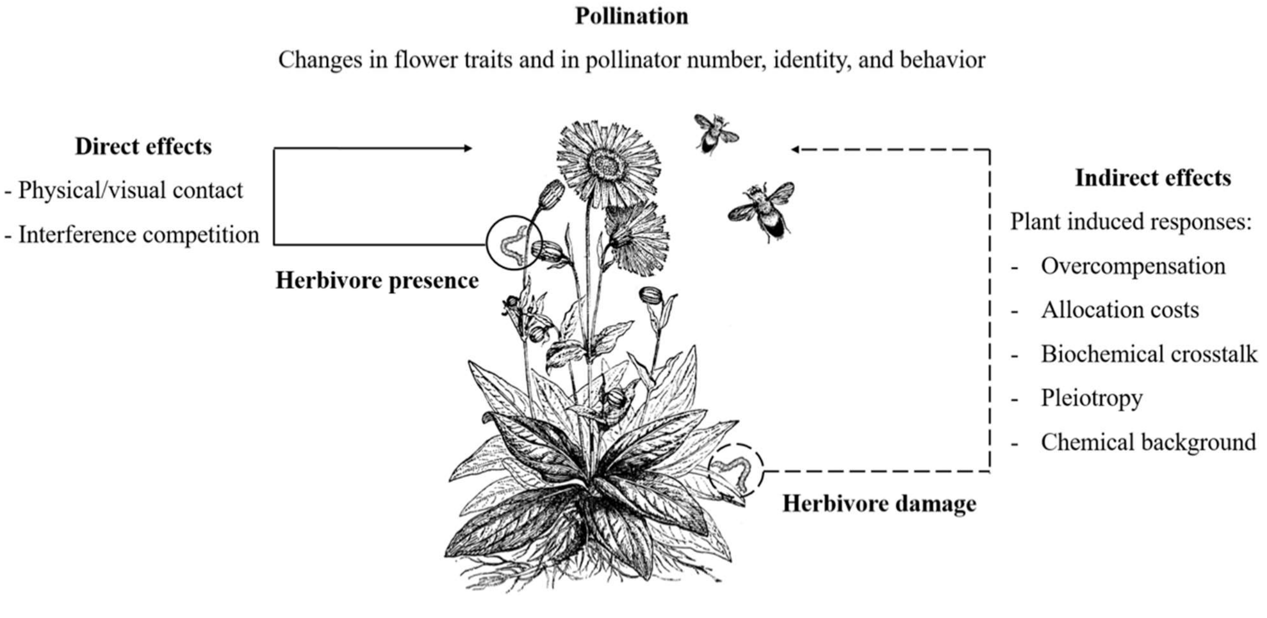

Figure 1. Mechanisms by which herbivory affects floral traits and pollination. This may happen through direct effects (full arrow), which involve the contact of pollinators with herbivores on flowers; and indirect effects (dashed arrow), through competition for floral rewards and or changes to floral signals, rewards and phenology caused by plant induced responses to damage. Illustrations from ClipArt ETC used with the permission of the Florida Center for Instructional Technology, University of South Florida – Bee (Mathews 1902); Caterpillar (Holst 1909); Plant (Whitney 1902).

Regarding overcompensation of herbivory as indirect effect, it is known that plants can respond to herbivory by increasing their productivity through higher growth rate, enhanced production of biomass and reproductive performance (Belsky 1986). Overcompensation is still a poorly understood phenomenon that has been reported in different plant-herbivore systems (Lennartsson *et al.* 1998, Poveda *et al.* 2003), and that may affect pollination by increasing the number of flowers available to interact with pollinators, which means enhancing biomass and consequently reproductive performance (Paige & Whitham 1987, Karban & Baldwin 1997). However, an overcompensation response may increase allocation costs associated to pollination, since plants tend to spend more resources on growth. Moreover, the evolutionary significance of these mechanism is highly debatable since it seems unlikely that there is a selective pressure on plants to attract herbivores that provide such a benefit (Bronstein *et al.* 2007). Despite the controversy, the ecological signifycance of overcompensation should be seen as its potential for indirect effects, which may be expressed at a later time. Due to the temporal lag between herbivore damage and plant overcompensation responses, effects of herbivory on pollination may occur during the next blooming season, or be relatively fast but long lasting (Danell & Bergström 2002).

Throughout their development, plants are exposed to periods of abundance and scarcity of resources that must be invested in growth, as well as resistance and tolerance to herbivores and other biotic and abiotic stresses (Karban & Baldwin 1997, Fornoni *et al.* 2003). Moreover, resources should be invested in the production of flowers, and afterwards for the maintenance of seeds and fruits. When resources are limiting, investment in defense given the need for reproduction may compromise the interaction of the plant with pollinators, either by the production of fewer flowers and/or less attractive flowers with a lower quality or amount of rewards (Strauss *et al.* 1996, Kessler & Halitschke 2009).

