A systematic review of the direct and indirect effects of herbivory on plant reproduction mediated by pollination: theories, methods, and challenges

Stephanie M Haas[1], Christopher Lortie[1,2]

[1] Department of Biology, York University, Toronto, Ontario, Canada
[2] The National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, California, United States

Corresponding Author:
Stephanie Haas[1]
4700 Keele St, Toronto, Ontario, M3J 1P3, Canada
Email address: shaas014@yorku.ca

Abstract

Background. Plant reproduction is influenced by the net outcome of plant-herbivore and plant-pollinator interactions. While both herbivore impacts and pollinator impacts on plant reproduction have been widely studied, few studies examine them in concert.

Methodology. Here, we review the contemporary literature that examines the net outcomes of herbivory and pollination on plant reproduction and the impacts of herbivores on pollination through damage to shared host plants using systematic review tools. The direct or indirect effects of herbivores on floral tissue and reported mechanisms were compiled including the taxonomic breadth of herbivores, plants, and pollinators.

Results. A total of 4304 studies were examined producing 61 relevant studies for synthesis that reported both pollinator and herbivore measures. A total of 53% of studies examined the impact of direct damage to floral tissue through partial florivory while 35% of studies also examined the impact of vegetative damage on pollination through folivory, root herbivory, and stem damage. Only 4 studies examined the effects of both direct and indirect damage to pollination outcomes within the same study.

Conclusions. It is not unreasonable to assume that plants often sustain simultaneous forms of damage to different tissues and that the net effects can be assessed through differences in reproductive output. Further research that controls for other relative drivers of reproductive output but examines more than one pathway of damage simultaneously will inform our understanding of the mechanistic relevance of herbivore impacts on pollination and also highlight interactions between herbivores and pollinators through plants. It is clear that herbivory can impact plant fitness through pollination; however, the relative importance of direct and indirect damage to floral tissue on plant reproduction is still largely unknown.

Introduction

41

42   Plant fitness is determined by the net outcome of interactions with other species. All
43 species within a community experience multiple direct interactions ranging from negative to
44 positive (García-cervigón et al. 2016, Pilosof et al. 2017). However, the sum of the direct
45 interactions between two species do not represent the net outcome of the relationship; these
46 direct interactions can in turn interact (Proulx, Promislow & Phillips, 2005). When each species
47 interacts with at least one third party species, indirect interactions quickly occur (Borrett,
48 Whipple & Patten, 2010). It is the sum of these direct and indirect interactions that represent the
49 net outcome of the interaction between any two species (Michalet et al., 2015).
50   For most angiosperms, interactions with herbivores and pollinators impact fitness.
51 Herbivory can be generally classified as having a direct negative effect on plants, while
52   pollinators can be similarly classified as having a direct positive effect on plants. Typically,
53 herbivory and pollination are examined one at a time; however, these effect pathways frequently
54 co-occur and therefore interact (Strauss, Conner & Rush, 1996; Vulliamy, Potts & Willmer,
55 2006; Tsuji et al., 2016; Chalcoff, Lescano & Devegili, 2019; Rusman et al., 2019; Scopece,
56 Frachon & Cozzolino, 2019). Most typically, damage to plants can reduce floral resources or
57 floral attractiveness to pollinators (Brody, 1997; Mothershead & Marquis, 2000; Rusman et al.,
58 2019). For instance, herbivory that removes flowers (complete florivory; Table 1) will remove the
59 possibility of pollination for those flowers and the possible source of nectar or pollen for
60 pollinators. This type of interaction between herbivory and pollination is obvious; however,
61 herbivory and pollination also interact in more subtle and indirect ways. Negative impacts to
62 pollinators can amplify the negative effects of herbivores on plant fitness by reducing both
63 potential seed set (e.g. number of flowers available to set seed) (Strauss, Conner & Rush, 1996;
64 Hambäck, 2001; Rusman et al., 2019) and actual seed set (i.e. flowers are not all pollinated due
65 to decreased pollinator visitation) (Adler, Karban & Strauss, 2001; Benning & Moeller, 2019).
66 Therefore, when the net outcome of herbivory on plants is examined, pollination must also be
67 considered. In this systematic review (Fig. 1), we have outlined a conceptual framework (Fig. 2)
68 to illustrate the direct and indirect ways in which the negative effects of herbivory can both
69 directly and indirectly effect plant fitness via animal pollinators and pollination. Here, we outline
70 the general ways in which different types of herbivory can impact plant fitness and how this
71 interacts with pollination as outlined in Fig. 2, followed by a synthesis of the contemporary
72 literature on herbivore-pollinator interactions.
73   Herbivory can impact plant reproduction both directly and indirectly, regardless of
74 pollination; herbivores can both directly consume plant reproductive structures through floral
75 herbivory and rob the plant of the resources needed to produce reproductive structures through
76 vegetative herbivory (e.g. folivory; see Lucas-Barbosa, 2016). Complete florivory is the
77 complete removal of flowers or reproductive structures such as ovules (see Table 1 for a list of
78 definitions). By entirely removing reproductive structures plant fitness can, by definition, directly
79 decrease. However, herbivores can also remove or damage non-floral (vegetative) structures
80 such as leaves (folivory), stems (stem damage), and roots (root herbivory). Damage to these
81 structures can cause a plant to either not produce flowers, fruits or seeds, or produce structures
82 of poor quality (i.e. non-viable seeds; Brody, 1997; Mothershead & Marquis, 2000; Lucas-
83 Barbosa 2016; Rusman et al., 2019). In more extreme cases vegetative herbivory could result in

84   the death of the plant. Regardless of any indirect interactions via pollinators herbivores can
85   result in a negative net outcome on plant fitness.
86   When examining plant fitness it is important to consider multiple interactions not only in
87   the sense of both positive and negative (e.g. herbivory and pollination), but also different
88   sources of the same type (i.e. different sources of herbivory). While it is true plants can be
89   subjected to damage to different tissues as discussed, herbivory is not a singular interaction–
90   damage by multiple herbivores or to multiple tissues can occur simultaneously (Althoff,
91   Segraves & Pellmyr, 2005; Barber, Adler & Bernardo 2011; Scopece, Frachon & Cozzolino,
92   2019). That is, the same herbivore can feed on multiple tissues (e.g. Lucas-Barbosa et al.,
93   2016) or multiple herbivores can feed on different tissues (or even the same tissue)
94   simultaneously (e.g. Barber, Adler & Bernardo, 2011). As opposed to generalizing on multiple
95   tissues at once, a singular herbivore may change what tissue is targeted ontogenetically or even
96   switch entirely to pollination (Lucas-Barbosa et al., 2016). This type of switch is commonly seen
97   in pollinating insects with a herbivorous larval form (Nakazawa, 2015). A common example is
98   the yucca moth that feeds on yucca plants as a juvenile and pollinates them as an adult
99   (Pellmyr, 2003). While the same herbivore may attack different tissues, different herbivores may
100 also attack the same tissue in different ways (Rusman et al., 2019). For instance, one folivore
101 may consume leaves along the edges, while another may create holes in the center of leaves.
102 The effects of these herbivores may compound upon each other (whether on the same or
103 differing tissues; Raffaele et al., 2011), or one may even deter the other. The damage of any
104 one herbivore species alone may not be significant enough to negatively impact plant fitness,
105 but the combined efforts of two or more species may cause a significant effect (Anderson &
106 Paige, 2003). Damage to different types of tissues may be of particular importance due to the
107 use of both direct and indirect effects on reproduction, as outlined in Fig. 2.
108 Before delving into how the negative effects of herbivory and different types of herbivory can
109 negatively impact pollination, it is important to acknowledge that the results of herbivory are not
110 always strictly negative. The net outcome of herbivory on pollination is mediated by plant
111 responses (Santangelo, Thompson & Johnson, 2019). While herbivory in itself is a negative
112 interaction (i.e. damage to or removal of plant tissue) the net outcome of herbivory on pollination
113 or plant reproduction is not only dependent on external factors (such as abiotic and biotic
114 interactions) but also on the response of the plant itself in terms of resistances, allocation
115 strategies, and defenses (see Hawkes & Sullivan, 2001). Plants often have defenses against
116 herbivory including constitutive (e.g. thorns) or inducible (e.g. volatile release) defenses that can
117 be both mechanical or chemical and can mitigate or reduce herbivory (Chen, 2008). Plants may
118 also reduce herbivory by interacting with other non-herbivore species (Ruttan & Lortie, 2013).
119 For instance, the attractant-decoy hypothesis states that plants that grow near preferred plants
120 can influence herbivore foraging choice when herbivores are selective (Ruttan & Lortie, 2013).
121 Similarly, the repellent-plant hypothesis states that associating with distasteful or well-defended
122 plants will cause herbivores to avoid the patch all together, also relieving the plant of herbivory
123 (Ruttan & Lortie, 2013). Plants can also release volatiles or produce food or shelter that, instead
124 of deterring herbivores, attract the predator of its herbivores (Heil, 2008). However, a cost to
125 some defenses include deterring pollinators (Lucas-Barbosa, Van Loon & Dicke, 2011). For
126 instance, volatiles released in response to herbivory may also repel pollinators (Lucas-Barbosa
127 et al., 2016), and predators of herbivores may also be predators of pollinators (Heil, 2008).

