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A meta-analysis of herbivore effects on plant attractiveness to pollinators

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Abstract. Herbivores may directly or indirectly affect plant attractiveness to pollinators. Although several studies have reported on these effects, there is yet no general consensus on the strength and sign of such interactions or their contingency on herbivory features such as the plant tissue attacked. We performed a meta-analysis of studies testing for effects of herbivores on floral traits, plant attractiveness to pollinators, and plant reproductive success. We also assessed whether herbivore effects depended on the plant tissue attacked by herbivores and if real or simulated herbivory was used. We found an overall significant negative effect of herbivores on floral traits, plant attractiveness to pollinators, and plant reproductive success. These effects were, however, contingent on the plant tissue attacked and on whether real or simulated damage was used. Real floral and leaf, but not root, herbivores showed detrimental effects on floral traits and plant attractiveness to pollinators. In addition, real leaf, but not floral or root herbivory, lowered plant reproductive success. Contrastingly, simulated leaf and floral herbivory showed no effect on any of the response variables. These findings help move forward our understanding of the strength and directionality of herbivore effects on plant attractiveness to pollinators and their underlying mechanisms.

Key words: floral traits; herbivory; indirect effect; plant compensation; pollinators; reproductive success; trait-mediated effect.

INTRODUCTION

Herbivores can directly or indirectly affect plant attractiveness to pollinators, and such effects may ultimately influence plant reproductive success (reviewed by Bronstein et al. 2007, Jones and Agrawal 2017). The outcome of these interactions between herbivores and pollinators is variable and ranges from studies showing the expected negative effects of herbivores (Karban and Strauss 1993, Strauss et al. 1996, Lehtilä and Strauss 1997, Barber et al. 2011, 2015), to studies showing positive effects (Ivey and Carr 2005, Zhu et al. 2017), no

effect (Gómez 2005, Pareja et al. 2012), or mixed patterns depending on the identity of the herbivore and pollinator species or guild (Poveda et al. 2003, 2005, Rusman et al. 2018). Thus, although herbivore–pollinator interactions are presumably widespread, there is yet no consensus on the nature (i.e., directionality) and strength of these effects.

Herbivores can influence plant attractiveness to pollinators in multiple and interdependent ways, and these frequently imply negative effects on pollinator attraction and plant reproduction. First, herbivores can directly alter plant attractiveness to pollinators when the latter avoid contact with herbivore-infested flowers or inflorescences ("pollinator avoidance mechanisms"; Lohmann et al. 1996). In these cases, herbivore presence may hinder pollinator access to flowers or signal increased risk of predation (Lohmann et al. 1996, Bronstein et al.

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2007). Second, herbivory may indirectly alter plant attractiveness to pollinators via changes in reproductive (or even vegetative) traits ("plant-mediated mechanisms"; Lehtilä and Strauss 1997, Krupnick and Weis 1999, Mothershead and Marquis 2000). For example, herbivore-damaged plants frequently produce fewer or smaller flowers as well as less nectar and pollen, and these changes may render plants less attractive to pollinators (Jones and Agrawal 2017). Likewise, herbivory can also alter plant reproductive phenology, which may produce plant–pollinator phenological mismatches (Louda and Potvin 1985). On the other hand, there are, however, cases where herbivores can have positive (or neutral) effects on pollinators. For instance, herbivory may indirectly positively affect plant attractiveness to pollinators when plants increase flower production in response to damage (Strauss et al. 2001, Irwin et al. 2008, Schiestl et al. 2014), with this resulting in increased pollinator attraction and this in turn potentially increasing plant reproductive success. Although plant reproductive overcompensation to herbivory is potentially widespread (Garcia and Eubanks 2019), the importance of these positive effects relative to other mechanisms linking herbivores and pollinators (either negatively or positively) is not well understood.