As argued by Strauss (1997), allocation costs of herbivory to pollination are difficult to detect, either because there are no costs, the magnitude of these costs are too small, or they are expressed in traits that are not assessed (see Bergelson & Purrington 1996 for the importance of genetic background). The latter case is probably the most common source of herbivory cost underestimation, since most studies address herbivory costs only on the female component of plant fitness (*i.e.*, seed production). Changes in male fitness can be specifically detected by effects in the quantity, size, and performance of pollen. As an example, Quesada *et al.* (1995) detected that individuals of *Cucurbita texana* whose branches were partially defoliated by beetles produced fewer staminate flowers, with fewer pollen grains that were less likely to sire seeds compared to undamaged branches. In turn, Strauss *et al.* (1999) showed that leaf damage on *Brassica rapa* by *Pieris rapae* decreased its petal size and tended to decrease the number of pollen grains produced per flower, but had no effect on pollen grain size.

Investing or not limiting resources in defense, growth or reproduction is also a matter of other factors such as competitive pressure by other plants and the dynamics of herbivore and pollinator communities (Junker *et al.* 2013, Hoffmeister *et al.* 2016). The context becomes more complex when we consider that competition pressure may not be only due to scarce resources in the soil, but also to pollinators (Levin & Anderson 1970). Thus, the most varied strategies of plants to survive herbivory and reproduce may rise, such as investing more in induced defenses, which have a lower allocation and ecological cost compared to constitutive defenses (Karban & Baldwin 1997, Agrawal & Karban 1999). Another possible strategy is that plants change their phenology to ensure that flowers are exposed at times that they are most likely to be pollinated (Freeman *et al.* 2003). Kessler *et al.* (2010) illustrates this temporal decoupling between pollinators and herbivores. *Nicotiana attenuata* damaged by hawkmoth larvae whose adults pollinate them at night produce flowers with reduced emission of volatile attractive to these moths and with morning anthesis, when they are preferentially pollinated by day-active hummingbirds.

Defenses against herbivores and floral attractiveness may be associated in other ways than through resource availability. A possibility that is less explored is the existence of crosstalk between biochemical pathways that produce chemical compounds for both defense and floral attractiveness (*e.g.*, color pigments and fragrance) (Pareja *et al.* 2012). In such a case, these paths may share enzymes or substrates so that the production of one compound affects the production of the other (Bostock 2005). An example is what happens with phenolic compounds: the biochemical pathway that synthetize anthocyanins (flavonoids that confer color to flowers and fruits) produces naringenin, 3-OH flavanones and flavan-3,4-diols as intermediate compounds, which are required for synthesis of defense compounds in transverse paths (flavones, flavonols and tannins, respectively) (Fineblum & Rausher 1997). Therefore, it is reasonable to say that plant chemical systems of defense and floral attractiveness interact so that the induction of defense compounds after damage can compromise or enhance the production of compounds involved in floral attractiveness and vice versa.

The interactions between chemical systems of defense and floral attractiveness is reinforced if both systems are controlled by genes that regulate the expression of only one trait, that is, genes that act only on the production of defensive or floral compounds. However, the same gene may control the expression of both traits, which is called pleiotropy (Simms & Bucher 1996, Irwin *et al.* 2004). This happens, for example, when a gene encodes a certain enzyme that acts early in a biochemical pathway that synthetizes both defense and floral attractive compounds (Johnson *et al.* 2015). Normal activity or even a mutation in these pleiotropic genes will affect the production of the two types of compounds and thus will impact plant traits with different ecological functions. This reinforces the idea that it does not make sense to consider plant traits that function for defense against herbivores and attractiveness of pollinators always independent from each other (Raguso 2009).

Finally, pollinators may use plant chemical signals to find the flowers they visit. These signals are composed of a blend of volatile compounds that can inform pollinators the availability of receptive flowers, as well as the presence and quality of its rewards (Kessler *et al.* 2008, Bruce & Pickett 2011, Kessler *et al.* 2011). Floral fragrance is commonly considered for this propose. However, vegetative volatiles may also be important for the interaction between plants and its pollinators (Caissard *et al.* 2004). According to Willmer (2011), vegetative volatiles that function to attract pollinators, although little explored, are relatively common, and the process may result in a specific relationship in which only leaves produce volatiles attractive to pollinators (Dufaÿ *et al.* 2003). The influence of vegetative volatiles has been also described for insect perception of sex pheromones near host plants (Schmidt-Büsser *et al.* 2009, Trona *et al.* 2010), which reinforces the idea that vegetative volatiles establish an important chemical background for ecological interactions to occur.