128   Other ways of resisting or mitigating herbivores include initial overproduction of
129   structures (e.g. producing more flowers than can be brought to fruit; Huth & Pellmyr, 1997) and
130   compensation for received herbivory (Garcia & Eubanks, 2019). Plants can often compensate
131   for damage they sustain by producing new flowers (in response to florivory) or further branching
132   stems (in response to stem damage; Garcia & Eubanks, 2019). In some cases, plants will
133   produce more flowers in the presence of herbivory than in the absence due to
134   overcompensation (Garcia & Eubanks, 2019). Therefore, not only is it possible that the negative
135   impact of herbivory can be mitigated, but herbivory could result in a net positive outcome in
136   terms of pollination and plant reproduction depending on the traits of the plant itself. In this
137   review, we specifically examine the indirect interactions of herbivores on pollinators mediated by
138   shared host plants.
139   Similar to how herbivory does not always result in a negative outcome, pollination (or
140   animal pollination) does not always result in a positive outcome on plant fitness. It has been
141   estimated that 87.5% of the world's angiosperms are pollinated by animals (Ollerton, Winfree &
142   Tarrant, 2011). Most angiosperms either require pollinators to reproduce or pollinators increase
143   the plants' fruit or seed set (Culley, Weller & Sakai, 2002). That is, many plants receive
144   pollination from animals but are still able to reproduce without pollinators by either wind
145   pollination or self-pollination (Culley, Weller & Sakai, 2002) and so pollinators in some case may
146   simply have a neutral effect on plant fitness, neither decreasing nor increasing plant fitness in
147   self-compatible plants (Dicenta et al., 2002). However, animal pollination can supplement wind
148   or self-pollination, increasing yields compared to the absence of pollinators (Klein et al., 2007;
149   Cardel & Koptur, 2010; Jorge, Loureiro & Castro, 2015). Pollinators can also provide important
150   increases in genetic diversity when self-pollination is prevalent (Vaughton & Ramsey, 2006)
151   Therefore, while plants that did not require any animal pollination were excluded from this
152   review, those that received at least some animal pollination were included (i.e. self-compatible
153   species were not excluded).
154   When plants are animal pollinated, the floral display presented by an individual,
155   population, or community can influence pollinator choice. Pollinators are often attracted to larger
156   flowers over smaller ones (Parachnowitsch & Kessler, 2010; Kaczorowski et al., 2012; Lavi &
157   Sapir, 2015), and more symmetrical flowers over those that have less or lost symmetry (Giurfa,
158   Dafni & Neal, 1999; Botto-Mahan et al., 2011). Pollinators are also often attracted to large floral
159   patches (Thompson, 2001; Fowler, Rotheray & Goulson, 2016). Many of these floral display
160   attributes can be indicators of floral quality or availability of resources (i.e. nectar and pollen;
161   Giurfa, Dafni & Neal, 1999; Parachnowitsch & Kessler, 2010; Fowler, Rotheray & Goulson,
162   2016), but regardless the innate preference for these floral traits mean that changes in them by
163   external factors such as herbivory can influence pollinator choice.
164   Herbivory can influence floral display both directly and indirectly depending on the tissue
165   (both floral and vegetative) targeted by herbivores. Herbivores can impact the reproduction of
166   plants (regardless of pollination or pollinators) by removing flowers or ovules via florivory
167   (complete florivory; Kelly et al., 2008; Table 1) but also by influencing pollinator visitation.
168   Removal of flowers not only eliminates a potential source of resources for pollinators, but also
169   decreases the overall size of the floral display. Rather than removing flowers, partial
170   consumption of floral tissue (incomplete florivory) can make flowers directly less attractive to
171   pollinators by reducing symmetry (Botto-Mahan et al., 2011). Conversely, consumption of

172   vegetative (non-floral) tissues can have an indirect effect on floral traits and pollinator attraction
173   (Fig. 2) by reducing the resources available to plants (Mothershead & Marquis, 2000).
174   Vegetative herbivory such as folivory, root herbivory, and stem damage (Table 1) can cause
175   plants to produce fewer and smaller flowers (Strauss, Conner & Rush, 1996; Hambäck, 2001;
176   Hladun & Adler, 2009). Similar to incomplete florivory, this vegetative herbivory can also change
177   the morphology of flowers including symmetry or architectural structure (Strauss, Conner &
178   Rush, 1996; Table 1; Mothershead & Marquis, 2000; Suárez, Gonzáles & Gianoli, 2009).
179   Phenology, sex ratio, and pollen production can further shift with vegetative herbivory (Strauss,
180   Conner & Rush, 1996; Mothershead & Marquis, 2000; Avila-Sakar, Simmers & Stephenson,
181   2003; Arceo-Gómez, Parra-Tabla & Navarro, 2009). In these ways, both vegetative and floral
182   damage can interact with pollination by changing aspects of floral display. Numerous
183   mechanistic pathways can integrate the direct and indirect impacts of herbivores on plant
184   reproduction through plant tissue, allocation strategies, and timing that impact plant pollination
185   (Strauss, Conner & Rush, 1996; Mothershead & Marquis, 2000; Kelly et al., 2008; Botto-Mahan
186   et al., 2011). The nature of how not only each type of herbivory, but also the joint impact of
187   multiple types of herbivory impact pollination and plant reproduction are the basis of Fig. 2.
188   The indirect effects of herbivory on pollination are the focus of this review; there are
189   other ways in which pollinators and herbivores interact. For instance, there are direct
190   interactions between herbivores and pollinators where the presence of herbivores actively
191   deters pollinators from approaching flowers (Canela & Sazima, 2003). While some studies in
192   our review include these direct interactions (e.g. Canela & Sazima, 2003), they are not a focus.
193   Additionally, given the cyclical nature of plant lifecycles, the successful reproduction of a plant
194   species is vital to the continued availability of its tissues as a food source for herbivores. While
195   this may be less relevant for generalist herbivores, the successful pollination of a plant could in
196   turn affect the future availability of resources for herbivores. These types of effects pollinators
197   may have on herbivores are not included in this review, nor are these types of interactions
198   between herbivory and pollination included in the conceptual framework since they are not the
199   focus of this review.
200   In this systematic review, we synthesize the contemporary literature on herbivore-plant-
201   pollinator interactions with a specific focus on studies that examined the joint impact of
202   herbivores and pollinators on plant reproduction or the impact of herbivores on pollination using
203   the mechanistic pathways proposed in our conceptual framework (Fig. 2). The frequency of
204   mechanisms tested and the frequency that direct vs indirect floral damage pathways are
205   contrasted is important to both ecology and evolution. This includes examining the diversity of
206   types of damage—both the tissue targeted and the taxa causing the damage. Finally, we
207   examine how each mechanism is tested.
208
209   Survey methodology
210   A search for papers that examine the impact of herbivores on pollinators or the
211   pollination of plants in October 2019 using Web of Science and the search terms "herbivor*
212   AND pollinat*", "floriv*", "foliv* AND pollinat*", "herbivor* AND flower*", and "foliv* AND flower"
213   was conducted by S. Haas (no review protocol was registered). This resulted in 3681 papers
214   (Fig. 1). Papers had to meet the criteria that they directly tested the impact of herbivory on
215   animal-mediated pollination. The indirect effect of herbivores on pollinators or the indirect effect

216 of herbivores on plants via pollinators must have been reported to be included in this synthesis
217 (e.g. through measuring pollen deposition or comparing open pollination to supplementary hand
218 pollination). After review, 59 papers were included in the final analysis (Fig. 1). Papers that were
219 excluded were reviews and descriptions of the natural history of plants or animals (including
220 diet). Studies were also excluded if they examined the impact of herbivores on plants but not
221 pollination. Data extracted included the physical location of all study sites and the taxa
222 examined, as well as the analyses performed (including type of herbivory, response variable,
223 and general direction of effect each variable had on each response) and the general structure of
224 the experimental design. Site biomes were calculated using biomes from Terrestrial Ecoregions
225 of the World, originating from the World Wildlife Fund (Olson et al., 2001; CC BY-NC 3.0) using
226 the software QGIS (QGIS Development Team, 2019).
227

228 **Results**
229   In total, 59 papers met all criteria to be included in the final analysis. These papers
230 ranged from 1995 to 2019 spanning 18 different countries and 11 (of 14) different biomes (Fig.
231 3). The majority were done in the United States and the temperate broadleaf & mixed forests
232 biome. The only biomes not represented were tropical & subtropical coniferous forests, tropical
233 & subtropical grasslands, savannas & shrublands, and tundra. Of the 51 papers in which site
234 information could be taken (that were not greenhouse experiments) all but three studies were
235 located within a single biome. A total of 47 plant taxa, 27 herbivore taxa, and 18 pollinator taxa
236 were studied in these papers (Table S1; Fig. 4). Almost all herbivores (81%) and pollinators
237 (78%) were insects. A total of 90% of studies (N=55) examined a single plant species while only
238 43% of studies (N=26) examined a single herbivore and 10% a single pollinator (N=6; Table S2
239 and S3). It was most common to examine the entire community of pollinators (72% of studies;
240 N=44). Pollination was most frequently measured through direct pollinator visitation (57% of
241 studies); however, 25% used supplemental pollination (Table 1). Herbivory was also most
242 frequently (67%) observed directly by animals although 33% of studies (N=20) applied some
243 form of artificial herbivory, and 22% artificially reduced herbivory by excluding herbivores or
244 applying pesticides.
245   The most common type of herbivory examined was florivory (49%; Fig. 5, Table 1). This
246 was followed by folivory (27%) and grazing (20%). However, stem damage (8%) and root
247 herbivory (5%) were also utilized. For 5% of studies, herbivory was non-specific (i.e. "open" to
248 all herbivores). Almost all studies (88%) looked at only one form of herbivory. Of the other 12%
249 of studies, two or three types of herbivory were examined. Hladun and Adler (2009) examined
250 the interaction between two types of vegetative herbivory—root herbivory and folivory.
251 Buchanan (2015) also compared two types of vegetative herbivory: leaf damage and meristem
252 damage, while Rusman et al. (2019) looked at all three types of vegetative herbivory (folivory,
253 stem damage, and root herbivory). Similarly, Sasal et al. (2017) looked at both general grazing
254 (in the form of ungulates) and specifically folivory (in the form of insect herbivory). Lucas-
255 Barbosa et al. (2013), Lucas-Barbosa et al. (2016), and Mothershead and Marquis (2000)
256 compared the effects of florivory and folivory representing the only papers that compared
257 vegetative and floral herbivory.
258   Florivory was found to have some negative impact on floral expression, pollination, or
259 seed production in 86% of papers (Supplemental Table S4). Some positive effect of florivory

260   was found in 24% of papers and a neutral effect in 48% of papers. For folivory, 81% of papers
261   each found some negative effect or neutral effect, while only 31% found any positive effect.
262   Grazing had 67% of papers each find some negative or neutral effect, and 33% found some
263   positive effect. Similar proportions were found in each of the other types of herbivory.
264   Only 19% of papers took a full mechanistic approach to the effects of herbivores on
265   pollinators (Table 2). These studies examined each point of the mechanism in Fig. 2: the effects
266   of herbivory on floral display, pollinators, and plant reproduction. Most frequently (24%), papers
267   examined the effect on pollinators and plant reproduction while skipping the mechanistic step of
268   the impact on the flower. Otherwise, there was an approximately equal split between only
269   examining effects on pollinators (15%), only examining the effect of supplemental pollination on
270   reproduction (12%), examining the floral attributes and reproduction without the pollinator
271   (15%), or the floral attributes and pollinator without reproduction (15%).