The effects of herbivores on plant attractiveness to pollinators are contingent on several key factors that could explain variable outcomes of these interactions. For example, pollinator traits (e.g., degree of specialization, foraging behavior) are an important determinant of changes in pollinator behavior in response to plant trait changes (Jones and Agrawal 2017). Likewise, the type of plant tissue or organ attacked by herbivores may be equally important and has received some attention in the past (Kessler and Halitschke 2009, Zangerl and Berenbaum 2009). Floral herbivores are expected to have particularly strong impacts on plant attractiveness to pollinators (relative to herbivores attacking other plant parts) because their direct (interference or repellence) and indirect (plant trait mediated) effects on floral visitors are produced by feeding on the same tissues used by pollinators. Accordingly, a quantitative review by Kessler and Halitschke (2009) reported a strong negative effect of floral herbivory on plant attractiveness to pollinators, but neutral and positive effects of leaf and root herbivory, respectively. However, their analysis only included 16 studies (floral herbivory = 4, leaf herbivory = 10, root herbivory = 2), therefore limiting conclusions about the relative importance of effects of herbivores feeding on different plant parts. In addition, the floral traits potentially associated with herbivore effects on plant attractiveness to pollinators and the implications of these effects for plant reproductive success remain to be evaluated.

Here we build from previous work by using a meta-analytical approach to assess the overall strength and sign of herbivore effects on plant attractiveness to pollinators. We also evaluated the effects of herbivores on floral traits

as a potential explanation for changes in pollinator responses, as well as herbivore effects on plant reproductive success to address the potential implications of herbivore–pollinator interactions for plant fitness. Our analysis included studies conducted from 1991 to 2018 testing for effects of damage on flowers, leaves and roots, using either real herbivores or simulated attack, on floral traits (e.g., flower number and size), plant attractiveness to pollinators (e.g., pollinator abundance, diversity, and visitation rates), and plant reproductive success (e.g., fruit and seed number and size). In addressing the above, we provide the most robust assessment to date on the sign and magnitude of herbivore effects on plant attractiveness to pollinators and potential underlying mechanisms and implications for plant fitness.

Material and Methods

Data collection

We carried out an extensive literature search in the ISI Web of Knowledge database using the following search criteria: "(Plant or tree or shrub) and (herbivore or herbivores or herbivorous) and (flower or floral or nectar or inflorescence or pollinator or pollination)." We retained only articles, book chapters, reviews, theses, dissertations, and abstracts published in English. To limit the search to relevant papers, we filtered outputs to consider only the following research areas: plant sciences, environmental sciences, ecology, agriculture, forestry, evolutionary biology, and entomology. The search included the period from 1950 to June 2018. Our initial search yielded 5,074 papers (see the PRISMA flow chart, Appendix S1: Fig. S1). We also surveyed the references in review papers on herbivore effects on floral traits and interactions between herbivores and pollinators in case some studies were not detected by our ISI search, namely: Bronstein et al. (2007), Kessler and Halitschke (2009), Lucas-Barbosa et al. (2011), Lucas-Barbosa (2016), Jogesh et al. (2017), Jones and Agrawal (2017), and Caruso et al. (2019).

Studies retained in our search had to meet the following criteria: (1) that the study reported floral traits and/or pollinator responses associated with plant attractiveness for control plants (undamaged) vs. plants damaged by real herbivores (insects or mammals) or simulated (mechanical) damage, and (2) that the study reported treatment-level means, some measure of variability (i.e., variance, standard error, or standard deviation), and sample sizes in either the text, figures, tables, or appendices. When needed, we extracted data from figures following digitalization using ImageJ 1.51j8 software. After these criteria were applied, the resulting data set consisted of 568 study cases from 88 studies (out of the initial 5,074) from the primary literature (i.e., papers) published between 1991 and 2018 in 36 scientific journals (see list of references in Appendix S2). Together, the selected studies included a total of 68 plant species (23

annual and 45 perennial). In addition to floral traits and responses associated with plant attractiveness to pollinators, we also extracted data on plant reproductive success for studies reporting on pollinator presence. In such studies, herbivore effects on reproductive success can be, at least partly, attributed to pollinator responses. Study cases represented data points, i.e., treatment vs. control comparisons, drawn from a single primary study, where a single study may have one or more study cases. The occurrence of more than one study case in a given study took place when more than one response was measured and/or more than one herbivory treatment level was tested (against a control), in which case the number of study cases in a given study equaled the number of responses by the number of treatment level vs. control comparisons. We used different approaches to account for both sources of nonindependence in our analyses and assessed the robustness of our conclusions to the inclusion of multiple study cases per primary study (see Statistical Analyses).

