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Evolutionary Interactions Between Plant Reproduction and Defense Against Herbivores

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Keywords

herbivory, inbreeding depression, induced response, mating system, plant–insect interactions, evolution of sex

Abstract

Coevolution is among the most important evolutionary processes that generate biological diversity. Plant–pollinator interactions play a prominent role in the evolution of reproductive traits in flowering plants. Likewise, plant–herbivore interactions select for myriad defenses that protect plants from damage. These mutualistic and antagonistic interactions, respectively, have traditionally been considered in isolation from one another. Here, we consider whether reproductive traits and antiherbivore defenses are interdependent as a result of pollinator- and herbivore-mediated selection. The evolution of floral traits, self-fertilization, and separate sexes frequently affects the expression and evolution of plant defenses. In turn, the evolution of defense can affect allocation to reproductive traits, and herbivores often impose strong selection directly on floral traits. Theory and empirical evidence suggest that herbivores can influence the evolution of selfing from outcrossing and potentially the evolution of separate sexes from combined sexes. We identify several areas in which future research is needed to increase our understanding of the evolutionary interplay between reproduction and defense in plants.

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1. INTRODUCTION

Herbivory: the consumption of plants by animals

Coevolution: reciprocal natural selection between two or more species that leads to evolutionary change within each species

Plants engage in a wide variety of mutualistic and antagonistic species interactions with significant ecological and evolutionary consequences. Animal pollination has played a major role in the diversification of reproductive traits in angiosperms, whereas herbivory is among the most important ecological interactions in most ecosystems. Ehrlich & Raven (1964) proposed that coevolution between plants and herbivores is also an important driver of diversification in plant defense, with corresponding evolutionary changes in herbivores. Although pollinators and herbivores are each recognized as agents of natural selection in plant populations, they are typically studied in relative isolation from one another, resulting in distinct communities of researchers addressing rather different questions (Strauss & Whittall 2006). In this review, we consider the interactions between the evolution of reproduction and defense in plants (**Figure 1**). We argue that greater integration between the study of plant reproductive biology and the study of defenses against herbivores and other plant parasites will provide new insight into the ecology and evolution of plants and plant–animal interactions.

1.1. Evolution of Plant Reproductive Diversity

Flowering plants exhibit exceptional reproductive diversity compared with most other groups of organisms. Their sessile habit requires agents for pollen dispersal, and this has resulted in the evolution of numerous floral adaptations that promote cross-pollination, particularly in

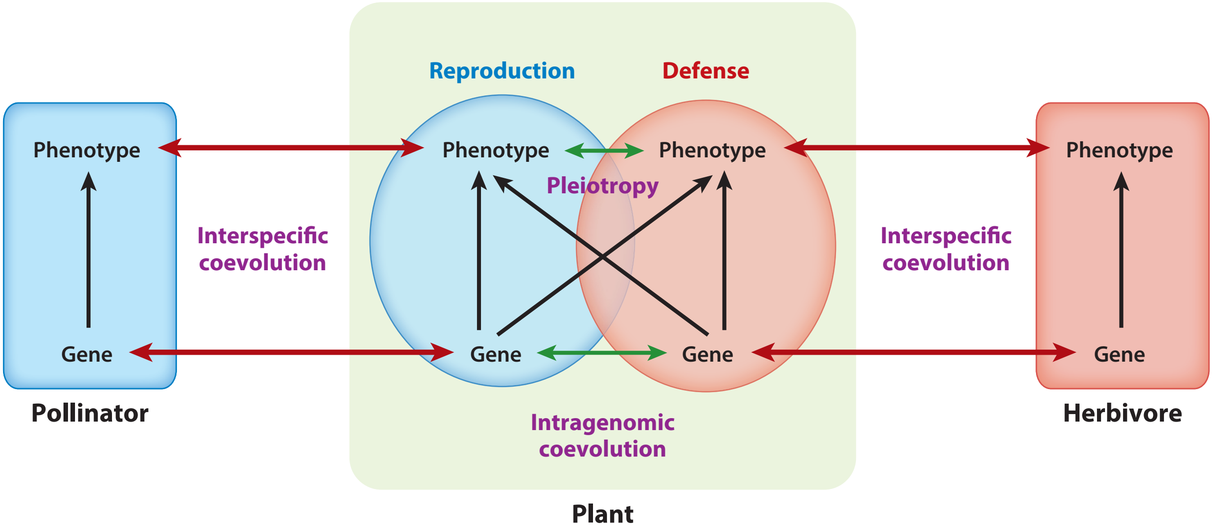

Figure 1

Conceptual illustration of how coevolution between species can lead to evolutionary interactions between reproduction and defense in plants. Traditionally, coevolution has been defined as reciprocal natural selection that causes evolutionary change in the phenotypes and underlying genes of interacting species (*red arrows*). Plant–pollinator and plant–herbivore interactions are classic examples of interspecific coevolution, yet these interactions have been studied in relative isolation from one another. Evidence reviewed here suggests that the evolution of the traits and genes associated with plant reproduction and defense may depend on one another and in some cases may involve intragenomic coevolution (*green arrows*). Evolution of reproductive and defense traits may be interdependent in one of two ways: First, when genes influence both reproductive traits and defense (due to pleiotropy or tight linkage), selection for increased or decreased expression of one trait can cause correlated changes in the other trait. Second, selection on reproductive traits can lead to fitness effects on defense traits and their underlying genes (or vice versa), which can lead to selection on compensatory mutations. The direct effects of structural and regulatory genes on an organism's phenotype are shown as black arrows.

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animal-pollinated lineages (Harder & Johnston 2009). However, not all variation in floral traits involves adaptation to pollen vectors, and a variety of floral strategies function to promote the quantity and quality of offspring, thus directly influencing fitness.

The hermaphroditic condition of most angiosperms provides opportunities for self-fertilization, often resulting in harmful genetic consequences for offspring in the form of inbreeding depression (ID) (Charlesworth & Charlesworth 1987). There is considerable evidence that the magnitude of ID plays a key role in maintaining high outcrossing rates in plant populations (Lande & Schemske 1985). Countervailing selection for reproductive assurance, when pollen vectors or mates are rare, probably accounts for frequent transitions to selfing in many angiosperm lineages. Shifts to selfing are the most common reproductive transitions in angiosperms, and they have profound consequences for floral morphology, sex allocation, life history, biogeography, population genetic structure, genome diversity, and rates of speciation and extinction (Wright et al. 2013).

Complex interactions between genetic and ecological factors cause variation in mating systems ranging from predominant selfing to mixed mating (both selfing and outcrossing) and obligate outcrossing (Goodwillie et al. 2005). Moreover, plasticity in sex allocation and the combination of hermaphroditic and unisexual flowers in various structural and temporal combinations have given rise to a wide range of sexual systems and gender strategies that affect mating (Geber et al. 1999). Despite sustained interest in plant reproductive diversity since Darwin's seminal work (Darwin 1876, 1877), there has been relatively little consideration of evolutionary interactions between reproduction and defense against enemies such as herbivores (Strauss 1997, Campbell 2014). However, growing evidence indicates that in addition to animal pollinators affecting floral evolution and plant mating in many groups, herbivores also impose selection on reproductive traits.

1.2. Herbivory and the Evolution of Plant Defenses

Herbivores and plants represent over 75% of the macroscopic diversity and biomass within terrestrial ecosystems, and herbivores include many arthropods, mollusks, vertebrates, and nematodes. These groups of animals consume between 5% and 20% of plant biomass annually (Turcotte et al. 2014) and can significantly reduce plant fitness (Hawkes & Sullivan 2001). Plants have many defenses to protect themselves against herbivores. A defense is defined as any trait that increases plant fitness in the presence of herbivores, with traits falling into three general categories: resistance, tolerance, and avoidance. Plant populations often contain heritable variation in defense traits (Geber & Griffen 2003), and herbivory can be a potent agent of selection driving the evolution of defense (Agrawal et al. 2012).