272

273   Discussion

274   Herbivory and reproduction in plants are intimately linked through interactions with
275   animals. In this systematic review, we examined the relative frequencies and the extent that
276   these important processes are studied in concert. While the effect of herbivores on plants have
277   long been studied, and it has been well shown that herbivores can directly and indirectly impact
278   plant reproduction, growth, and population dynamics (Hawkes & Sullivan, 2001; Ohgushi, 2005;
279   Boivin, Doublet & Candau, 2019; Garcia & Eubanks, 2019), the small number of studies that
280   were located within this review indicate how infrequently the effects of herbivores on pollination
281   are studied. These studies were also heavily biased towards damage done by insects,
282   temperate biomes, and the effects of a single herbivore species on a single plant species.
283   Furthermore, only a handful of studies compared direct and indirect effects of herbivory on floral
284   traits and pollination. Given that most animal-pollinated plants likely experience damage to
285   multiple tissues as well as pollination (Lucas-Barbosa, 2016), this is an unfortunate gap in the
286   literature. In addition, those few studies that do examine both herbivory and pollination
287   frequently examine only the net outcome and not the underlying mechanism (i.e. how herbivory
288   impacts floral traits and how floral traits impact pollination). That is, most studies do not fully
289   examine the interaction network outlined in our framework (Fig. 2). Examining the impacts of
290   multiple herbivores as well as multiple types of herbivory is important in determining how plants
291   and pollinators are impacted by real communities of herbivores.
292   Direct damage to floral tissue is an important factor in determining plant reproductive
293   output. Complete florivory has been shown to have direct impacts on floral abundance. The net
294   outcome of this form of direct damage is dependent on the strategy of the plant (Juenger &
295   Bergelson, 1997; Wise, Cummins & De Young, 2008; Garcia & Eubanks, 2019). In some cases,
296   plants will over-produce flowers as a defense against florivory creating more flowers than the
297   plant is able to bring to seed (e.g. Huth & Pellmyr, 1997). Therefore, florivory frequently results
298   in no net loss in reproductive output for the plant. In other cases, plants are able to compensate
299   or overcompensate for herbivory, replacing the flowers lost (sometimes producing more flowers
300   than initially), or delaying phenology (Wise, Cummins & De Young, 2008; Garcia & Eubanks,
301   2019). If the plant is able to completely compensate (reproduce flowers of equal or greater
302   quality and quantity) then the net effect of complete florivory is neutral or even positive. How
303   plants interact with florivores can influence communities and population resilience through these

304   differences in reproductive output. While the impact of removal of flowers on overall plant
305   reproduction has been studied numerous times (See McCall & Irwin, 2006), the impact of this
306   removal specifically on pollination or pollinator visitation is rarely studied. Out of the 29 papers
307   that examined the impact of florivory on pollination found in this review, only one examined
308   complete florivory (Sutter & Albrecht, 2016). Changes in plant population and community
309   dynamics due to changes in reproduction have the potential to impact pollinators, for instance
310   patches with more flowers tend to attract more pollinators (Lazaro & Totland, 2010). Pollinators
311   in turn interact with plants to determine reproductive output. Therefore, the indirect interactions
312   between herbivores and pollinators fosters even further co-evolutionary processes such that
313   plants not only sufficiently compensate for lost reproductive structures due to herbivores, but
314   also to produce flowers of quality and quantity sufficient to attract pollinators. This interaction
315   requires further research into the implications of complete florivory on plant compensation,
316   pollination, and reproduction.
317   Incomplete florivory can also impact both pollination and plant reproduction. Incomplete
318   florivory can result in flowers that are less attractive to pollinators despite offering the same
319   reward. (Mothershead & Marquis, 2000). Pollinators can use visual cues such as floral
320   symmetry to choose between flowers (Rodríguez et al., 2004). A loss of symmetry can result in
321   decreased visitation (McCall, 2010). When other cues are more important, there may be no
322   effect of incomplete florivory (Malo, Leirana-Alcocer & Parra-Tabla, 2001) and plants can
323   mitigate or eliminate the negative effects of herbivory on floral display by reproducing via self-
324   pollination (with or without pollinators) in some cases including several species in this
325   systematic review (e.g. Cardel & Koptur, 2010). However, since animal pollination frequently
326   increases plant fitness this strategy may only limit the effects of incomplete florivory as opposed
327   to eliminating them. In addition, the actual presence of florivores in flowers can deter pollinators.
328   For example, Canela and Sazima (2003) found that florivorous crabs not only decreased
329   attraction of flowers to pollinators through damage but that pollinators were less likely to visit
330   flowers while the crabs were present. All of the 29 studies we found that examined the impact of
331   florivory on pollination examined partial florivory. In most studies, partial florivory was found to
332   decrease pollinator visitation or pollen deposition as well as plant reproduction (fruit set or seed
333   set). By decreasing pollinator visitation, incomplete florivory can indirectly decrease plant
334   reproduction (via pollen limitation). As with complete florivory decreases in reproduction can
335   impact population dynamics, while indirect effects on pollinators can drive the coevolutionary
336   arms race between herbivores and plants that might not otherwise occur under the limited
337   damage of incomplete florivory (that is, florivory that keeps ovules and stigmas intact).
338   While direct damage to floral tissue is the most common way to examine the effects of
339   herbivores on pollinators (Fig. 4), damage to vegetative tissue also had indirect effects on floral
340   attributes. The main mechanism that folivory, root damage and stem damage impact pollinators
341   is through decreasing both resources and the ability for plants to produce resources
342   (Mothershead & Marquis, 2000). By decreasing the amount of photosynthetic and absorptive
343   area available to a plant or siphoning off xylem or phloem, fewer or smaller flowers may be
344   produced (Mothershead & Marquis, 2000; Hambäck, 2001; Hladun & Adler, 2009). These
345   flowers may be less attractive to pollinators (Mothershead & Marquis, 2000) or theoretically be
346   less fertile, producing fewer seeds. While plants are also able to compensate for vegetative
347   damage, resources are often allocated to regrowth instead of reproduction and so vegetative

348 damage can still decrease fitness (Pratt et al., 2005; Garcia & Eubanks, 2019). Root herbivory
349 can also change how the plant interacts with aboveground herbivores and mutualists (Barber et
350 al., 2015). For instance, root herbivory can decrease aboveground herbivory and increase the
351 nectar in extrafloral nectaries (Hladun & Adler, 2009; Soler et al., 2012). While folivory, root
352 herbivory, and stem damage can decrease reproductive output (Mutikainen & Delph, 1996;
353 Lehtilä & Strauss, 1999; Pratt et al., 2005; Lopez-Toledo et al., 2018), it is less clear whether
354 they impact pollinators or pollination. Folivory, root damage, and stem damage were found to
355 negatively impact several floral traits, as well as pollinator visitation and reproduction
356 (Mutikainen & Delph, 1996; Strauss, Conner & Rush, 1996; Mothershead & Marquis, 2000;
357 Hambäck, 2001; Arceo-Gómez, Parra-Tabla & Navarro, 2009; Hladun & Adler, 2009; Barber &
358 Gorden, 2013; Sasal, Farji-Brener & Raffaele, 2017). However, vegetative damage was also
359 frequently observed to have no effect on each of these traits. It is also possible that plants are
360 better able to compensate for or resist vegetative damage such that there will be no change in
361 floral display or reproduction. For instance, (as with incomplete florivory) plants may switch to
362 self-pollination if floral display is compromised or pollination is limited.
363   While it is clear that vegetative damage can impact pollination and plant reproduction,
364 vegetative damage was also frequently observed to have no effect. This lack of effect may be
365 only representative of small sample size and more studies would find the proportions more
366 similar to what is found with florivory. However, the decrease in the number of studies to find an
367 effect of vegetative herbivory on pollination may be because few studies examined different
368 types of herbivory (Fig. 5) or different taxa simultaneously (Fig. 4; Supplemental Table S3).
369 Therefore, it is difficult to determine whether different types of herbivory may act synergistically
370 or if they interfere with each other (as seen between root herbivory and aboveground herbivory
371 in Barber et al. 2015). The larger proportion of neutral effects of vegetative herbivory on
372 pollination may only be an indication of not considering damage to all types of vegetative
373 tissues. This lack of directly comparing individual species is one weakness of some of the
374 papers included in this study. While comparing the effects of a broader taxonomic scope or
375 community of herbivores or pollinators is good for comparing the net outcomes of interactions,
376 the exact effects and net outcomes of individual species is lost. More research that examine
377 specific species, especially multiple specific species could help illuminate these differences.
378 This is particularly prevalent with how few studies examined individual pollinator species
379 compared to those that studied the entire community (Fig. 4). In contrast, the indirect pathway
380 from vegetative damage to changes in pollination may simply be more heavily regulated by
381 plant physiological responses (Fig. 2) as outlined above and considering multiple species may
382 not change this result. Regardless, the small sample size makes any conclusions about the
383 relative proportion of studies to find significant or neutral effects of vegetative damage dubious.
384   Vegetative herbivory can impact plant populations and communities through plant
385 reproduction, but the role of the indirect effect of vegetative herbivory on pollinators and the role
386 of pollinators in driving co-evolution between plants and non-floral herbivores is less distinct
387 than when examining florivores. In order to determine the relative effect of direct and indirect
388 damage to floral tissue on pollination, these two mechanisms need to be compared more
389 frequently. In this systematic review, only three studies examined the direct and indirect effects
390 of herbivory on floral display and pollination (Fig. 5). Specifically, these three studies compared
391 florivory to folivory. Lucas-Barbosa et al. (2013) examined the behaviour of pollinators of