For each study case, we compiled the following information: plant identity and life cycle (annual or perennial), type of damage applied (real herbivory vs. simulated mechanical damage), plant tissue damaged (flowers, roots or leaves), floral traits (number of flowers, flower and/or corolla size, nectar concentration and volume, number of flowering days, and/or time to flowering), pollinator responses associated with plant attractiveness (pollinator abundance and species richness, number of plants or flowers probed or visited, visit duration of pollinators, and/or plant or flower visitation rate), and plant reproductive success (number of fruits or seeds, fruit or seed weight, and seed germination rate). It is important to note that flower number and size accounted for >80% of the study cases for measurements of floral traits. Similarly, pollinator abundance and number of plants or flowers probed or visited accounted for >80% of the study cases of measurements of plant attractiveness to pollinators. Unfortunately, >80% of the studies that reported the type of pollinator (e.g., bees, flies, birds) measured responses by bees, so we did not have enough studies to test for effects of herbivory on pollinator type. Finally, fruit and seed number and size accounted for >80% of the study cases for measurements of plant reproductive success.

Statistical analyses

For each study case, we estimated effect sizes using Hedges' d metric and a confidence interval (CI; Hedges 1981) using the "metafor" package 1.9-8 version in R 3.2.3 (Viechtbauer 2010, R Core Team 2017). Hedges' d is calculated as the standardized mean difference between herbivore-damaged and control plants, such that negative values indicate that floral traits, plant attractiveness to pollinators, and plant reproductive success had lower mean values on damaged plants compared to control plants, whereas positive values indicate the inverse. For

flowering phenology and corolla tube length, increased time to flowering reduces the effective pollination period (Rafferty and Ives 2012), whereas increased corolla tube length reduces the efficiency of pollinators with a short proboscis by reducing their ability to collect nectar (Nilsson 1988). In both cases, we therefore multiplied the effect size by -1 such that the interpretation of the direction of the effect on these variables was in the same sense than all other variables (i.e., lower values indicative of reduced plant attractiveness to pollinators).

We first estimated the grand mean effect size and 95% confidence interval (CI) across all studies to assess whether there was an overall effect of herbivory on the three types of response variables measured (Koricheva et al. 2013). This grand effect size does not separate herbivore effects on plant attractiveness to pollinators vs. other response types measured or responses to different types of herbivory. Rather, the main purpose of this analysis was to estimate the degree of consistency among studies by means of the between-studies heterogeneity (τ^2 and associated Q statistics), an important overall estimator for our analysis. High heterogeneity can be accounted for by using explanatory variables (referred to as "moderators" in meta-analysis literature). Total heterogeneity is split into among-group heterogeneity (i.e., among treatments) and within-group heterogeneity (i.e., variance of effect sizes within moderator level). The τ^2 and associated Q statistics for heterogeneity aim at determining whether among-group heterogeneity is large enough as compared to within-group heterogeneity to conclude on the significant effect of the moderator tested. Because τ^2 is dependent on sample size, we also calculated I^2 value, which is a standardized estimate of total heterogeneity ranging from 0 and 1 (Koricheva et al. 2013, Nakagawa et al. 2017).

Following from the foregoing (overall) analysis, we evaluated the overall effects of herbivores (i.e., across all types of herbivory) separately for each type of response (i.e., floral traits, plant attractiveness to pollinators, and plant reproductive success) by estimating mean effect sizes and 95% CIs in each case. We then further investigated whether herbivore effects were contingent on the plant tissue attacked by herbivores (roots, flowers, or leaves) and type of damage applied (real or simulated). To this end, we ran a model including the type of response variable, plant tissue attacked, and type of damage applied as moderators and also tested for their two-way and three-way interactions. In addition, we estimated the mean effect sizes and 95% CIs from the complete model for each type of response, focal tissue, and type of damage. The effect of type of damage was only evaluated for flowers and leaves as we only found one primary study (with two study cases) using simulated root herbivory, which precluded drawing any inference about the effects of type of damage for this plant tissue. We report results from the omnibus test (i.e., overall effect of all moderators) as well as from the coefficient parameter estimate and associated confidence interval.