Several factors have been hypothesized to explain the wide variation in plant defense strategies among species; these factors include the intensity of herbivory, the fitness value of the attacked plant part, and constraints imposed by the abiotic environment (Stamp 2003). However, defense theories struggle toward generality, particularly when considering variation within and among species or higher taxonomic groups. Although few hypotheses on the evolution of defense explicitly incorporate features of plant reproduction (but see Levin 1975), recent studies suggest that reproductive systems and defense traits may not evolve independently (Strauss & Whittall 2006, Campbell 2014, Carr & Eubanks 2014). This growing body of literature motivates our review.

1.3. Scope of Review

We consider the evolutionary interdependence of plant reproduction and antiherbivore defenses by considering evidence in support of the following two complementary hypotheses.

Inbreeding depression (ID): reduction in viability and fertility of inbred compared with outcrossed offspring as a result of the expression of deleterious recessive genes in homozygous genotypes

Mating system: the relative frequency of selfing and outcrossing practiced by a plant or a population

Sexual system: relative production of female, male, and hermaphrodite flowers within and among plants in a population and how these ratios influence mating patterns

Resistance: traits of a plant that reduce damage by decreasing herbivore preference, consumption, and/or performance

Tolerance: traits that reduce the fitness impacts of damage but not the amount of damage

Avoidance: traits that make a plant less apparent to herbivores, allowing them to escape damage in space or time

Reproductive system: mechanisms and modes of reproduction in a population including the relative importance of sexual versus asexual reproduction and the frequencies of outcrossing and selfing

- **Hypothesis 1.** The evolution of reproductive traits directly or indirectly alters selection and evolution of defense traits, and this selection can involve changes in the levels, types, or diversity of plant defenses against herbivores. We consider evidence for this hypothesis in Section 2.
- **Hypothesis 2.** Herbivores and the evolution of plant defense directly or indirectly alter selection and evolution of plant reproductive traits, including flowering time, floral traits, mating patterns, and sexual systems. We review support for this hypothesis in Section 3.

Support for these two hypotheses implies that consideration of the joint evolution of reproduction and defense is necessary to understand the factors driving the evolutionary diversification of plants.

2. EFFECTS OF REPRODUCTION ON EVOLUTION OF DEFENSE

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In this section, we evaluate whether the evolution of reproductive traits affects the evolution of defense traits (Hypothesis 1). This is most likely when investment in floral traits influences herbivory and the expression of defense. This can arise directly when floral traits provide cues to both pollinators and herbivores and indirectly when investment in floral cues (e.g., flower color) and rewards (e.g., nectar) share developmental or biosynthetic pathways with defense traits. There is also growing evidence that transitions in mating patterns and sexual systems affect the ability of plant populations to maintain and evolve defenses against their enemies. Thus, if Hypothesis 1 is supported it will be necessary to consider plant reproductive traits when studying the evolution of plant defense.

2.1. Floral Traits and Susceptibility to Herbivores

The role of floral characters in attracting pollinators is well known, but only recently has it been appreciated that the same traits also attract herbivores (Strauss & Whittall 2006). Floral traits are most likely to affect susceptibility to herbivores when adult insects pollinate the plants their larvae use as hosts (i.e., pollinating herbivores). Examples include several obligate plant–pollinator mutualisms (Dufaÿ & Anstett 2003), such as the interactions between figs and fig wasps (Cook & Rasplus 2003) or yucca and yucca moths (Pellmyr 2003), in which the larvae feed directly on ovules and developing seeds. Most pollinating herbivores are less specialized, with pollinators visiting several plant species and their larvae feeding on multiple hosts and plant tissues. For example, hornworm moths (*Manduca* spp., Sphingidae) pollinate a variety of night-flowering species in the nightshade family (Solanaceae), and larval *Manduca* frequently consume the plants they pollinate (Adler & Bronstein 2004). Variation in floral traits may also attract nonpollinating herbivores, especially those that consume flowers (florivores) or fruits (frugivores and predispersal seed predators). Thus, both pollinating and nonpollinating herbivores have the potential to act as agents of selection on floral traits.

A diversity of floral traits influence the susceptibility of plants to herbivores. Floral volatile organic compounds (VOCs) are among the strongest cues for herbivores (Schiestl 2015). For example, Canada thistle (*Cirsium arvense*, Asteraceae) emits 13 floral VOCs that attract 16 herbivore species (Theis 2006), and night-flowering *Petunia* emits at least one VOC (methyl benzoate) that attracts pollinators and herbivores and two compounds (benzyl benzoate and isoeugenol) that deter florivores (Kessler et al. 2013). Large nectar volumes increase herbivory by pollinating *Manduca* herbivores in several species of Solanaceae (Adler & Bronstein 2004, Kessler 2012). Both visual and morphological floral traits affect apparency to herbivores, which can then reduce plant fitness (Theis & Adler 2012). For example, variation in flower color in purple morning glory (*Ipomoea purpurea*, Convolvulaceae) and wild radish (*Raphanus sativus*, Brassicaceae) has been linked to herbivory (Simms & Bucher 1996, Strauss et al. 2004, McCall et al. 2013). Increased flower size (Theis et al. 2014), large floral displays (Brody & Mitchell 1997), and taller inflorescences often result in greater herbivory (Ågren et al. 2013). The best-studied floral trait that affects risk to herbivory is flowering phenology (Elzinga et al. 2007). Plants that flower early or late typically receive less damage than plants that flower during peak flowering; this pattern is reversed when synchronous flowering satiates herbivores. Given the abundant evidence that floral traits affect herbivory, we next ask how floral traits might influence the evolution of defense.

Antagonistic pleiotropy: opposing fitness effects of a locus on multiple traits

2.2. Effects of Floral Traits on the Evolution of Defense

In support of the hypothesis that evolution of reproductive traits affects selection on plant defense (Hypothesis 1), there is evidence that pleiotropy and allocation trade-offs cause floral evolution to affect the evolution of defense.

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2.2.1. Pleiotropic effects on floral and defense traits. Genes controlling floral traits can have pleiotropic effects on the expression of defense traits. A striking example is reported in bird's-eye primrose (*Primula farinosa*, Primulaceae), in which a single locus controls inflorescence height through variation in scape length (Ågren et al. 2013). Tall inflorescences attract more pollinators but are also more susceptible to grazing compared with short inflorescences, leading to opposing selection by mutualists and antagonists on the same trait and locus—an example of antagonistic pleiotropy (**Figure 1**). As a consequence, the relative frequencies of tall and short inflorescences in populations depend on spatial and temporal variation of these opposing selective forces (Ågren et al. 2013). Although this is a clear example of pleiotropy, in most cases defense and floral traits are under polygenic control, potentially leading to more diverse outcomes.