392 *Brassica nigra* in response to the specialist caterpillar *Pieris brassicae. Pieris brassicae* feeds
393 on the leaves of *B. nigra* at a younger stage, and progress later to consuming flowers.
394 Therefore, while examining damage to two types of tissues, the damage was done by the same
395 individuals. They found there was no effect of *P. brassicae* on pollinators during the folivory
396 stage, while there was an effect at the florivory stage. In a study with the same system by many
397 of the same authors (Lucas-Barbosa et al. 2016) where the effect of damage to vegetative and
398 floral tissues on floral volatiles detected by pollinators was studied, neither folivory nor florivory
399 influenced pollinators. Finally, Mothershead and Marquis (2000) examined the effect of artificial
400 damage to both leaves and buds to the floral traits and seed set of *Oenothera macrocarpa* in
401 the presence and absence of supplemental hand pollination. Both folivory and florivory affected
402 floral traits (both morphology and size), that in turn impacted pollination and seed set. Folivory
403 was not found to directly reduce seed set through reduced floral resources, but rather only
404 indirectly through floral morphology. However, floral damage decreased fruit set (68% reduction)
405 more than foliar damage (18% reduction). While two of these studies point towards florivory
406 having a greater impact on pollination than folivory, two of three studies is not sufficient sample
407 size to determine the relative importance of direct (florivory) over indirect (vegetative herbivory)
408 damage. Only multiple studies that directly compare florivory and other types of herbivory within
409 the same system will be sufficient to determine their relative importance.
410   Similarly, the larger proportion of papers that examined florivory over other forms of
411 herbivory (Fig. 5) or the greater proportion of studies with a negative impact on pollination or
412 reproduction due to florivory is not sufficient to make the claim that florivory has a greater impact
413 on pollination than damage to vegetative tissue. Florivory is the more obvious choice when
414 studying the effects of herbivory on pollination and so a bias in papers towards florivory is
415 expected. Similarly, the sample size of studies that examine any other form of herbivory is
416 particularly low, and so proportions are not necessarily representative. While it is intuitive and
417 may be true that direct damage to floral tissue has a greater impact than indirect damage on
418 pollination, there is not sufficient evidence to make this claim.
419   As mentioned previously, some herbivores act as both herbivores and pollinators at
420 different ontogenetic stages. However, only a single species, the *B. nigra* specialist *P.*
421 *brassicae,* was examined as both a herbivore and a pollinator. Furthermore, *P. brassicae* was
422 only examined as both herbivore and pollinator of *B. nigra* in a single study (Lucas-Barbosa et.
423 Al 2016), although it was also used as a herbivore in Lucas-Barbosa et al. (2013) and as a
424 pollinator in Rusman et al. (2019). The intricate relationship and co-evolution between species
425 that change between negative and positive interactions is not one that is unstudied (see
426 Nakazawa, 2015). Strategies that reduce the impact of herbivores at an early stage that might
427 negatively impact the later production of floral resources would be beneficial to both plant and
428 herbivore in this case, even more so than with species that do not share this relationship.
429 However, clearly the net outcome of early stage herbivory on plant reproduction and late stage
430 pollination is lacking within the literature.
431   The joint impact of damage to multiple tissues can be extended to the effects of
432 herbivores that do not have a plant tissue preference. Most studies examined damage to
433 specific tissues; however, a number of studies examined damage to unspecified tissues,
434 representing both direct and indirect mechanisms that are not differentiated. Grazing
435 encompasses possible damage to flowers, leaves, and stems. Grazing is of particular import

436   because of its potential severity and anthropogenic causes. The agricultural industry plays a
437   large role in the impact humans have in creating disturbed ecosystems (Kitzes et al., 2008).
438   Most studies that examined direct or indirect damage to floral tissue used insects as focal
439   herbivores, those that looked at unspecified damage exclusively used mammals (Fig. 4). While
440   studies frequently look at grazing by large mammals such as deer and cattle at a community
441   level—examining the plant, or even floral diversity of a system (Olff & Ritchie, 1998; Kohyani et
442   al., 2008; Herrero-Jáuregui & Oesterheld, 2018), it is rare for these studies to further examine
443   the pollination consequences of grazing. Studies that examined grazing reported some negative
444   effect of grazing on plant reproduction or pollinator visitation. Grazing also impacted floral
445   morphology, number, phenology, and pollen production, but the mechanisms were not clearly
446   reported in primary studies. By studying the synergistic effects of multiple effect pathways, we
447   can better understand how grazing can impact vegetation.
448   The overall impact of the community of herbivores can impact plant resource allocation,
449   compensation and therefore pollination. However, the effects of herbivores on pollination are
450   frequently examined through a single herbivore and feeding strategy. Interactions do not exist in
451   isolation: plants generally experience damage from multiple herbivorous taxa (often including
452   both insects and mammals) and damage to multiple vegetative and floral tissues (Maddox &
453   Root, 1987; Farré-Armengol et al., 2015; Wise & Rausher, 2016). While examining the impact of
454   individual herbivores is important, in order to study the resilience and community dynamics of
455   plants and pollinators in relation to herbivores, it is important to consider multiple herbivores as
456   well as both direct and indirect impacts on floral tissue, following the conceptual framework
457   outlined in Fig. 2. The indirect effect of herbivores on pollinators can mediate co-evolutionary
458   processes between plants and herbivores and plants and pollinators. Therefore, understanding
459   how different types and forms of herbivory impact pollinators is important for understanding both
460   ecological and evolutionary stability.

461

Conclusions

463   Both direct and indirect damage to floral tissue can impact pollination and plant
464   reproduction. However, direct and indirect damage to floral tissue is rarely examined in concert.
465   The relative importance of the direct and indirect mechanisms and synergistic effects have
466   important implications for ecological resilience and stability in evolutionary processes. However,
467   this relative importance is almost never examined with the focus lying on each type individually.
468   The collection of herbivores that interact with plants can include species that feed on all types of
469   tissue either simultaneously or temporally separated that the plant then integrates into growth,
470   allocation, defense, or phenology. This in turn can impact pollinators and pollination, making
471   these two plant-animal interactions intimately linked.

472

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475

References

477   Adler LS. 2000. Alkaloid uptake increases fitness in a hemiparasitic plant via reduced herbivory
478   and increased pollination. *The American Naturalist* 156:92–99. DOI: 10.1086/303374.

479   Adler LS, Karban R, Strauss SY. 2001. Direct and indirect effects of alkaloids on plant fitness
480   Via herbivory and pollination. *Ecology* 82:2032–2044.
481   Agrawal AA, Rudgers JA, Botsford LW, Cutler D, Gorin JB, Lundquist CJ, Spitzer BW, Swann
482   AL. 2000. Benefits and constraints on plant defense against herbivores: spines influence
483   the legitimate and illegitimate flower visitors of yellow star thistle , *Centaurea solstitialis* L.
484   (Asteraceae). *The Southwestern Naturalist* 45:1–5. DOI: 10.2307/3672545.
485   Åhman I, Lehrman A, Ekbom B. 2009. Impact of herbivory and pollination on performance and
486   competitive ability of oilseed rape transformed for pollen beetle resistance. *Arthropod-Plant*
487   *Interactions* 3:105–113. DOI: 10.1007/s11829-009-9061-z.
488   Arceo-Gómez G, Parra-Tabla V, Navarro J. 2009. Changes in sexual expression as result of
489   defoliation and environment in a monoecious shrub in Mexico: implications for pollination.
490   *Biotropica* 41:435–441. DOI: 10.1111/j.1744-7429.2009.00502.x.
491   Anderson LL, Paige KN. 2003. Multiple herbivores and coevolutionary interactions in an
492   Ipomopsis hybrid swarm. *Evolutionary Ecology* 17:139–156. DOI:
493   10.1023/A:1023066101074.
494   Aschero V, Vázquez DP. 2009. Habitat protection, cattle grazing and density-dependent
495   reproduction in a desert tree. *Austral Ecology* 34:901–907. DOI: 10.1111/j.1442-
496   9993.2009.01997.x.
497   Avila-Sakar G, Simmers SM, Stephenson AG. 2003. The interrelationships among leaf damage,
498   anther development, and pollen production in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae).
499   *International Journal of Plant Sciences* 164:395–404. DOI: 10.1086/374196.
500   Barber NA, Gorden NLS. 2013. How do belowground organisms influence plant-pollinator
501   interactions? *Journal of Plant Ecology* 8:1–11. DOI: 10.1093/jpe/rtu012.
502   Barber NA, Milano NJ, Kiers ET, Theis N, Bartolo V, Hazzard R V., Adler LS. 2015. Root
503   herbivory indirectly affects above- and below-ground community members and directly
504   reduces plant performance. *Journal of Ecology* 103:1509–1518. DOI: 10.1111/1365-
505   2745.12464.
506   Benning JW, Moeller DA. 2019. Maladaptation beyond a geographic range limit driven by
507   antagonistic and mutualistic biotic interactions across an abiotic gradient. *Evolution*:1–16.
508   DOI: 10.1111/evo.13836.
509   Boivin T, Doublet V, Candau JN. 2019. The ecology of predispersal insect herbivory on tree
510   reproductive structures in natural forest ecosystems. *Insect Science* 26:182–198. DOI:
511   10.1111/1744-7917.12549.
512   Borrett SR, Whipple SJ, Patten BC. 2010. Rapid development of indirect effects in ecological
513   networks. *Oikos* 119:1136–1148. DOI: 10.1111/j.1600-0706.2009.18104.x.
514   Botto-Mahan C, Ramírez PA, Ossa CG, Medel R, Ojeda-Camacho M, González A V. 2011.
515   Floral herbivory affects female reproductive success and pollinator visitation in the
516   perennial herb *Alstroemeria ligtu* (Alstroemeriaceae). *International Journal of Plant*
517   *Sciences* 172:1130–1136. DOI: 10.1086/662029.
518   Brody AK. 1997. Effects of pollinators, herbivores, and seed predators on flowering phenology.
519   *Ecology* 78:1624–1631. DOI: 10.1890/0012-9658(1997)078{[}1624:EOPHAS]2.0.CO;2.
520   Brody AK, Irwin RE. 2012. When resources don't rescue: flowering phenology and species
521   interactions affect compensation to herbivory in *Ipomopsis aggregata*. *Oikos* 121:1424–
522   1434. DOI: 10.1111/j.1600-0706.2012.20458.x.