As suggested by Raguso (2008), floral volatiles can act synergistically with other floral traits to create a multimodal attractive signal. Thus, it is intuitive to think that traits like floral size, shape and color could also act synergistically with vegetative volatiles from leaves around them on reproductive branches or the whole plant to interact with pollinators. Such complex chemical background upon which flowers are presented could be affected by herbivory in many ways. One of them lies on the potential for leaf damage to change the volatile profile on floral headspace by reducing or inducing the emission of vegetative volatiles (Kessler & Halitschke 2009). This may change the behavior of pollinators that use chemical signals to locate the flowers, thus being more susceptible to changes in these signals. This mechanism is fundamentally different of those in which herbivory affects pollinator behavior through changes on plant resource allocation or pleotropic effects and biochemical crosstalk.

GAPS IN THE KNOWLEDGE AND FUTURE DIRECTIONS

Although most of the papers reviewed report a negative effect of herbivory on pollination, this should not be a generalization. As pointed out by Bronstein *et al.* (2007), herbivory may have neutral or even positive effects on pollination. Positive effects may happen when the herbivore is also an effective pollinator (*e.g.*, figs and fig wasps – Cook & Rasplus 2003; yuccas and yuccas moths – Pellmyr 2003), or when pollination is enhanced by an overcompensation plant response after damage (Paige & Whitham 1987). Moreover, pollinators in a community certainly vary in their resource requirements and respond differently to changes in floral traits (Junker *et al.* 2013, Lemaitre *et al.* 2014). In addition, pollinator species also vary in pollination effectiveness (Olsen 1997, Castro *et al.* 2013, Padyšáková *et al.* 2013), which adds uncertainty to the consequences of indirect effects of herbivory. What is even less considered is the possibility of a change in a community or turnover among pollinators sensitive to changes in flowers, but that do not differ in pollination effectiveness. Therefore, there may be a change in pollinator community without change in pollination outcome (Hoffmeister *et al.* 2016). Considering these possibilities would help us to better understand the ecological costs of herbivory for pollination and for community dynamics.

Among the studies that assessed the effects of herbivory on pollination, most have focused on plants from temperate ecosystems and with few pollinators. Therefore, little is known about effects of herbivory for pollination of tropical plants, particularly those interacting with a wide community of floral visitors. Thus, it would be interesting that future studies explore the direct and indirect effects of herbivory for plants that interact with a greater diversity of pollinators, besides comparing the outcomes for specialized and generalized pollination systems.

Regarding the mechanisms, an approach yet to be explored is how herbivory change the chemical background upon which flowers are presented to pollinators. There can be effects of floral and leaf damage on the synthesis and emission of volatile organic compounds (VOCs) by flowers (Zangerl & Berenbaum 2009, Pareja *et al.* 2012, Cozzolino *et al.* 2015), but also through VOCs emitted after damage by leaves around the flower that become part of the floral headspace (Kessler & Halitschke 2009). Although this approach is relatively new, the idea that vegetative VOCs may impact plant-pollinator interaction has been discussed for almost three decades (Beker *et al.* 1989).

Finally, the herbivore community associated with plants and herbivory patterns should also be assessed in more detail. In natural environments, plants are subject to attack by herbivores that vary in their feeding mode (*e.g.*, sap-suckers and chewers), and in their dietary specificity, ranging from extremely polyphagous to strictly monophagous. This variation may lead to differential effects of herbivory on floral traits, and differential indirect effects on pollination. Knowing the biology of herbivores associated not just with plants in natural systems but in crop systems as well is an important step to detect and interpret indirect ecological effects. As one of the bases for experimental studies, natural history data are indispensable. From them, we establish a broad perspective of ecological interactions in the study systems.

CONCLUSION

We presented a brief review of the scientific literature on how herbivory may affect pollination. We discussed this theme within the perspective of indirect ecological effects caused by plant response to damage, and which elements confer to plants the potential to mediate such effects. The review was carried out for studies published since the theme began to be explored (1980s), and we conclude that the most commonly reported result from experimental studies is a negative effect of herbivory on floral traits that are somehow important for pollinator attraction. Nevertheless, the negative effect on pollinators does not always lead to a negative impact on plant seed set. These results encourage further studies, particularly those that consider differential effects of herbivory on different pollinator taxa that vary in pollination effectiveness. We believe that advances in knowledge on this topic will be enhanced by studies that: (1) use tropical plants that interact with a diverse community of floral visitors as experimental systems; (2) explore new mechanisms of herbivory effects, such as the role of the vegetative volatiles in the communication between plants and pollinators; and that (3) frame their research questions with natural history data, such as specificities of the herbivore community and patterns of damage. Such studies will contribute to the foundation of theoretical ideas that integrate areas of ecology and improve our knowledge about insect-plant interactions.

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