Flower color variation due to anthocyanin pigments provides an example of how a polygenic floral trait can have pleiotropic effects on defense (**Figure 2*a***). Variation in flower color within (Strauss & Whittall 2006) and among (Rausher 2008) species is often controlled by variation in the production of anthocyanin pigments from the flavonoid pathway, which also produces a wide diversity of defense-related secondary metabolites including condensed tannins, flavonol glycosides, flavones, and isoflavones (Harborne & Williams 2000). When variation in floral pigmentation is caused by the nonfunctionalization of a core enzyme within the flavonoid pathway, a complete loss of anthocyanin and defensive metabolites can result (**Figure 2*b***). Similarly, changes in enzyme expression or specificity can alter the flux of metabolites among different branches of the flavonoid pathway (**Figure 2*c***). Pleiotropic effects of anthocyanin genes on resistance to herbivores have been demonstrated in some studies (Simms & Bucher 1996, Irwin et al. 2003, McCall et al. 2013) but not others (Fineblum & Rausher 1997), and the frequency with which flower color transitions result directly in defense evolution is not well understood. Thus, further research that integrates chemical and molecular analyses within field studies is required.

Florivory can select for correlated evolution of floral morphology and chemical defenses due to pleiotropic control of these traits, as in *Dalechampia* (Euphorbiaceae) (Armbruster 1997). The ancestral structure of *Dalechampia* inflorescences includes resin-secreting floral bracts that protect flowers from herbivores. Early diverging lineages evolved modified resin-secreting tissues that act as rewards for pollinating bees (Armbruster et al. 2009). Transition in resin function also involved changes to the shape of inflorescences (e.g., bilateral symmetry, which is more attractive to pollinating bees) (Armbruster 1997) but with multiple reversions to more defended ancestral phenotypes. Thus, it would seem that antagonistic pleiotropy mediates an evolutionary seesaw within *Dalechampia* between attractive and defensive floral phenotypes, which is driven by the relative strength of selection by pollinators and florivores.

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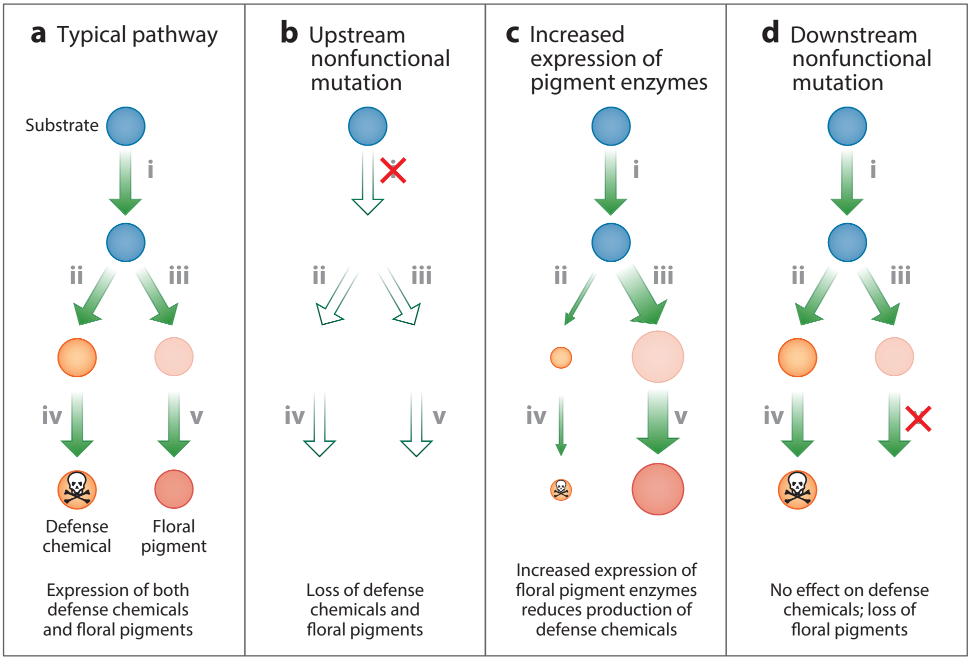

Figure 2

A hypothetical metabolic pathway illustrating how pleiotropy can potentially affect the evolution of floral pigments and defense chemicals. In this pathway, defensive chemicals and floral pigments share an upstream enzyme (*i*) and substrates (*circles*) but have unique downstream enzymes (*ii*–*v*) and products. (*a*) A typical pathway with functional enzymes that produce both defensive chemicals and floral pigments. (*b*) An upstream mutation that causes nonfunctionalization of enzyme *i*, which causes the complete loss of defense chemicals and floral pigments. (*c*) Increased expression of a floral enzyme (*iii*) that competes for substrates with a defense enzyme (*ii*); this increased expression leads to increased production of floral pigments and a decrease in the expression of defense chemicals. (*d*) A downstream mutation that causes nonfunctionalization in an enzyme (*v*) specific to the floral pigment pathway. This mutation does not affect the expression of defense chemicals. This pathway is conceptually similar to the flavonoid pathway, which produces floral pigments and defense metabolites, but these same principles can be applied to any biosynthetic or developmental pathway that influences both reproductive traits and defense.

Selection can reduce negative fitness effects of pleiotropy between defense and floral traits in at least three ways. First, beneficial mutations that affect floral phenotypes may have a negligible influence on defense when they occur within enzymes and transcription factors that are downstream within metabolic pathways (**Figure 2*d***) (Fineblum & Rausher 1997). Second, gene duplication can allow selection to favor a more specialized function of a paralogous gene copy (Des Marais & Rausher 2008). Third, structural enzymes and transcription factors frequently show tissue- or environment-specific expression (Berger & Dubreucq 2011), causing the decoupling of floral and defense traits (Dron et al. 1988). These mechanisms may explain cases in which variation in floral phenotypes does not affect resistance (Fineblum & Rausher 1997) or examples of weak correlation in a defense metabolite between floral and nonfloral tissues (Adler et al. 2012, Theis et al. 2014). The molecular basis for the decoupling of floral and defense traits that share biosynthetic pathways represents an important area for future research.

2.2.2. Allocation trade-offs between reproduction and defense. Allocation trade-offs are pervasive in nature and have the potential to drive evolutionary interactions between reproduction and defense. Classic plant defense theories propose that increased investment in growth and reproduction comes at a cost in allocation to defense (Coley et al. 1985, Herms & Mattson 1992). This theory is primarily supported by comparisons of distantly related taxa within communities (Endara & Coley 2011) but has not been supported by studies that focus on species within specific genera or families (Agrawal & Fishbein 2008, Adler et al. 2012). However, the latter studies focused on correlations between defense and growth rate. Future investigations that explicitly measure allocation to reproductive and defense traits are needed to determine whether limited energy budgets could drive trade-offs in the evolution of reproduction and defense.

Constitutive resistance: the level of resistance against herbivores in undamaged plants prior to herbivore attack

Induced resistance: a change in the expression of a plant trait in response to herbivory that affects resistance against herbivores

2.3. Mating System and Resistance Against Herbivores

Investigations of ID in plants have largely focused on fitness components such as survival, growth rate, flower number, and seed production (Husband & Schemske 1996). However, inbreeding increases genome-wide homozygosity and should affect any phenotype harboring recessive, deleterious mutations—including those influencing defense (Charlesworth & Charlesworth 1999). The fitness consequences of these effects will depend on the particular interaction of defense traits with herbivore species. Thus, quantifying how inbreeding affects specific defense traits such as resistance is important for understanding how mating systems could modify selection on defense.

At least 22 studies of 9 plant species have tested the prediction that inbreeding negatively affects resistance to herbivores (**Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). Tests of this prediction were recently reviewed by Carr & Eubanks (2014). Thus, we focus on this literature from two perspectives: First, we consider the importance of alternative strategies of defense when comparing the effects of inbreeding on specific defense traits. Second, we consider how the effect of inbreeding on resistance differs with mating system (selfing versus outcrossing populations). The mating system's influence is important because highly selfing populations are more likely to purge deleterious mutations, whereas outcrossing populations will have fewer opportunities to expose deleterious mutations to selection (Barrett & Charlesworth 1991).