523   Buchanan AL. 2014. Effects of damage and pollination on sexual and asexual reproduction in a
524   flowering clonal plant. *Plant Ecology* 216:273–282. DOI: 10.1007/s11258-014-0434-8.
525   Caballero P, Ossa CG, Gonzáles WL, González-Browne C, Astorga G, Murúa MM, Medel R.
526   2013. Testing non-additive effects of nectar-robbing ants and hummingbird pollination on
527   the reproductive success of a parasitic plant. *Plant Ecology* 214:633–640. DOI:
528   10.1007/s11258-013-0195-9.
529   Canela MBF, Sazima M. 2003. Florivory by the crab *Armases angustipes* (Grapsidae)
530   influences hummingbird visits to *Aechmea pectinata* (Bromeliaceae). *Biotropica* 35:289–
531   294. DOI: 10.1111/j.1744-7429.2003.tb00287.x.
532   Cardel YJ, Koptur S. 2010. Effects of florivory on the pollination of flowers: an experimental field
533   study with a perennial plant. *International Journal of Plant Sciences* 171:283–292. DOI:
534   10.1086/650154.
535   Cares-Suárez R, Poch T, Acevedo RF, Acosta-Bravo I, Pimentel C, Espinoza C, Cares RA,
536   Muñoz P, González A V, Botto-Mahan C. 2011. Do pollinators respond in a dose-
537   dependent manner to flower herbivory?: an experimental assessment in *Loasa tricolor*
538   (Loasaceae). *Gayana. Botánica* 68:176–181. DOI: 10.4067/S0717-66432011000200007.
539   Cariveau DP, Norton AP. 2014. Direct effects of a biocontrol agent are greater than indirect
540   effects through flower visitors for the alien plant Dalmatian toadflax (Linaria dalmatica:
541   Scrophulariaceae). *Biological Invasions* 16:1951–1960. DOI: 10.1007/s10530-013-0638-1.
542   Chalcoff VR, Lescano MN, Devegili AM. 2019. Do novel interactions with local fauna have
543   reproductive consequences for exotic plants? A case study with thistles, ants, aphids, and
544   pollinators. *Plant Ecology* 220:125–134. DOI: 10.1007/s11258-019-00907-2.
545   Chen M. 2008. Inducible direct plant defense against insect herbivores : A review. *Insect*
546   *Science* 15:101–114.
547   Culley TM, Weller SG, Sakai AK. 2002. The evolution of wind pollination in angiosperms.
548   *Trends in Ecology & Evolution* 17:361–369.
549   Cunningham SA. 1995. Ecological constraints on fruit initiation by *Calyptrogyne ghiesberghtiana*
550   (Arecaceae): floral herbivory, pollen availability, and visitation by pollinating bats. *American*
551   *Journal of Botany* 82:1527–1536.
552   Danderson CA, Molano-Flores B. 2010. Effects of herbivory and inflorescence size on insect
553   visitation to *Eryngium yuccifolium* (Apiaceae) a prairie plant. *The American Midland*
554   *Naturalist* 163:234–246. DOI: 10.1674/0003-0031-163.1.234.
555   Dicenta F, Ortega E, Cánovas JA, Egea J. 2002. Self-pollination vs. cross-pollination in almond:
556   Pollen tube growth, fruit set and fruit characteristics. *Plant Breeding* 121:163–167. DOI:
557   10.1046/j.1439-0523.2002.00689.x.
558   Enri SR, Probo M, Farruggia A, Lanore L, Blanchetete A, Dumont B. 2017. A biodiversity-
559   friendly rotational grazing system enhancing flower-visiting insect assemblages while
560   maintaining animal and grassland productivity. *Agriculture, Ecosystems and Environment*
561   241:1–10. DOI: 10.1016/j.agee.2017.02.030.
562   Farré-Armengol G, Filella I, Llusia J, Primante C, Peñuelas J. 2015. Enhanced emissions of
563   floral volatiles by *Diplotaxis erucoides* (L.) in response to folivory and florivory by *Pieris*
564   *brassicae* (L.). *Biochemical Systematics and Ecology* 63:51–58. DOI:
565   10.1016/j.bse.2015.09.022.
566   Fowler RE, Rotheray EL, Goulson D. 2016. Floral abundance and resource quality influence

567   pollinator choice. *Insect Conservation and Diversity* 9:481–494. DOI: 10.1111/icad.12197.

568   García-cervigón, AI, Iriondo JM, Linares JC, and Olano JM. 2016. Disentangling Facilitation
569   Along the Life Cycle : Impacts of Plant – Plant Interactions at Vegetative and Reproductive
570   Stages in a Mediterranean Forb. *Frontiers in Plant Science* 7:1–11. DOI:
571   10.3389/fpls.2016.00129.

572   Garcia LC, Eubanks MD. 2019. Overcompensation for insect herbivory: a review and meta-
573   analysis of the evidence. *Ecology* 100:02585. DOI: 10.1002/ecy.2585.

574   Garrido P, Mårell A, Öckinger E, Skarin A, Jansson A, Thulin CG. 2019. Experimental rewilding
575   enhances grassland functional composition and pollinator habitat use. *Journal of Applied*
576   *Ecology* 56:946–955. DOI: 10.1111/1365-2664.13338.

577   Giurfa M, Dafni A, Neal PR. 1999. Floral Symmetry and Its Role in Plant-Pollinator Systems.
578   *International Journal of Plant Sciences* 160:S41–S50. DOI: 10.1086/314214.

579   Hambäck PA. 2001. Direct and indirect effects of herbivory: Feeding by spittlebugs affects
580   pollinator visitation rates and seedset of *Rudbeckia hirta*. *Ecoscience* 8:45–50. DOI:
581   10.1080/11956860.2001.11682629.

582   Hawkes C V., Sullivan JJ. 2001. The impact of herbivory on plants in different resource
583   conditions: a meta-analysis. *Ecology* 82:2045–2058.

584   Heil M. 2008. Indirect defence via tritrophic interactions. *New Phytologist* 178:41–61. DOI:
585   10.1111/j.1469-8137.2007.02330.x.

586   Herrero-Jáuregui C, Oesterheld M. 2018. Effects of grazing intensity on plant richness and
587   diversity: a meta-analysis. *Oikos* 127:757–766. DOI: 10.1111/oik.04893.

588   Hladun KR, Adler LS. 2009. Influence of leaf herbivory, root herbivory, and pollination on plant
589   performance in *Cucurbita moschata*. *Ecological Entomology* 34:144–152. DOI:
590   10.1111/j.1365-2311.2008.01060.x.

591   Huth CJ, Pellmyr O. 1997. Non-random fruit retention in *Yucca filamentosa*: consequences for
592   an obligate mutualism. *Oikos* 78:576–584. DOI: 10.2307/3545620.

593   Jorge A, Loureiro J, Castro S. 2015. Flower biology and breeding system of *Salvia sclareoides*
594   Brot. (Lamiaceae). *Plant Systematics and Evolution* 301:1485–1497. DOI:
595   10.1007/s00606-014-1169-7.

596   Juenger T, Bergelson J. 1997. Pollen and resource limitation of compensation to herbivory in
597   scarlet gilia, *Ipomopsis aggregata*. *Ecology* 78:1684–1695.

598   Kaczorowski RL, Seliger AR, Gaskett AC, Wigsten SK, Raguso RA. 2012. Corolla shape vs.
599   size in flower choice by a nocturnal hawkmoth pollinator. *Functional Ecology* 26:577–587.
600   DOI: 10.1111/j.1365-2435.2012.01982.x.

601   Kelly D, Ladley JJ, Robertson AW, Crowfoot L. 2008. Flower predation by *Zelleria maculata*
602   (Lepidoptera) on *Peraxilla* mistletoes: effects of latitude and fragmentation, and impact on
603   fruit set. *New Zealand Journal of Ecology* 32:186–196.

604   Kitzes J, Wackernagel M, Loh J, Peller A, Goldfinger S, Cheng D, Tea K. 2008. Shrink and
605   share: humanity's present and future Ecological Footprint. *Philosophical Transactions of*
606   *the Royal Society B: Biological Sciences* 363:467–475. DOI: 10.1098/rstb.2007.2164.

607   Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke
608   T. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of*
609   *the Royal Society B: Biological Sciences* 274:303–313. DOI: 10.1098/rspb.2006.3721.

610   Knight TM. 2004. The effects of herbivory and pollen limitation on a declining population of

611   *Trillium grandiflorum*. *Ecological Applications* 14:915–928. DOI: 10.1890/03-5048.

612 Kohyani PT, Bossuyt B, Bonte D, Hoffmann M. 2008. Grazing as a management tool in dune

613   grasslands: Evidence of soil and scale dependence of the effect of large herbivores on

614   plant diversity. *Biological Conservation* 141:1687–1694. DOI:

615   10.1016/j.biocon.2008.04.010.

616 Krupnick GA, Weis AE. 1999. The effect of floral herbivory on male and female reproductive

617   success in *Isomeris arborea*. *Ecology* 80:135–149. DOI: 10.1890/0012-

618   9658(1999)080[0135:TEOFHO]2.0.CO;2.

619 Krupnick GA, Weis AE, Campbell DR. 1999. The consequences of floral herbivory for pollinator

620   service to Isomeris arborea. *Ecology* 80:125–134.

621 Lavi R, Sapir Y. 2015. Are pollinators the agents of selection for the extreme large size and dark

622   color in Oncocyclus irises? *New Phytologist* 205:369–377. DOI: 10.1111/nph.12982.

623 Lazaro A, Totland O. 2010. Local floral composition and the behaviour of pollinators: attraction

624   to and foraging within experimental patches. *Ecological Entomology* 35:652–661. DOI:

625   10.1111/j.1365-2311.2010.01223.x.

626 Leavitt H, Robertson IC. 2006. Petal herbivory by chrysomelid beetles (*Phyllotreta* sp.) is

627   detrimental to pollination and seed production in *Lepidium papilliferum* (Brassicaceae).

628   *Ecological Entomology* 31:657–660. DOI: 10.1111/j.1365-2311.2006.00820.x.

629 Lehtilä K, Strauss SY. 1999. Effects of foliar herbivory on male and female reproductive traits of

630   wild radish, Raphanus raphanistrum. *Ecology* 80:116–124. DOI: 10.1890/0012-

631   9658(1999)080[0116:EOFHOM]2.0.CO;2.

632 Liao K, Gituru RW, Guo YH, Wang QF. 2013. Effects of floral herbivory on foraging behaviour of

633   bumblebees and female reproductive success in Pedicularis gruina (Orobanchaceae).

634   *Flora* 208:562–569. DOI: 10.1016/j.flora.2013.08.007.

635 Lohman DJ, Zangerl AR, Berenbaum MR. 1996. Impact of floral herbivory by parsnip webworm

636   (Oecophoridae: *Depressaria pastinacella* Duponchel) on pollination and fitness of wild

637   parsnip (Apiaceae: *Pastinaca sativa* L.). *The American Midland Naturalist* 136:407–412.

638 Lopez-Toledo L, Perez-Decelis A, Macedo-Santana F, Cuevas E, Endress BA. 2018. Chronic

639   leaf harvesting reduces reproductive success of a tropical dry forest palm in northern

640   Mexico. *PLoS ONE* 13:1–16. DOI: 10.1371/journal.pone.0205178.

641 Louthan A, Valencia E, Martins DJ, Guy T, Goheen J, Palmer T, Doak D. 2019. Large mammals

642   generate both top-down effects and extended trophic cascades on floral-visitor

643   assemblages. *Journal of Tropical Ecology* 35:185–198. DOI:

644   10.1017/S0266467419000142.