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In all the above models, we performed multilevel error meta-analyses (Nakagawa et al. 2017) with the *rma.mv* function of the R package metafor v. 2.0-0 (Viechtbauer 2010, R Core Team 2017), and included the primary study and study case nested within primary study as random factors in order to account for nonindependence among multiple effect sizes drawn from a single primary study (Moreira et al. 2018). Multiple comparisons of herbivore-damaged plants with the same control plant were accounted for by computing the variance–covariance matrix among all effect sizes. We considered an effect size as significant if its 95% confidence interval did not overlap with zero (Koricheva et al. 2013). Preliminary analyses testing for an effect of plant life cycle (annual or perennial) indicated that this factor did not significantly influence herbivore effects on any of the responses types measured ($Q_M = 0.14$, $P = 0.704$). We therefore pooled all data on annual and perennial plants and did not consider this effect in the Results section.

To ensure that our findings were robust, we conducted a sensitivity analysis in which we sequentially removed one primary study at a time. This analysis was aimed at testing whether the main result could have emerged from the inclusion of any particularly influential study, for instance one providing a large number of study cases. For each of the 88 runs, corresponding to removing each of the 88 primary studies included in the main analysis, we checked that model parameter estimates for each herbivory treatment (control vs. herbivore damaged) were comparable, regardless of whether each study was later included or not in the analyses. This analysis indicated that our findings were robust and unbiased by nonindependence among effect sizes (Appendix S3: Figs. S1 and S2). In addition, we used several approaches to verify that our results were not affected by publication bias (Koricheva et al. 2013): (1) inspection of funnel plots, (2) cumulative meta-analysis, (3) calculation of fail-safe number, and (4) exploration of the relationship between effect sizes and journal impact factor. These analyses indicated that our findings were robust to selective reporting and dissemination bias (Appendix S4: Figs. S1–S3).

RESULTS

The grand mean effect size (±95% CI) for the effect of herbivores (across all response types) was significant and negative (−1.28 ± [−1.99; −0.56]). This global analysis indicated a substantial amount of total heterogeneity ($\tau^2 = 18.15$, $Q_T = 24087.74$, $P < 0.001$), most of which (96%) was attributable to among-study heterogeneity ($I^2 = 0.96$). Further analyses indicated a significant negative effect of herbivores (across plant tissue types, $Q_M = 12.08$, $P = 0.001$) on floral traits, plant attractiveness to pollinators, and plant reproductive success (Fig. 1). These effects were, however, contingent on the plant tissue attacked by herbivores (significant response type by plant tissue interaction: $Q_M = 11.01$, $P = 0.026$) and type of damage applied (significant response type by

damage type interaction: $Q_M = 6.34$, $P = 0.042$). Real floral and leaf herbivores had significant negative effects on floral traits (Fig. 2a) and plant attractiveness to pollinators (Fig. 2b), and real leaf (but not floral) herbivores additionally decreased plant reproductive success (Fig. 2c). Real root herbivores did not significantly influence floral traits, plant attractiveness to pollinators, or reproductive success (Fig. 2a–c). Finally, and in contrast to effects of real (leaf and floral) herbivores, simulated leaf and floral herbivory showed no significant effects on floral traits (Fig. 2a), plant attractiveness to pollinators (Fig. 2b), or plant reproductive success (Fig. 2c).