Supplemental Material

2.3.1. Effects of inbreeding on plant defense traits. Inbreeding influences the expression of traits that underlie multiple defensive strategies, including constitutive resistance, induced resistance, and tolerance. These effects have been best studied in horsenettle (*Solanum carolinense*, Solanaceae) (Campbell 2014) and yellow monkeyflower (*Mimulus guttatus*, Phrymaceae) (Ivey & Carr 2012). In *S. carolinense*, inbreeding negatively affects induction of foliar VOCs, spine density, and defense-related secondary metabolites and the production of jasmonic acid (JA), the plant hormone that regulates the expression of most resistance traits (Campbell et al. 2014). Tolerance to herbivory is variably affected by inbreeding: Inbred *M. guttatus* (Ivey et al. 2004) and *S. carolinense* (Campbell 2014) show reductions in tolerance to damage, whereas white swallowwort (*Vincetoxicum hirundinaria*, Apocynaceae) does not show any change in tolerance with inbreeding (Muola et al. 2011). Finally, there is limited support for the effects of inbreeding on so-called indirect defense—the recruitment of natural enemies of herbivores by induced VOCs. Inbred *S. carolinense* and field pumpkin (*Cucurbita pepo*, Cucurbitaceae) show reduced induction of VOCs and recruitment of putative enemies, but this recruitment was not linked to plant fitness (Ferrari et al. 2006, Kariyat et al. 2012). Overall, these studies confirm that the majority of plant defense strategies have the potential to be negatively influenced by inbreeding.

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Studies examining the effects of inbreeding on defense often confound constitutive and induced resistance. Over half of the studies described above were conducted in the field, where resistance is measured as natural damage, and were often conducted without a herbivore removal treatment (**Supplemental Table 1**). Measures of natural damage frequently underestimate the effects of inbreeding if levels of constitutive and induced resistance are negatively genetically correlated or if variation in the mating system is correlated with the defense strategy (Campbell & Kessler 2013). Conversely, glasshouse estimates of resistance traits, or short-term bioassays, often do not measure induced resistance. Presently, only the studies of *S. carolinense* explicitly compare the effects of inbreeding on constitutive and induced trait values (Kariyat et al. 2012, Campbell & Kessler 2013, Campbell et al. 2013), and future work is needed to disentangle how selfing affects these defensive strategies in more plant species.

Genetic load: the collection of deleterious mutations within the genome of individuals or populations

Monoecy: a sexual system in which individuals produce separate female and male flowers

Andromonoecy: a sexual system in which individuals produce hermaphrodite and male flowers

Dioecy: a sexual polymorphism in which populations are composed of female and male plants

Gynodioecy: a sexual polymorphism in which populations are composed of female and hermaphrodite plants

Plant gender: the relative contribution to fitness from maternal versus paternal investment

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2.3.2. Effects of inbreeding on defense differ with mating system. The strongest effects of inbreeding on resistance against herbivores are expected from species that are predominantly outcrossing. Of the species investigated, only *S. carolinense* has this mating system (Travers et al. 2004). As predicted, this species harbors significant genetic load at resistance genes, as indicated by reduced chemical resistance (Campbell et al. 2013), increased herbivore performance or consumption on inbred progeny (Kariyat et al. 2011, Campbell et al. 2013), and reduced preference of ovipositing adults for inbred plants (Kariyat et al. 2014). The recent results from *S. carolinense* therefore support the hypothesis that inbreeding reduces resistance to herbivores in outcrossing species.

In contrast, the effects of inbreeding are more variable in species with predominant selfing or mixed-mating populations. For example, jimsonweed (*Datura stramonium*, Solanaceae) exhibited selfing rates ≥90% in natural populations, and experimental self-fertilization of jimsonweed resulted in either a decrease (Bello-Bedoy & Núñez-Farfán 2010) or no change in resistance (Núñez-Farfán et al. 1996). Plants with mixed-mating systems also exhibited variation in the effects of inbreeding on resistance (Leimu et al. 2008), although this variation appeared less extreme compared with selfing species (Carr & Eubanks 2014). Mating system may therefore be a predictor of the effects of inbreeding on resistance, especially for populations at the extremes of the outcrossing–selfing continuum. However, there are still insufficient numbers of studies to draw firm conclusions (**Supplemental Table 1**). A major priority for future research is to examine how interpopulation and interspecific variation in mating system influences the effect of inbreeding on defense using a comparative approach.

Supplemental Material

2.4. Plant Gender and Resistance Against Herbivores

Flowering plants exhibit a wide range of gender strategies because of the opportunities to combine female, male, and hermaphrodite flowers at the plant (e.g., monoecy, andromonoecy) and population (e.g., dioecy, gynodioecy) levels (Barrett 2002). Despite the complexity of plant sexual systems, all species can be distinguished by whether populations are monomorphic or dimorphic for gender (Lloyd 1979). A growing literature has revealed that plant gender can influence the susceptibility of plants to herbivores and the expression of defense.

The first survey of herbivory in dioecious species indicated that male plants were more likely to exhibit damage in comparison with females (Ågren et al. 1999). Male-biased herbivory was confirmed by a meta-analysis involving a larger sample of species (Cornelissen & Stiling 2005). These studies also showed that male plants exhibited larger and more numerous leaves, lower concentrations of secondary metabolites, and reductions in other putative defenses like leaf toughness and trichomes, in comparison with female plants. These findings led Cornelissen & Stiling (2005,

p. 495) to suggest that "male-biased herbivory is a rule" and that differential herbivory between the sexes may play a significant role in the evolution of sexual systems, a topic we return to in Section 3.4.

In a later examination of the origins of sex-biased herbivory in dioecious plants, Avila-Sakar & Romanow (2012) questioned whether male-biased herbivory is a general rule. They identified empirical and conceptual shortcomings of earlier studies, particularly taxon sampling and limited mechanistic data. It is true that both ultimate and proximate explanations for sex-biased herbivory are largely lacking. Differential herbivory could be the product of greater selection for defense in females to protect their ability to mature fruits or the product of indirect selection in males for lower investment in defense because of allocation to faster growth. For example, the greater cost of reproduction in females (Barrett & Hough 2012) should limit growth and thereby select for greater defense, as predicted by the Growth Rate Hypothesis (Coley et al. 1985). There is evidence of faster growth in males compared with females (Jing & Coley 1990), but it remains unclear whether the putative trade-off between growth and defense differs between sexes in most dioecious systems (but see Stevens & Esser 2009). Comparative data on sexual dimorphism in defense traits, including information on growth rates of the sexes, from a large sample of unrelated dioecious species would help place these patterns into context and indicate whether they are explained by classic hypotheses for defense evolution or by other mechanisms.

Permanent translocation heterozygosity (PTH): functionally asexual genetic system caused by multiple reciprocal chromosome translocations and balanced lethal mortality of gametes

Gynodioecy, the coexistence of females and hermaphrodites in populations, is a frequent intermediate stage in the evolution of dioecy. Whether the sexual morphs in gynodioecious populations experience differences in resistance to herbivores is important, as it could have consequences for the maintenance of the polymorphism (Ashman 2002; see Section 3.4). There is some evidence that herbivory is biased toward pollen-producing plants (hermaphrodites) and is most pronounced in seeds. For example, Douglas iris (*Iris douglasiana*, Iridaceae) hermaphrodites reached peak flowering after females and suffered greater seed loss to dipteran larvae (Uno 1982). Similarly, weevils imposed gender-specific seed predation of hermaphrodite plants of Henderson's checkerbloom (*Sidalcea hendersonii*, Malvaceae) (Marshall & Ganders 2001) and Virginia strawberry (*Fragaria virginiana*, Rosaceae) (Ashman 2006), which may contribute to the maintenance of females in populations. In contrast to dioecy, however, there are still too few data to speculate on the mechanisms underlying gender-specific variation in defense within gynodioecious species or on the evolutionary consequences of this variation (see Section 3.4).