645 Lucas-Barbosa D. 2016. Integrating studies on plant-pollinator and plant-herbivore interactions.

646   *Trends in Plant Science* 21:125–133. DOI: 10.1016/j.tplants.2015.10.013.

647 Lucas-Barbosa D, Van Loon JJA, Dicke M. 2011. The effects of herbivore-induced plant

648   volatiles on interactions between plants and flower-visiting insects. *Phytochemistry*

649   72:1647–1654. DOI: 10.1016/j.phytochem.2011.03.013.

650 Lucas-Barbosa D, van Loon JJA, Gols R, van Beek TA, Dicke M. 2013. Reproductive escape:

651   annual plant responds to butterfly eggs by accelerating seed production. *Functional*

652   *Ecology* 27:245–254. DOI: 10.1111/1365-2435.12004.

653 Lucas-Barbosa D, Sun P, Hakman A, van Beek TA, van Loon JJA, Dicke M. 2016. Visual and

654   odour cues: plant responses to pollination and herbivory affect the behaviour of flower

655   visitors. *Functional Ecology* 30:431–441. DOI: 10.1111/1365-2435.12509.

656   Maddox GD, Root RB. 1987. Resistance to 16 diverse species of herbivorous insects within a

657   population of goldenrod , *Solidago Mtissima*: genetic variation and heritability. *Oecologia*

658   72:8–14.

659   Malo JE, Leirana-Alcocer J, Parra-Tabla V. 2001. Population fragmentation, florivory, and the

660   effects of flower morphology alterations on the pollination success of *Myrmecophila tibicinis*

661   (Orchidaceae). *Biotropica* 33:529–534. DOI: 10.1111/j.1744-7429.2001.tb00207.x.

662   McCall AC. 2010. Does dose-dependent petal damage affect pollen limitation in an annual

663   plant? *Botany* 88:601–606. DOI: 10.1139/B10-032.

664   McCall AC, Irwin RE. 2006. Florivory: The intersection of pollination and herbivory. *Ecology*

665   *Letters* 9:1351–1365. DOI: 10.1111/j.1461-0248.2006.00975.x.

666   Michalet R, Chen SY, An LZ, Wang XT, Wang YX, Guo P, Ding CC, Xiao S. 2015.

667   Communities: Are they groups of hidden interactions? *Journal of Vegetation Science*

668   26:207–218. DOI: 10.1111/jvs.12226.

669   Missagia CCC, Alves MAS. 2017. Florivory and floral larceny by fly larvae decrease nectar

670   availability and hummingbird foraging visits at *Heliconia* (Heliconiaceae) flowers. *Biotropica*

671   49:13–17. DOI: 10.1111/btp.12368.

672   Moranz RA, Fuhlendorf SD, Engle DM. 2014. Making sense of a prairie butterfly paradox: the

673   effects of grazing, time since fire, and sampling period on regal fritillary abundance.

674   *Biological Conservation* 173:32–41. DOI: 10.1016/j.biocon.2014.03.003.

675   Mothershead K, Marquis RJ. 2000. Fitness impact of herbivore through indirect effects on plant-

676   pollinator interactions in *Oenothera macrocarpa*. *Ecology* 81:30–40. DOI: 10.1890/0012-

677   9658(2000)081[0030:FIOHTI]2.0.CO;2.

678   Motzke I, Tscharntke T, Wanger TC, Klein AM. 2015. Pollination mitigates cucumber yield gaps

679   more than pesticide and fertilizer use in tropical smallholder gardens. *Journal of Applied*

680   *Ecology* 52:261–269. DOI: 10.1111/1365-2664.12357.

681   Munguía-Rosas MA, Arias LM, Jurado-Dzib SG, Mezeta-Cob CR, Parra-Tabla V. 2015. Effects

682   of herbivores and pollinators on fruit yield and survival in a cleistogamous herb. *Plant*

683   *Ecology* 216:517–525. DOI: 10.1007/s11258-015-0455-y.

684   Mutikainen P, Delph LF. 1996. Effects of herbivory on male reproductive success in plants.

685   *Oikos* 75:353–358.

686   Nakazawa T. 2015. Ontogenetic niche shifts matter in community ecology: a review and future

687   perspectives. *Population Ecology* 57:347–354. DOI: 10.1007/s10144-014-0448-z.

688   Ohgushi T. 2005. Indirect interaction webs: herbivore-induced effects through trait change in

689   plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81–105. DOI:

690   10.1146/annurev.ecolsys.36.091704.175523.

691   Olff H, Ritchie ME. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology*

692   *and Evolution* 13:261–265. DOI: 10.1016/S0169-5347(98)01364-0.

693   Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals?

694   *Oikos* 120:321–326. DOI: 10.1111/j.1600-0706.2010.18644.x.

695   Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC,

696   D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnut TF, Ricketts TH, Kura Y,

697   Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001. Terrestrial Ecoregions of the

698   World: A New Map of Life on Earth. *BioScience* 51:933-938. CC BY-NC 3.0

699   https://creativecommons.org/licenses/by-nc/3.0/.

700   Parachnowitsch AL, Kessler A. 2010. Pollinators exert natural selection on flower size and floral
701   display in Penstemon digitalis. *New Phytologist* 188:393–402. DOI: 10.1111/j.1469-
702   8137.2010.03410.x.

703   Pellmyr O. 2003. Yuccas, Yucca Moths, and Coevolution: A Review. *Annals of the Missouri*
704   *Botanical Garden* 90:35–55.

705   Pilosof S, Porter MA, Pascual M, Kéfi S. 2017. The multilayer nature of ecological networks.
706   *Nature Ecology & Evolution* 1:1–35. DOI: 10.1038/s41559-017-0101.

707   Pratt PD, Rayamajhi MB, Van TK, Center TD. 2005. Herbivory alters resource allocation and
708   compensation in the invasive tree *Melaleuca quinquenervia*. *Ecological Entomology*
709   30:316–326.

710   Proulx SR, Promislow DEL, Phillips PC. 2005. Network thinking in ecology and evolution.
711   Trends in Ecology and Evolution 20:345–353. DOI: 10.1016/j.tree.2005.04.004.

712   QGIS Development Team. 2019. QGIS Geographic Information System. *Open Source*
713   *Geospatial Foundation Project.* http://qgis.osgeo.org.

714   Raffaele E, Veblen TT, Blackhall M, Tercero-Bucardo N. 2011. Synergistic influences of
715   introduced herbivores and fire on vegetation change in northern Patagonia, Argentina.
716   *Journal of Vegetation Science* 22:59–71. DOI: 10.1111/j.1654-1103.2010.01233.x.

717   Rodríguez I, Gumbert A, De Ibarra NH, Kunze J, Giurfa M. 2004. Symmetry is in the eye of the
718   "beeholder": Innate preference for bilateral symmetry in flower-naïve bumblebees.
719   *Naturwissenschaften* 91:374–377. DOI: 10.1007/s00114-004-0537-5.

720   Rusman Q, Poelman EH, Nowrin F, Polder G, Lucas-Barbosa D. 2019. Floral plasticity:
721   Herbivore-species-specific-induced changes in flower traits with contrasting effects on
722   pollinator visitation. *Plant Cell and Environment* 42:1882–1896. DOI: 10.1111/pce.13520.

723   Ruttan A, Lortie CJ. 2013. A systematic review of the attractant-decoy and repellent-plant
724   hypotheses: Do plants with heterospecific neighbours escape herbivory? Journal of Plant
725   *Ecology* 8:337–346. DOI: 10.1093/jpe/rtu030.

726   Santangelo JS, Thompson KA, Johnson MTJ. 2019. Herbivores and plant defences affect
727   selection on plant reproductive traits more strongly than pollinators. *Journal of Evolutionary*
728   *Biolog*y 32:4–18. DOI: 10.1111/jeb.13392.

729   Sasal Y, Farji-Brener A, Raffaele E. 2017. Fire modulates the effects of introduced ungulates on
730   plant–insect interactions in a Patagonian temperate forest. *Biological Invasions* 19:2459–
731   2475. DOI: 10.1007/s10530-017-1455-8.

732   Scopece G, Frachon L, Cozzolino S. 2019. Do native and invasive herbivores have an effect on
733   *Brassica rapa* pollination? *Plant Biology* 21:927–934. DOI: 10.1111/plb.12985.

734   Sõber V, Moora M, Teder T. 2010. Florivores decrease pollinator visitation in a self-incompatible
735   plant. *Basic and Applied Ecology* 11:669–675. DOI: 10.1016/j.baae.2010.09.006.

736   Sõber V, Teder T, Moora M. 2009. Contrasting effects of plant population size on florivory and
737   pollination. *Basic and Applied Ecology* 10:737–744. DOI: 10.1016/j.baae.2009.06.003.

738   Soler R, van der Putten WH, Harvey JA, Vet LEM, Dicke M, Bezemer TM. 2012. Root herbivore
739   effects on aboveground multitrophic interactions: patterns, processes and mechanisms.
740   *Journal of Chemical Ecology* 38:755–767. DOI: 10.1007/s10886-012-0104-z.

741   Soper Gorden NL, Adler LS. 2016. Florivory shapes both leaf and floral interactions. *Ecosphere*
742   7:1–15. DOI: 10.1002/ecs2.1326.