DISCUSSION

Overview

The overall negative effects of herbivores on pollinator attraction were contingent on the plant tissue attacked by herbivores. Whereas real floral and leaf herbivores negatively influenced plant attractiveness to pollinators, root herbivores showed no such effect. These results were concordant with studies conducted over the last decade showing that effects of leaf and floral herbivores on pollinators are in most cases consistently negative
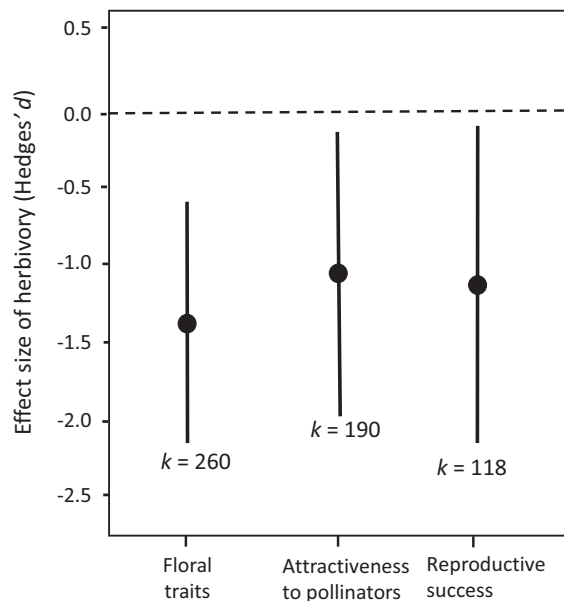

FIG. 1. Mean effect size of herbivory on floral traits (e.g., flower number and size), plant attractiveness to pollinators (e.g., abundance, number of visits, and visit duration), and plant reproductive success (e.g., fruit and seed number and size). Dots and error bars represent model parameter estimates and corresponding 95% bias-corrected confidence intervals (CI). k = number of study cases. The vertical dashed line centered on zero represents the null hypothesis (i.e., no difference in floral traits, plant attractiveness to pollinators, and plant reproductive success between control and herbivore-damaged plants). The effect size of each plant tissue damaged by herbivory is significant if the 95% CI does not include zero.
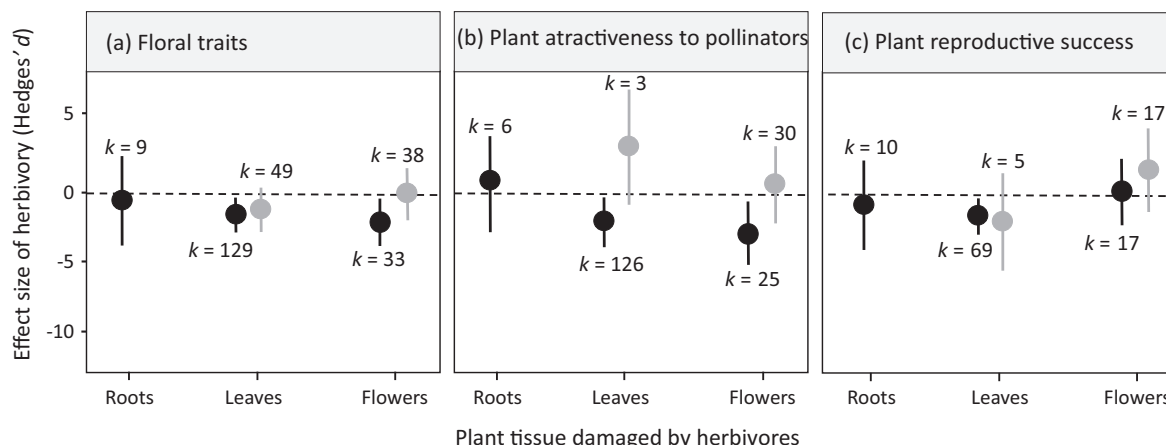
FIG. 2. Mean effect size of the plant tissue damaged by herbivory (roots, leaves, or flowers) and type of damage (real herbivory or simulated mechanical damage) on floral traits (e.g., flower number and size), plant attractiveness to pollinators (e.g., abundance, number of visits, and visit duration), and plant reproductive success (e.g., fruit and seed number and size). Dots and error bars represent model parameter estimates and corresponding 95% bias-corrected confidence intervals (CI). k = number of study cases. Black dots represent real herbivory, whereas gray dots represent simulated herbivory. Only damage on flowers and leaves was analyzed, as there were no replicated studies using simulated root herbivory. The vertical dashed line centered on zero represents the null hypothesis (i.e., no difference in floral traits, plant attractiveness to pollinators, and plant reproductive success between control and herbivore-damaged plants). The effect size of each plant tissue damaged by herbivory and each type of damage is significant if the 95% CI does not include zero.