2.5. Consequences of Reproductive Systems for Defense Evolution

In an influential paper, Levin (1975) proposed that reproductive systems play a prominent role in the evolution of plant defense against parasites. He hypothesized that reproductive systems that limit effective rates of recombination [e.g., selfing, apomixis, and permanent translocation heterozygosity (PTH)] compromise the evolution of defense. Subsequent theoretical models have established how transitions between sexual and asexual reproduction affect the evolution of defense and also how parasites influence the evolution of sex and recombination (Salathé et al. 2008). Two general conclusions from these models are that a loss of sex frequently constrains adaptive defense responses to parasites (similar to genome-wide expectations; see Wright et al. 2013), whereas strong selection by parasites can maintain sexual reproduction (Lively 2010).

There has been considerably less work examining how variation in selfing rate affects the evolution of defense. Like asexuality, selfing should lead to reduced effective rates of recombination; however, theoretical models suggest that any resulting constraint on the evolution of defense may depend greatly on the fitness costs of herbivory and the rate at which these costs lead to purging of deleterious alleles (Koslow & DeAngelis 2006). DeAngelis and colleagues (Koslow & DeAngelis

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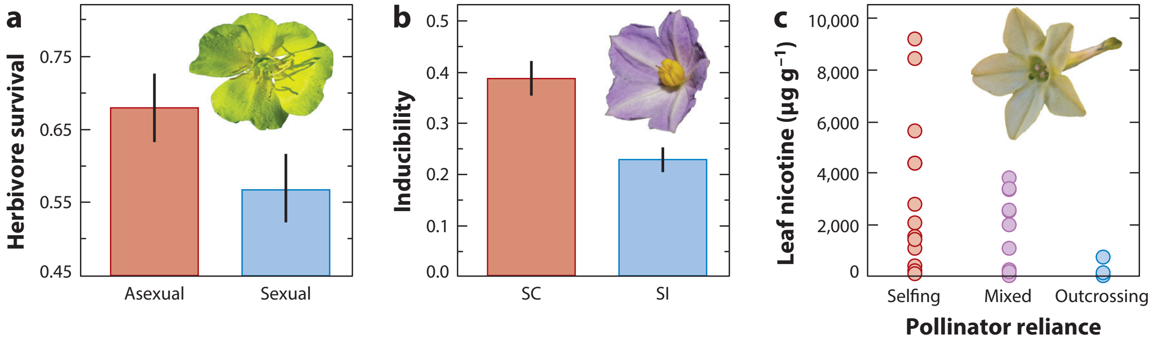

Figure 3

Examples of the effects of plant reproductive systems on the evolution of resistance to herbivores. Each study used comparative phylogenetic methods to examine how resistance or susceptibility varied across multiple plant species. (*a*) Two-spotted spider mites (*Tetranychus urtica*) exhibit higher survival on functionally asexual than sexual *Oenothera* species, indicating that sexual species are more resistant to this generalist herbivore (image of *O. biennis*). (Panel *a* modified from Johnson et al. 2009 with permission.) (*b*) Self-compatible (SC) plant species in the Solanaceae family exhibit higher rates of induced resistance to *Manduca sexta* caterpillars than self-incompatible (SI) relatives (image of *Solanum bahamense*). (Panel *b* modified from Campbell & Kessler 2013 with permission.) (*c*) Tobacco (*Nicotiana*) species that self-pollinate exhibit higher constitutive nicotine levels in leaves than outcrossing species, whereas species with intermediate self-fertility have intermediate levels of nicotine (image of *N. alata*). The same pattern was observed in flower tissue and nectar. (Panel *c* modified from Adler et al. 2012 with permission.)

2006, DeAngelis et al. 2008) modeled resistance as a single locus diallelic genetic system in which resistance is dominant. Although intended for pathogens, their model is informative for the evolution of antiherbivore defenses with a similar genetic basis. Contrary to initial models (Levin 1975), DeAngelis and colleagues found that selfing is associated with the evolution of increased resistance. This resistance evolves because selfing leads to homozygous populations, which allows selection to purge susceptible genotypes. By contrast, sexual populations have a higher frequency of heterozygotes in which the recessive susceptible allele is protected from selection. In these models, increased selfing can lead to decreased resistance, but this occurs only when there is low transmission of parasites between plants and when resistance carries a high cost. The models indicate that the evolution of decreased resistance is not an inevitable consequence of increased selfing and that under some circumstances selfing may facilitate the evolution of increased defense.

Studies of evening primroses (*Oenothera* spp., Onagraceae) have provided insights into how transitions from sexual to functionally asexual reproduction influence phenotypic and molecular evolution of defense. *Oenothera* has undergone multiple independent transitions between sexual and the functionally asexual PTH genetic system (Cleland 1972). A comparison of 32 sexual and PTH *Oenothera* spp. demonstrated that sexual species are consistently more resistant to generalist herbivores than asexual species (**Figure 3*a***) (Johnson et al. 2009). By contrast, PTH *Oenothera* are more resistant to at least one specialist beetle. The results of this study can be explained, in part, by higher concentrations of tannins in sexual *Oenothera*, which were negatively correlated with performance of generalist herbivores and positively correlated with susceptibility to the specialist beetle (Johnson et al. 2009). Subsequent phytochemical analyses revealed that transitions to PTH are associated with altered phenolic composition and a greater diversity of flavonoids (Johnson et al. 2014). At the molecular level, sexual *Oenothera* exhibit nonsynonymous substitution rates higher than PTH species in chitinase, a defense enzyme effective against pathogens and some insects (Hersch-Green et al. 2012). This observation is consistent with faster adaptive evolution in response to selection by parasites in sexual lineages, which in combination with greater accumulation of deleterious mutations in PTH lineages (Hollister et al. 2015) may explain variation in resistance between sexual and functionally asexual plant species.

Recent studies provide more general insight into how the evolution of reproductive systems can influence the evolution of plant defense. A comparison of constitutive and induced resistance in 56 species of Solanaceae, representing multiple transitions from self-incompatibility (SI) to self-compatibility (SC), revealed that SI species exhibited slightly greater constitutive resistance than SC species (Campbell & Kessler 2013). By contrast, SC species exhibited greater inducibility of resistance following damage by *Manduca sexta* (**Figure 3*b***). At this stage it is unclear whether increased inducibility is an adaptation to reduce defense costs in selfing species, which tend to occur in disturbed environments with unpredictable herbivore populations, or whether inducibility is more costly to outcrossing species, which rely more on pollinators and may have less variable herbivore populations. Conversely, increased selfing in tobacco (*Nicotiana* spp., Solanaceae) was associated with the evolution of greater constitutive investment in chemical resistance (Adler et al. 2012). These authors examined concentrations of two alkaloids (nicotine and anabasine) in each of three tissues (leaf, flower, and nectar) among 32 species that varied in their ability to self-pollinate. Nicotine content was negatively correlated with the likelihood of outcrossing, whereas nicotine concentration was positively correlated between leaves and flowers (**Figure 3*c***), suggesting that pollinators select for low nicotine in the nectar and flowers of outcrossing species and cause indirect selection on leaf nicotine via pleiotropy (Adler et al. 2012). These differences may occur because there is little capacity for independent expression in different tissues in *Nicotiana* species, which could explain why the patterns in this genus are partially inconsistent with the findings of Campbell & Kessler (2013).