743   Strauss SY. 1997. Floral characters link herbivores, pollinators, and plant fitness. *Ecology*
744   78:1640–1645.
745   Strauss SY, Conner JK, Rush SL. 1996. Foliar herbivory affects floral characters and plant
746   attractiveness to pollinators: implications for male and female plant fitness. *The American*
747   *Naturalist* 147:1098–1107.
748   Strauss SY, Murch P. 2004. Towards an understanding of the mechanisms of tolerance:
749   Compensating for herbivore damage by enhancing a mutualism. *Ecological Entomology*
750   29:234–239. DOI: 10.1111/j.0307-6946.2004.00587.x.
751   Suárez-Esteban A, Delibes M, Fedriani JM. 2014. Unpaved roads disrupt the effect of
752   herbivores and pollinators on the reproduction of a dominant shrub. *Basic and Applied*
753   *Ecology* 15:524–533. DOI: 10.1016/j.baae.2014.08.001.
754   Suárez LH, Gonzáles WL, Gianoli E. 2009. Foliar damage modifies floral attractiveness to
755   pollinators in *Alstroemeria exerens*. *Evolutionary Ecology* 23:545–555. DOI:
756   10.1007/s10682-008-9254-4.
757   Sutter L, Albrecht M. 2016. Synergistic interactions of ecosystem services: pest control boosts
758   crop yield increase through insect pollination. *Proceedings of the Royal Society B*. DOI:
759   10.1098/rspb.2015.2529.
760   Thompson JD. 2001. How do visitation patterns vary among pollinators in relation to floral
761   display and floral design in a generalist pollination system? *Oecologia* 126:386–394. DOI:
762   10.1007/s004420000531.
763   Torres I, Salinas L, Lara C, Castillo-Guevara C. 2008. Antagonists and their effects in a
764   hummingbird–plant interaction: Field experiments. *Ecoscience* 15:65–72. DOI:
765   10.2980/1195-6860(2008)15[65:AATEIA]2.0.CO;2.
766   Tsuji K, Dhami MK, Cross DJR, Rice CP, Romano NH, Fukami T. 2016. Florivory and pollinator
767   visitation: A cautionary tale. *AoB PLANTS* 8. DOI: 10.1093/aobpla/plw036.
768   Vaughton G, Ramsey M. 2006. Selfed seed set and inbreeding depression in obligate seeding
769   populations of *Banksia marginata*. *Proceedings of the Linnean Society of New South*
770   *Wales* 127:19–25.
771   Valdivia CE, Niemeyer HM. 2005. Reduced maternal fecundity of the high Andean perennial
772   herb *Alstroemeria umbellata* (Alstroemeriaceae) by aphid herbivory. *New Zealand Journal*
773   *of Ecology* 29:321–324.
774   Vallius E, Salonen V. 2006. Allocation to reproduction following experimental defoliation in
775   *Platanthera bifolia* (Orchidaceae). *Plant Ecology* 183:291–304. DOI: 10.1007/s11258-005-
776   9040-0.
777   Vazquez DP, Simberloff D. 2004. Indirect effects of an introduced ungulate on pollination and
778   plant reproduction. *Ecological Monographs* 74:281–308.
779   Vulliamy B, Potts SG, Willmer PG. 2006. The effects of cattle grazing on plant-pollinator
780   communities in a fragmented Mediterranean landscape. *Oikos* 114:529–543. DOI:
781   10.1111/j.2006.0030-1299.14004.x.
782   Wise MJ, Cummins JJ, De Young C. 2008. Compensation for floral herbivory in *Solanum*
783   *carolinense*: Identifying mechanisms of tolerance. *Evolutionary Ecology* 22:19–37. DOI:
784   10.1007/s10682-007-9156-x.
785   Wise MJ, Rausher MD. 2016. Costs of resistance and correlational selection in the multiple-
786   herbivore community of *Solanum carolinense*. *Evolution* 70:2411–2420. DOI:

787   10.1111/evo.13035.

788   Zangerl AR, Berenbaum MR. 2009. Effects of florivory on floral volatile emissions and

789   pollination success in the wild parsnip. *Arthropod-Plant Interactions* 3:181–191. DOI:

790   10.1007/s11829-009-9071-x.

791

Figure 1

PRISMA diagram for the progression of papers included in the analyses.

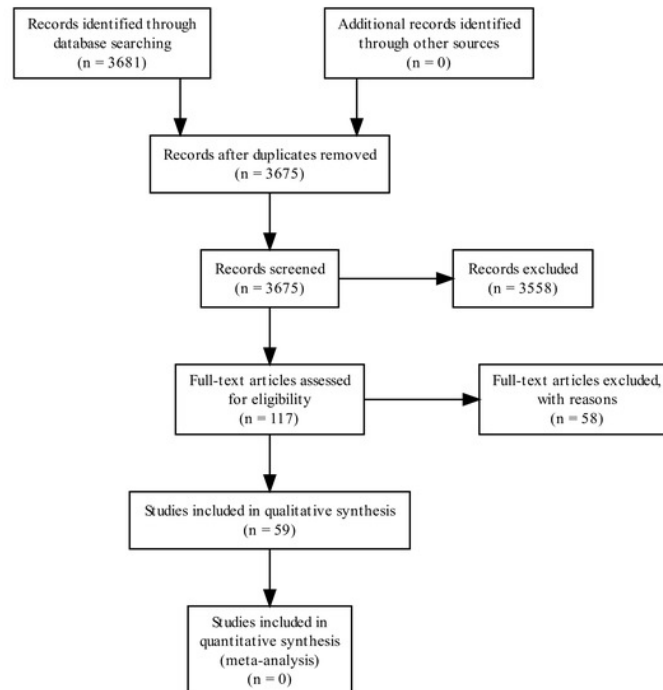



Figure 2

Mechanisms of damage by herbivores that can impact pollination and therefore seed set.

Solid lines represent direct interactions and dotted lines indirect interactions. The two main pathways are direct (direct damage to floral tissue influences pollinators; shown lighter in orange) and indirect (damage to vegetative tissue indirectly effects floral traits; shown in darker in blue). Lines and boxes in black represent interactions and steps shared by both pathways. The thick dotted lines represent the net indirect interaction of plant damage on pollinators (and pollination) that was the focus of this review.

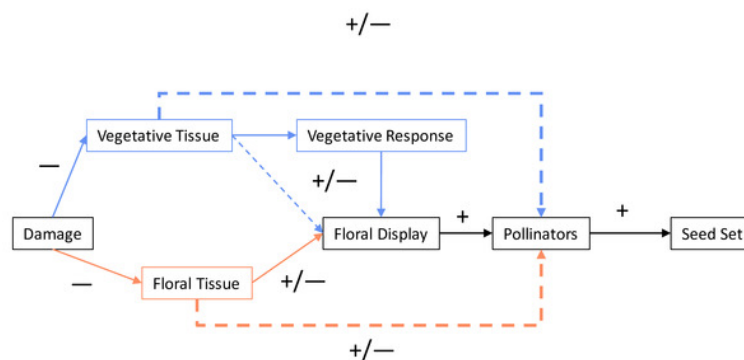



Figure 3

Geographical distribution of studies (N=56; 3 studies had no geographic information) across biomes that examined the impact of both herbivores and pollinators.

Studies spanned over 20 countries and 11 biomes. Biomes were generated from Terrestrial Ecoregions of the World, originating from the World Wildlife Fund (Olson et al. 2001; CC BY-NC 3.0 https://creativecommons.org/licenses/by-nc/3.0/).

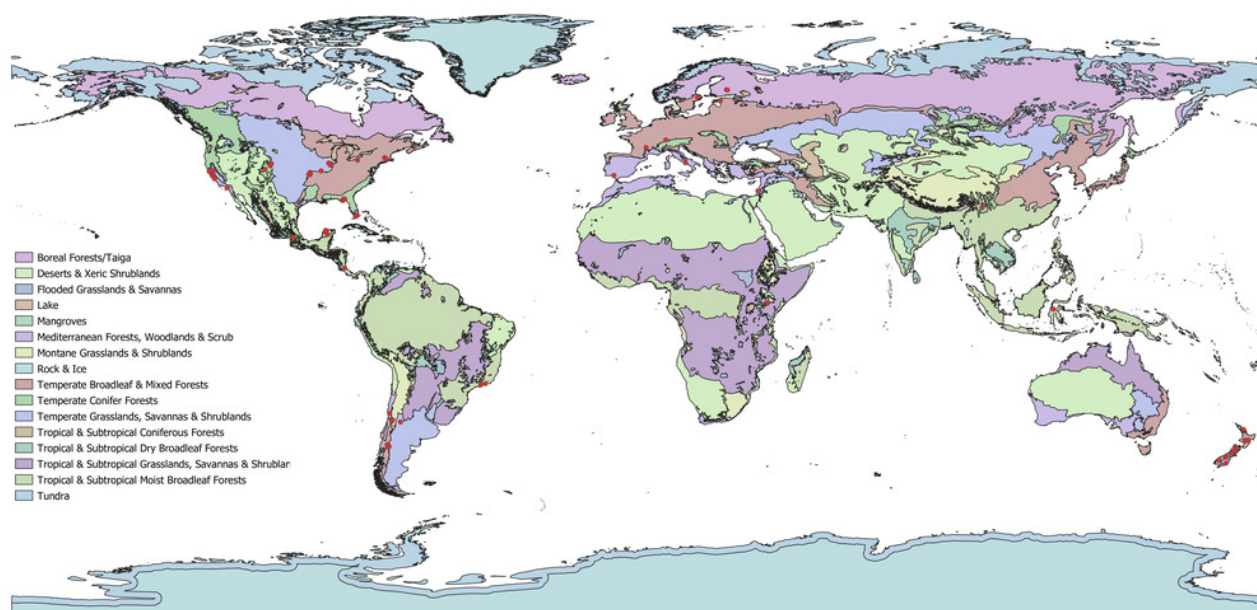



Figure 4

Network showing the interactions between herbivores, plants, and pollinators found within the 61 studies included in this review.

Links are coloured by whether herbivores had a direct, indirect, or unspecified effect (or both direct and indirect) on floral tissue within the study. Line thickness represents multiple interactions between those two species. Community refers to studies where the herbivores, plants, or pollinators consisted of whatever species were found within the natural community and not restricted. Plant species in which no herbivores or pollinators were used within the study (e.g. herbivory was artificially mimicked and pollination was measured passively through hand pollination) are not included.