(reviewed by Jones and Agrawal 2017), whereas the direction of root herbivore effects appears to be more variable (e.g., Barber et al. 2011, 2015; albeit with a considerably lower number of studies). We also found negative effects of real floral and leaf herbivores on floral traits (e.g., smaller flower size or display size), which could potentially explain their negative effects on plant attractiveness to pollinators. Further, leaf herbivores negatively influenced plant reproductive success (i.e., lower fruit and seed production and size) which might be at least partly attributable to the negative effects of these herbivores on pollinators. Interestingly, floral herbivores did not have a significant mean effect on plant reproductive success despite reducing plant attractiveness to pollinators, suggesting that compensatory mechanisms in plant reproduction may have come into play. Root herbivores, on the other hand, did not have a significant mean effect on floral traits, plant attractiveness to pollinators, or plant reproductive success. Finally, and in sharp contrast with these results with real herbivory, the lack of effect of simulated leaf and floral damage on floral traits, plant attractiveness to pollinators, or plant reproductive success, indicates that results based on simulated herbivory treatments should be taken with caution, as they may underestimate herbivore effects on pollinators.

Potential mechanisms explaining herbivore effects on pollinators

The effects of herbivores on plant attractiveness to pollinators are argued to be strongly contingent on the plant or organ attacked, and a previous meta-analysis by Kessler and Halitschke (2009) reported negative effects of (real) floral herbivory but no effect of leaf herbivory on plant attractiveness to pollinators. However, our updated results based on a larger number of studies indicated that *both* floral and leaf (real) herbivores decrease in pollinator attraction. Leaf herbivores thus also appear to have relatively consistent negative effects on pollinators, even though they do not directly feed on the same plant tissues used by pollinators. This suggests that systemic plant-induced responses from leaf to reproductive tissues are widespread and important in mediating folivore–pollinator interactions (Bronstein et al. 2007); direct mechanisms such as interference or chemical cues for increased predation cannot, however, be discarded (Kessler et al. 2011) and may also be at play, depending on features such as plant size and architecture influencing proximity between leaves and flowers. In contrast, our finding that real root herbivores had no effect on pollinators suggest that links between belowground herbivory and aboveground plant–pollinator interactions are weaker. This could be explained, at least partly, because effects of root herbivores are exclusively plant mediated and do not act via direct mechanisms, which may limit the overall strength of their effects. Having said this, we caution about these results, because the number of studies testing for (real) root herbivory was low (N = 6, study cases = 27), which prevents reaching strong conclusions. Further studies addressing the concomitant effects of below- and aboveground herbivory on pollinators are clearly needed.

The observed negative effects of leaf and floral herbivores on plant attractiveness to pollinators are presumably mediated, at least partly, by negative effects of

such herbivores on plant traits, particularly floral features (i.e., plant-mediated effects). Accordingly, a number of experimental studies have demonstrated that herbivory negatively affects plant reproductive traits such as flower display size, flower size, and rewards for pollinators (Karban and Strauss 1993, Strauss et al. 1996, Lehtilä and Strauss 1997, Barber et al. 2011, 2015). In contrast, root herbivores did not appear to influence floral traits, which could explain their lack of effect on plant attractiveness to pollinators. Negative direct effects of floral herbivory may take place through avoidance mechanisms, where pollinators evade flowers with herbivore presence (Lohmann et al. 1996, Bronstein et al. 2007), whereas indirect mechanisms may arise through changes in volatile organic compounds (VOCs) emitted by flowers that reduce floral attractiveness to pollinators (Kessler et al. 2011). In the latter case, several studies have reported that leaf herbivory alters floral scents and these changes in turn correlate with reduced pollinator attraction (Kessler et al. 2011, Schiestl et al. 2014). Although, we found no studies reporting effects of floral herbivores on floral VOCs and pollinator attraction, evidence that leaf herbivores influence pollinators via changes in floral volatile emissions suggests that parallel effects by floral herbivores may be just as (or more) likely due to local induction. Future work testing the effects of different types of herbivory on floral volatiles and associating these changes with pollinator visitation is needed.