Theory and empirical research indicate that variation in reproductive systems can have significant influence on the evolution of defense. Decreased sex or increased selfing can lead to the evolution of decreased resistance (Johnson et al. 2009), increased resistance (Johnson et al. 2009, Adler et al. 2012), or transitions in defensive strategies (Campbell & Kessler 2013). In addition, the effects of reproductive systems on the evolution of defense may depend on herbivore specialization (Johnson et al. 2009), the genetic architecture of resistance (Koslow & DeAngelis 2006), the specific defensive traits examined (Adler et al. 2012, Campbell & Kessler 2013), and the relative importance of resistance traits to herbivores and pollinators (Adler et al. 2012). Thus, effects of the reproductive mode on defense evolution may not be as straightforward as Levin (1975) envisioned, and further research may reveal general patterns that are not yet apparent from the small number of existing studies.

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3. EFFECTS OF HERBIVORES AND DEFENSE ON THE EVOLUTION OF REPRODUCTIVE DIVERSITY

In this section we consider how herbivores and the evolution of plant defenses alter selection and the evolution of reproductive traits (Hypothesis 2). As we show below, herbivory and investment in defense can alter the expression of plant reproductive traits, including the size of flowers and floral displays, allocation to rewards, and the timing of flowering. These effects may in turn alter pollinator visitation and selection on reproductive traits. Similarly, herbivory can magnify the effects of ID with potential consequences for contemporary mating patterns. Whether herbivores exert consistent selection on plant reproductive systems over longer timescales, resulting in significant changes to mating and sexual systems, is less clear and represents a critical gap in considering the evolutionary interactions between reproduction and defense.

3.1. Effects of Herbivory and Induced Responses on Floral Traits and Pollinators

Induced response: a change in the expression of a plant trait in response to damage

Herbivores can directly and indirectly alter floral traits, and this alteration can influence pollinator visitation and plant fitness. Florivores modify floral traits directly by consuming flowers and other reproductive tissues (McCall & Irwin 2006) and can have indirect effects when they induce metabolic responses (Kessler & Baldwin 2002) that then influence floral traits, pollination, and mating (Strauss & Whittall 2006, Campbell 2014). We focus here on herbivore-induced changes to floral characters, which remain poorly characterized compared with the direct effects of florivory and the consumption of fruits and seeds.

Preliminary evidence suggests that induced responses from herbivory can alter many floral traits. For example, leaf damage can cause subsequent reductions in corolla size and floral display, resulting in negative effects on pollinator visitation and plant fitness (Strauss et al. 1996, 1999). Herbivores can also induce changes to the rewards collected by pollinators, including pollen size (Lehtilä & Strauss 1999), and can result in the transport of defensive metabolites to pollen (Kessler & Halitschke 2009) and nectar (Adler et al. 2006, McCall & Karban 2006). These induced biochemical changes can repel pollinators (Kessler & Halitschke 2009) and influence mating patterns by changing pollinator behavior (Kessler et al. 2012) and by modulating the rate and selective benefits of selfing. Herbivores can also induce changes to floral VOCs (Theis et al. 2009, Lucas-Barbosa et al. 2011), but how these induced VOCs affect mutualists and antagonists remains unclear (see Section 2.1). How herbivory impacts attraction of pollinators through VOCs represents an important question for understanding the consequences of herbivores for the evolution of floral traits (Kessler et al. 2011).

The mechanisms underlying induced effects of herbivores on floral traits are also poorly understood. Damage can cause reallocation of resources from reproductive to storage tissues (e.g., roots) (Babst et al. 2005). Alternatively, changes to floral and leaf VOCs (Kessler et al. 2010), reward chemistry (Kessler & Halitschke 2009), and floral pigments (Tamari et al. 1995) could be driven by herbivore induction of JA (Kessler & Baldwin 2002). This raises the question of how plants independently control responses of leaf and reproductive tissues to maximize fitness, because constitutive correlations between leaf and reward chemistry may not predict induced responses (Kessler et al. 2010). For example, folivory induces VOC emissions from flowers but not leaves of black mustard (*Brassica nigra*, Brassicaceae) (Bruinsma et al. 2014), whereas herbivory induces glucosinolate production in leaves and not flowers of *R. sativus* (Strauss et al. 2004). Our limited understanding of the extent of induced responses, and the shared hormonal mechanisms regulating defense and plant reproductive traits (Kessler et al. 2010, Campbell et al. 2014), indicates that future research should consider both constitutive and induced responses when evaluating how herbivores affect floral traits.

3.2. Selection on Reproductive Traits by Herbivores

Herbivores may influence the evolution of plant reproductive traits both directly and indirectly. Herbivores can impose selection directly on floral traits when (*a*) genetic variation in floral traits affects the preference or performance of florivores and seed predators (see Section 2.1) and (*b*) genetic variation in floral traits is related to plant fitness. Conversely, herbivores can impose selection indirectly on floral traits by altering the behavior or efficacy of pollinators that facilitate mating (Section 3.1). Indirect selection by herbivores on floral traits occurs when four conditions are satisfied: (*a*) Seed production is pollen limited, (*b*) phenotypic variation in floral traits affects the efficacy of pollinators in facilitating mating, (*c*) genetic variation underlies this phenotypic variation in floral traits, and (*d*) herbivores alter floral traits that attract pollinators (Section 3.1).

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Given these conditions, we ask: What is currently known about the importance of selection on floral traits by herbivores?

We identified 21 studies involving 107 estimates of phenotypic selection on 28 floral traits by a variety of mammalian and invertebrate herbivores (**Supplemental Table 2**). Herbivores imposed significant selection on at least one floral trait in most studies (91%) (**Supplemental Table 2**). One-quarter of the estimates of selection were significantly different from zero. Importantly, the strength of selection by herbivores on floral traits was as strong or stronger than pollinator-mediated selection in 67% of cases that detected significant selection by either herbivores or pollinators. Although there are examples of herbivores and pollinators imposing selection in the same direction on floral traits (Sletvold et al. 2014), our analysis suggests they more commonly select in opposite directions (**Figure 4**). Herbivores frequently selected for shorter inflorescences, fewer flowers, and smaller flowers or showy bracts (**Supplemental Table 2**), whereas pollinators often selected for increases in these traits. These examples of opposing selection may result in

Supplemental Material

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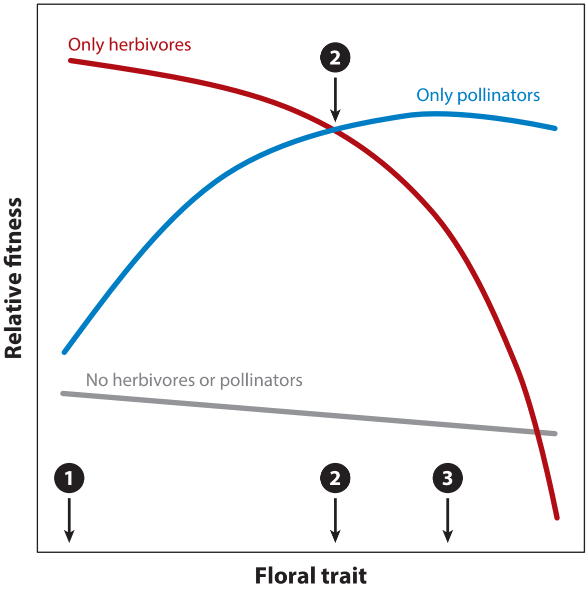