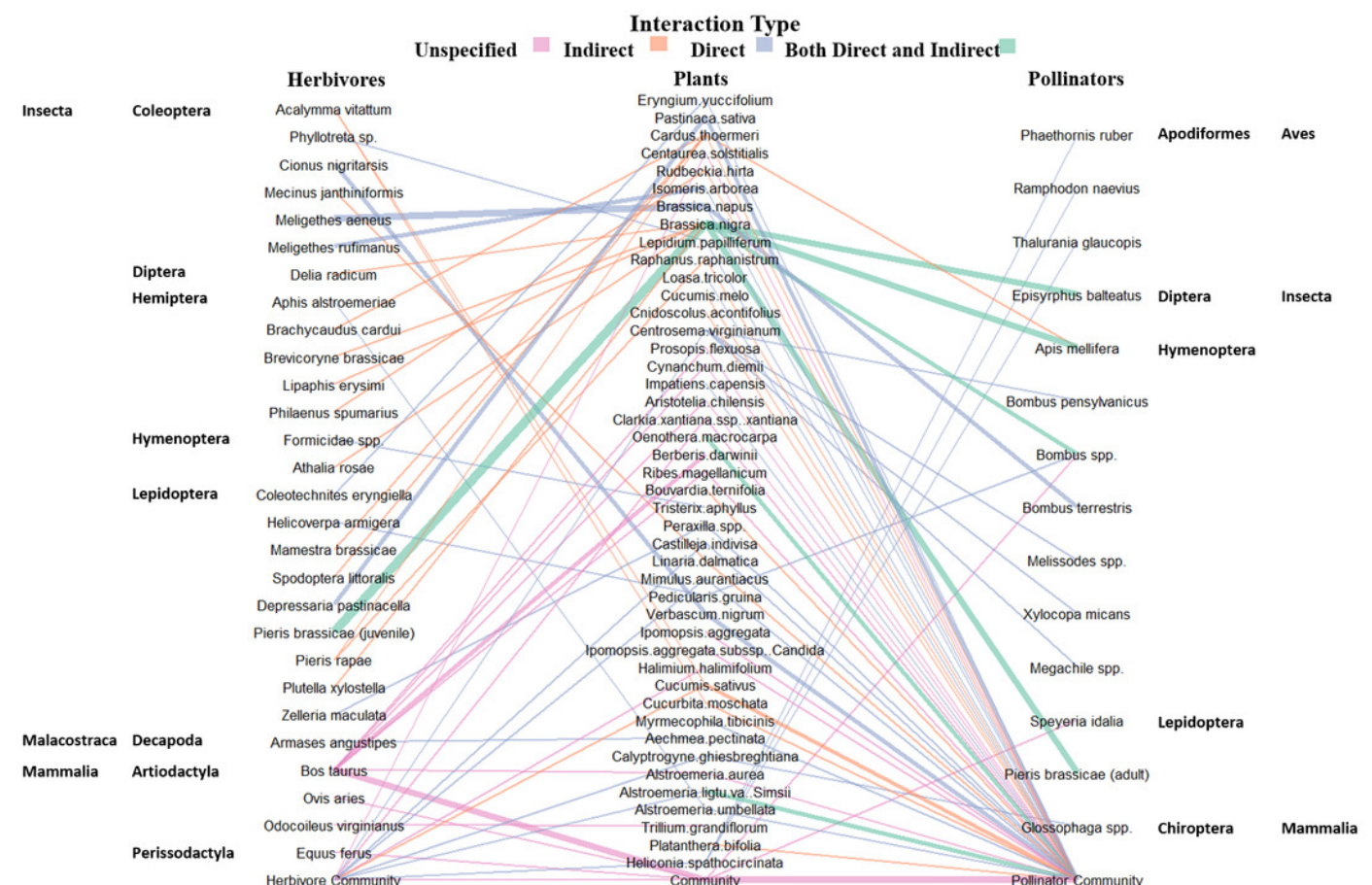
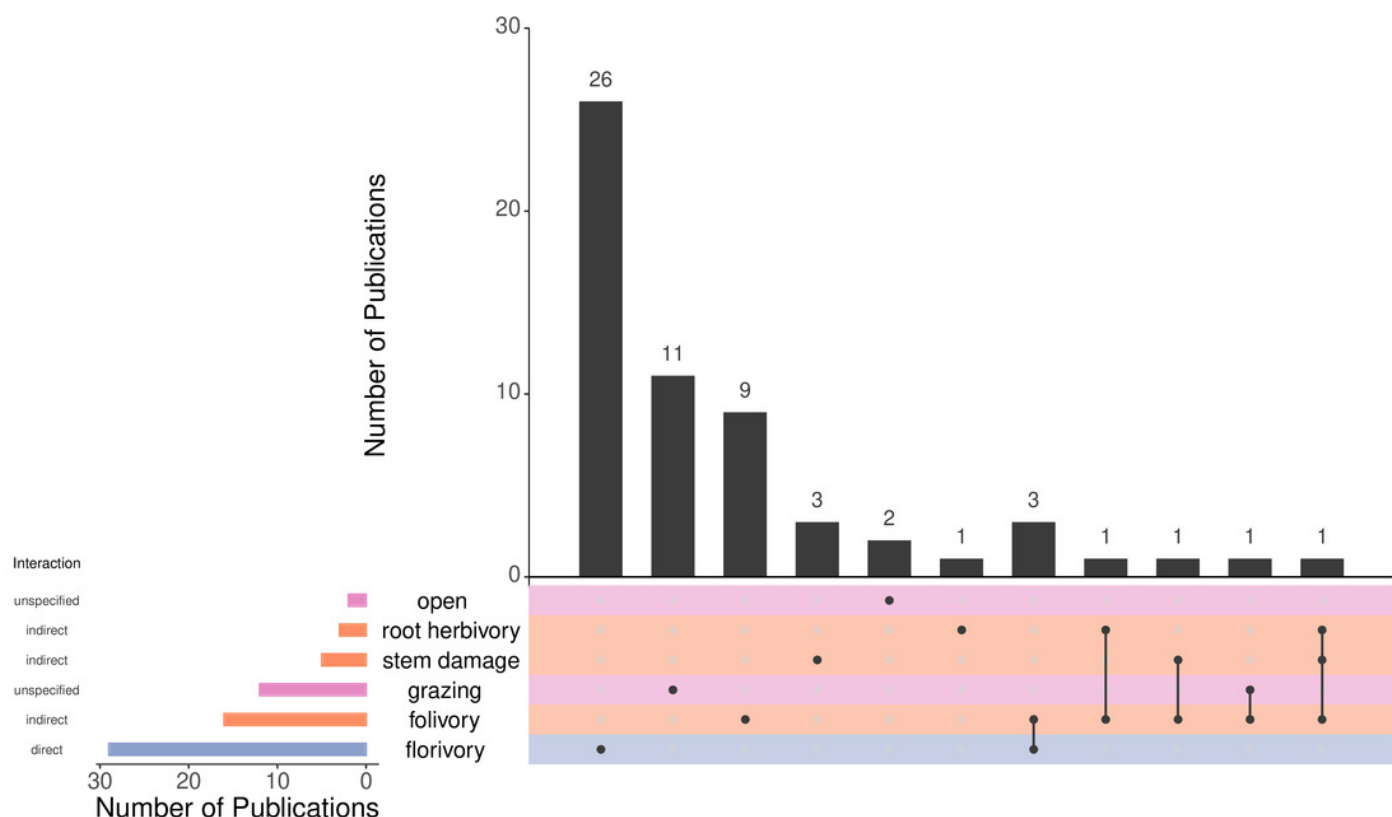



Figure 5

UpSet plot showing the number of publications (N=61) that examined each type of herbivory both individually and simultaneously.

The black vertical bars represent the number of publications that looked at exactly one, two or three types of herbivory. The dots directly below black bars correspond to which type(s) of herbivory are represented within that category. The coloured horizontal bars to the left of the list of herbivory types show the number of publications that included each herbivory type (regardless of whether another type of herbivory was also examined). Horizontal bars and rows are coloured according to the interaction type of each form of herbivory (i.e. direct, indirect, or unspecified). Unspecified interaction pathways are those in which one or both of direct and indirect pathways are possible, but not specified.

Definitions and study counts of all types of herbivory as well as floral, pollinator, and plant responses included in this review.

Study counts include artificial herbivory versions for each herbivory category (e.g. both floral herbivory done by animals and human removal of petals would be included under florivory).

Term	Definition	Category	Number of Studies
Florivory	Flower consumption, including removal of flowers and inflorescences (complete florivory) and partial removal of flowers and petals (partial florivory)	Floral Herbivory	29
Folivory	Leaf consumption	Vegetative Herbivory	16
Stem damage	Damage to the stem, including puncture damage and meristem removal.	Vegetative Herbivory	5
Root herbivory	Damage to or consumption of roots	Vegetative Herbivory	3
Open (herbivory)	Open to all herbivores that could consume any or all plant tissues.	Both Vegetative and Floral Herbivory with unknown proportions	3
Grazing	Indiscriminate consumption of plants by mammalian herbivores.	Both Vegetative and Floral Herbivory with unknown proportions	12
Flower morphology/architecture and size	Refers to flower symmetry (both due to faulty growth and partial floral damage), inflorescence shape, and architecture, as well as aspects of floral morphology relating to size including diameter, surface area, and corolla length	Floral Response	16
Flowering phenology	The timing of flowers, including when flowers are produced and when they open	Floral Response	5
Flower abundance	The number of flowers in total. Also includes the presence/absence of flowers when flowers are considered individually	Floral Response	24

sex ratio	The relative proportion of male and female flowers	Floral Response	1
Floral diversity	Number of species or other diversity metric of flowering species	Floral Response	2
Pollen production	The amount of pollen produced by a flower or stigma	Floral Response	5
Pollen deposition	The amount of pollen deposited by a pollinator	Pollinator Effect	6
Pollinator visitation	The frequency with which a flower or plant is visited by pollinators	Pollinator Effect	35
Pollinator abundance	The abundance of pollinators found in the local environment	Pollinator Effect	4
Pollinator diversity	The number of pollinator species (or other diversity metric) that either visit a flower/plant or are found in the local environment	Pollinator Effect	3
Fruit set	A number of measures that represent the amount of fruit produced including number of fruits, fruit size, and fruit mass	Plant Response	26
Seed set	A number of measures that represent the amount of seed produced including number of seeds, seed size, and seed mass. In some cases, only viable seeds are considered.	Plant Response	29

Distribution of studies based on herbivore-pollinator mechanism examined.

Unspecified refers to damage that may include either of vegetative and floral tissue, both or neither (damage was mimicked by the application of chemicals).

Indirect	n	Direct	n	Unspecified	n
Vegetative Damage-Floral Response-Pollinator	5	Floral Damage-Floral Response-Pollinator	1	Unspecified Damage-Floral Response-Pollinator	6
Vegetative Damage-Floral Response-Pollinator-Seed Set	9	Floral Damage-Floral Response-Pollinator-Seed Set	6	Unspecified Damage-Floral Response-Pollinator-Seed Set	2
Vegetative Damage-Pollinator	3	Floral Damage-Pollinator	7	Unspecified Damage-Pollinator	0
Vegetative Damage-Pollinator-Seed Set	4	Floral Damage-Pollinator-Seed Set	13	Unspecified Damage-Pollinator-Seed Set	6