Pollinator-mediated effects of herbivory on plant reproduction

Our analysis indicated that leaf herbivores negatively influence plant reproductive success, concordant with their negative effect on floral traits and pollinator attraction. This result could be explained by reduced plant allocation to reproduction following damage (subsequent flower production or fruit filling), and/or lower pollinator attraction. The relative importance of these two mechanisms probably depends on plant-based (e.g., mating system and functional strategies related to induced responses) and pollinator-based (e.g., pollinator species composition and behavior) characteristics. Unfortunately, we cannot assess the relative importance of these mechanisms based on the current data and the number of available studies. We therefore call for studies comparing plants with contrasting mating features such as the presence/absence of reproductive assurance mechanisms that experimentally manipulate plant reproductive success (e.g., via hand-pollination) and pollinator presence in addition to herbivory.

Contrary to expectations, floral herbivores did not show an overall relevant effect on plant reproductive success, which suggests that plant compensation dampens the negative effects of herbivory on flower output and pollinator attraction. A number of studies have reported overcompensation in flower production

(Strauss et al. 2001, Irwin et al. 2008, Schiestl et al. 2014), and although floral herbivores showed a mean negative effect on floral traits, it is possible that plants increase allocation to fruit and seed formation following herbivore attack (Garcia and Eubanks 2019). In this sense, a number of plant species included in our analysis are self-compatible and undergo self-pollination (e.g., *Mimulus guttatus*, *Raphanus raphanistrum*, *Isomeris arborea*, and *B. rapa*), which could have offset the negative effects of floral herbivores on display size and pollinator attraction. A recent meta-analysis found strong evidence of plant reproductive overcompensation to insect herbivory (Garcia and Eubanks 2019), suggesting that this could represent a potentially important phenomenon. In addition, compensation to herbivory might be more common in reproductive than vegetative tissues because plants usually allocate more resources to reproductive structures after herbivore damage (Irwin et al. 2008), combined with the fact that reproductive tissues are energetically more costly and more directly related to plant fitness than vegetative tissues (McCall and Fordyce 2010). On a closing note, it is worth pointing out that root herbivores had weak and/or variable effects on plant reproductive success despite the fact that root damage can have negative effects on allocation to reproduction (e.g., reduced root growth and nutrient storage; Núñez-Farfán et al. 2007). It is therefore possible that plant compensation frequently buffers root herbivory and this leads to no overall effect of such herbivores on plant reproductive success as observed from our analyses. Alternatively, it is also plausible that low statistical power may have prevented the detection of such negative effects. More studies involving root herbivores are needed to obtain more robust conclusions. Measurements of plant reproductive output conducted over longer periods of time are also needed, particularly in cases of high or recurrent herbivory. This would increase the chance of detecting negative effects on pollinator attraction and allocation to reproduction due to the depletion of plant reserves and failure of plants to achieve full compensation.

Conclusions and future directions

Our findings deliver valuable insight into our understanding of herbivore–pollinator interactions, and also point at several lines for further inquiry. Controlled experiments including replication of species with different pollination or mating systems (e.g., contrasting level of self-compatibility presence/absence of reproductive assurance) while manipulating pollinators and herbivores will advance our understanding of how plant-based features affect herbivore–pollinator interactions. Likewise, manipulations of effects of herbivore guilds would be highly valuable for a more detailed understanding of species- or guild-specific effects on different plant parts. In the case of perennial plants, longer-term measurements of herbivore effects, pollinator responses,

and reproductive success are necessary to improve understanding of the consequences of these interactions for plant fitness, and to provide a better assessment of the potential role of plant compensatory mechanisms in determining how these interactions play out. Work addressing the influence of abiotic factors on plant compensatory responses to herbivory is also needed, including comparisons of plant species with different growth forms or functional strategies expected to differ in compensatory capacity and tolerance mechanisms. Finally, a stronger emphasis on root herbivores is needed, given the lack of studies involving this type of herbivory and the potentially widespread effects on plant-associated aboveground interactions (as shown for plant–herbivore and plant–herbivore–enemy interactions). In all of the above cases, the identification of plant traits mediating these indirect effects will be of key importance, as will the separation of direct and indirect effects of different herbivore species or guilds on pollinators.

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