Figure 4

Predicted influences of herbivores and pollinators as agents of selection on a hypothetical floral trait (e.g., display size) in a self-compatible plant population. When no herbivores or pollinators are present (*gray line*) the fitness optimum is at arrow ➊, yet such plants experience low fitness due to inbreeding depression and pollen limitation, and selection on the floral trait is negative due to the costs of floral allocation. When pollinators are present but herbivores are absent (*blue line*), selection shifts the fitness optimum to arrow ➌, at which point greater investment in floral traits increases attractiveness to pollinators and thus plant fitness. The fitness optimum occurs at arrow ➌ (and not higher) in this example because of the costs of increased investment in floral structures and the asymptotic relation between the floral trait and pollinator attraction. When herbivores are present but pollinators are absent (*red line*), the fitness optimum is at arrow ➊ because herbivores have a negative effect on plant fitness and risk to herbivore attack increases with greater investment in the floral trait. When pollinators and herbivores are both present, the fitness optimum occurs at arrow ➋ (i.e., the intersection of the *blue* and *red lines*) because herbivores and pollinators select on the trait in opposite directions, thus causing stabilizing selection. This is a hypothetical example, and numerous variations in predicted relationships are possible; however, on the basis of the results presented in **Supplemental Table 2**, the combined effects of herbivores and pollinators may frequently cause stabilizing selection for intermediate floral trait values.

stabilizing selection on floral traits (Pérez-Barrales et al. 2013) (**Figure 4**) and may maintain genetic variation within and between populations (Ågren et al. 2013). These data clearly show that herbivores can be potent agents of natural selection on floral traits and are likely to play a significant role in floral evolution.

Experimental manipulation of herbivores allows for the dissection of the direct versus indirect effects of herbivore-mediated selection (Gómez 2003, Ågren et al. 2013). For example, flower and seed predator moths preferentially attacked early-flowering common evening primrose (*O. biennis*) genotypes, resulting in a direct fitness advantage to late-flowering genotypes (Agrawal et al. 2012). Other studies revealed that the effects of herbivores are indirect. Mothershead & Marquis (2000) experimentally manipulated leaf herbivory and pollination in Missouri evening primrose (*Oenothera macrocarpa*) and demonstrated that leaf herbivory reduced flower size, which decreased pollinator visitation and resulted in indirect selection on this trait. Despite these examples, most studies in **Supplemental Table 2** are correlative; thus, it is unclear whether direct or indirect herbivore-mediated selection is more common.

Supplemental Material

There still exist large gaps in our understanding of these interactions. First, all but one study (Agrawal et al. 2012) used phenotypic rather than genotypic selection analyses. Environmental variation can inflate the magnitude of phenotypic selection (Stinchcombe et al. 2002), so it is possible that the importance of herbivore-mediated selection has been exaggerated in some studies. Second, most investigations measured selection on phenological and morphological traits, with few examining whether herbivores select on other traits, particularly floral volatiles (Ehrlén et al. 2012). Third, most studies focus on the role of seed predators and florivores as selective agents on floral traits, whereas only a single investigation examined the role of leaf herbivores (Mothershead & Marquis 2000). Herbivores that feed directly on reproductive structures are expected to be the most important agents of selection on floral traits, but indirect effects by folivores may still be pervasive and require examination. Finally, only two studies have examined whether selection by herbivores results in evolutionary changes of these floral traits within populations (Agrawal et al. 2012, Ågren et al. 2013). More population-level studies are needed to determine the role of herbivores in driving floral evolution.

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3.3. Herbivory, Defense, and Mating System Evolution

The effects of inbreeding on defense trait expression (Section 2.3) and herbivory on variation in floral traits (Section 3.1) suggest two complementary processes by which herbivory could play a role in the evolution of selfing from outcrossing. First, differential herbivory between inbred and outcrossed offspring could change the fitness cost of selfing and lead to herbivore-mediated ID. Second, herbivore-induced changes to floral traits could alter the rate and quality of pollinator visitation and lead to pollen limitation. As detailed below, there is evidence that both of these processes affect the fitness consequences of inbreeding.

3.3.1. Herbivore-mediated inbreeding depression. In basic models of mating system evolution, selfing is favored when ID reduces the fitness of inbred offspring to <50% of outbred offspring (Lande & Schemske 1985). The reduction in fitness of selfed offspring leads to the hypothesis that ecological factors could modulate the magnitude of ID and influence mating system evolution. A variety of environmental stressors are known to exacerbate ID (Cheptou & Donohue 2011), yet the role of herbivores in affecting ID remains poorly understood.

Testing the hypothesis that herbivory alters the strength of ID requires the simultaneous manipulation of inbreeding and the presence of herbivores. This comparison should ideally be performed across a large number of genetic families and several populations to avoid biasing estimates of ID from sampling a small number of genotypes. In glasshouse studies that manipulated the presence of herbivores, inbred plants suffered greater reductions in fitness (Carr & Eubanks 2002, Leimu et al. 2008) and biomass (Hull-Sanders & Eubanks 2005) compared with outbred plants. These effects varied considerably among populations, likely reflecting variation in inbreeding history and the frequency of deleterious mutations. Field studies have the advantage of testing herbivore-mediated fitness consequences of inbreeding in natural settings and have mostly supported the hypothesis that herbivores increase ID, albeit with considerable variation in results among selfing and mixed-mating taxa (see Section 2.3).

Variation in the effects of herbivores on ID would appear to argue against a strong role for herbivores in mating system evolution. However, a primary goal of many early studies was to examine only one aspect of the interaction (e.g., effects on resistance), and these studies often did not manipulate herbivory (e.g., Bello-Bedoy & Núñez-Farfán 2010) or used only a single replicate of the herbivore manipulation (e.g., Kariyat et al. 2011). Thus, few robust tests of herbivore-mediated ID exist, despite many early studies. Ivey & Carr (2005) reported significantly greater ID caused by herbivory in a large field experiment of the mixed-mating *M. guttatus*. In the outcrossing *S. carolinense*, ID exceeded 50% for several fitness components after 3 years of herbivory in the field, but ID was not significantly different from zero when plants were protected from herbivores (Campbell et al. 2013). This finding supports the hypothesis that herbivores can select against the transition to selfing (see also Kariyat et al. 2011). Although discrete transitions in mating system caused by herbivory have not, as yet, been reported, the strength of herbivore-mediated selection to maintain outcrossing (Campbell et al. 2013) suggests this may be an important avenue for future research, particularly in highly outcrossing populations. Conversely, the evolution of selfing in mixed-mating populations is likely affected by the interplay between the level of herbivory and the amount of genetic load. There remains considerable scope to examine the conditions under which herbivores influence the evolution of selfing across a range of mating systems.

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3.3.2. Herbivore effects on selfing rates and pollination. Herbivore-induced changes to floral morphology (Steets & Ashman 2004), floral rewards (Krupnick et al. 1999), or volatiles can influence pollinators and plant mating (see Section 3.1). These induced responses can limit outcrossing opportunities through induction of repellent or toxic compounds (Kessler et al. 2011), promote outcrossing by attracting pollinators (Schiestl 2015), or limit geitonogamous self-pollination by altering pollinator behavior (Steets et al. 2006, Kessler et al. 2012). Herbivores have been shown to both increase (Ivey & Carr 2005, Steets et al. 2006) and decrease (Elle & Hare 2002) selfing rates. However, the evolutionary consequences of herbivore-induced changes to floral traits remain largely unexplored (Steets et al. 2007), particularly in terms of linking induced changes to selfing with subsequent herbivore-mediated ID. In general, upregulation of defense chemistry in reward tissues (e.g., nectar, pollen) after damage should select for increased selfing by limiting the recruitment of new pollinators; this selection suggests a trade-off between inducibility and outcrossing.

3.4. Herbivory and Evolutionary Transitions in Sexual Systems

Gender strategies involve three distinct sexual morphs—hermaphrodite, female, and male—with their relative frequencies defining plant sexual systems. The evolution of separate sexes from combined sexes is puzzling for several reasons. Although dioecy has evolved from hermaphroditism numerous times (Renner 2014), unisexuality involves the risk of reproductive failure and causes up to a 50% reduction in genetic transmission compared with hermaphroditism. Theoretical models identify three parameters that help resolve these problems and govern the transition to gender dimorphism: (*a*) sex allocation and the relative fertility of sex types, (*b*) selfing rates and ID in hermaphrodites (Section 3.3), and (*c*) the genetics of sex determination (Charlesworth 1999). Empirical studies focus on measuring these parameters in species with gender variation and determining the factors that shift fitness gain curves from convexity to concavity (Charnov et al. 1976) as well as the ecological context in which this occurs (Ashman 2006). A dominant theme has been the role of stressful abiotic conditions in favoring dioecy, but relatively little attention has been focused on the potential role of enemies as agents of selection.

The first hypotheses on the role of herbivores in the evolution of dioecy were based on natural history observations of sex-biased herbivory in tropical dioecious species (Janzen 1971, Bawa 1980, Cox 1982). As reviewed in Section 2.4, male-biased herbivory has been demonstrated in numerous dioecious populations, but efforts to extrapolate the selective forces driving unisexuality from these observations may be misleading. The observed patterns in herbivory could result from differences in the life history and reproductive traits of the sexes, whereas other selective forces may drive the origin of dioecy.

A more fruitful approach may be to determine how herbivory influences the key parameters in models for the evolution of dioecy. Investigating these parameters is best accomplished by studying populations that represent stages along the two main evolutionary pathways to dioecy: the gynodioecy and monoecy pathways (Barrett 2002). Identifying how enemies influence morph-specific fitness through female and male function can provide insight into whether herbivory promotes or prevents the evolution of dioecy (Ashman 2002). Exemplary studies involve *Fragaria* spp. in which dioecy evolves via the gynodioecy pathway with the occurrence of hermaphrodite, gynodioecious, subdioecious (all sex types), and dioecious species (Liston et al. 2014). Transitions to dioecy in *Fragaria* spp. may be favored by sex-specific weevil herbivory on hermaphrodites, when this reduces floral display and pollinator attraction and causes increased selfing, as observed in *F. virginiana* (Penet et al. 2009). However, the same type of male-biased herbivory by weevils in *F. virginiana* (weevils are thought to require pollen to complete development) also favors individual hermaphrodites with female-biased sex allocation over those that produce more pollen (Ashman et al. 2004). This scenario causes a deceleration of the male fitness gain curve (see Ashman 2002) and can reduce the fitness advantage to hermaphrodites with increased allocation to male function and effectively oppose the spread of males in populations (Ashman et al. 2004, Ashman & Penet 2007). Consequently, this form of selection may outweigh any potentially negative effects of selfing on hermaphrodite fitness and explain why the full transition from subdioecy to dioecy is not evident in *F. virginiana*.

The transition to dioecy via the monoecy pathway may be at least as common as those involving the gynodioecy pathway (Renner 2014) but less is known about the ecological mechanisms involved. In broadleaf arrowhead (*Sagittaria latifolia*, Alismataceae), vertical gradients of weevil herbivory on inflorescences have the potential to select for unisexuality (Muenchow & Delesalle 1992), and this may explain the transition from monoecy to dioecy that occurs in this species. This hypothesis is plausible but would be strengthened by studies of herbivory in ancestral monoecious populations. A second example involves figs (*Ficus*, Moraceae), in which monoecy is ancestral and dioecy has evolved once or twice, with reversions back to monoecy at least twice (Weiblen 2000). Two studies have implicated herbivores in the transition to dioecy (Kerdelhué & Rasplus 1996, Greef & Compton 2002). Unfortunately, the small number of evolutionary transitions to dioecy in both *Sagittaria* and *Ficus* limits opportunities for a rigorous assessment of the mechanisms causing these transitions. Moreover, because abiotic selection has frequently been implicated in the evolution of gender dimorphism (Ashman 2006), a major future challenge is to determine the relative contributions of abiotic and biotic selection in this transition.

Finally, herbivores could influence transitions between gender strategies by directly altering sex allocation. Plasticity in sex allocation is a characteristic feature of monoecious and

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andromonoecious populations, in which individuals differentially allocate resources to female and male function depending on environmental circumstances (Lloyd & Bawa 1984). Herbivory could contribute to this variation, either by causing a reduction in resource acquisition and increased allocation to male rather than female function (Krupnick & Weis 1998) or by influencing sex expression through the induction of phytohormones (Golenberg & West 2013). However, the consequences of these effects remain poorly understood.

Intragenomic coevolution: evolution at two or more loci within a single genome as a result of reciprocal selection among loci

4. CONCLUSIONS

We have considered evidence for evolutionary interactions between the traits and genes controlling reproductive systems and defense strategies (**Figure 1**). There are a growing number of examples of reproductive traits influencing the evolution of plant defenses and susceptibility to herbivores (Section 2, Hypothesis 1). Moreover, herbivores frequently affect the expression of floral traits, plant–pollinator interactions, and the costs and benefits of alternative reproductive systems (Section 3, Hypothesis 2). We conclude that there appears to be strong support for the two complementary hypotheses proposed here. Furthermore, we suggest that in some cases, tight reciprocal feedbacks between defense and reproduction could lead to intragenomic coevolution between reproduction and defense (i.e., reciprocal selection between traits and genes within species) (**Figure 1**). This may be particularly likely in systems with tight interspecific coevolution like nursery pollination systems. Consistent with this notion, well-studied plant lineages, including *Ficus* (Cook & Rasplus 2003), *Dalechampia* (Armbruster et al. 2009), *Protea* (Hanley et al. 2009), and *Yucca* (Pellmyr 2003), provide compelling examples of pollinators and herbivores that appear to drive evolutionary interactions between reproductive and defense traits. How general this process is among angiosperm lineages when one considers the diversity of herbivores, pollination systems, defense strategies, and reproductive strategies remains to be determined. Large gaps remain in our understanding of the evolutionary interactions between plant reproductive biology and defense. These represent exciting areas for future research because an integrated view of the evolution of plant reproduction and defense could help to explain the patterns and processes that have shaped these plant traits and how they influence biotic interactions.

FUTURE ISSUES

1. How does the outcrossing rate of populations modify the effects of inbreeding on constitutive resistance, induced resistance, and tolerance against generalist and specialist herbivores?
2. To what extent does variation in floral traits influence indirect selection of pollinators on plant defense strategies?
3. To what extent does variation in reproductive system (e.g., sexual versus asexual, outcrossing versus selfing, hermaphroditism versus dioecy) influence the phenotypic and molecular evolution of plant defense?
4. What role does pleiotropy play in causing evolutionary interactions between reproductive and defense traits? What are the molecular, metabolic, and development mechanisms involved?
5. How often does herbivore-mediated ID lead to purging of deleterious alleles in natural populations?

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6. Can herbivores drive evolutionary transitions in reproductive systems, including transitions from outcrossing to selfing and from hermaphroditism to dioecy? Conversely, does herbivory constrain evolutionary transitions among reproductive systems?
7. Do genes underlying reproductive traits show evidence for molecular coevolution with defense genes (i.e., intragenomic coevolution)?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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