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## Review

# Sex-specific patterns of antagonistic and mutualistic biotic interactions in dioecious and gynodioecious plants

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### ABSTRACT

A major transition in flowering plants has been the evolution of separate sexes from hermaphroditism via gynodioecy which is considered to be the most important route. Biotic interactions, both antagonist and mutualistic, have been proposed to influence this transition which is generally accompanied by the evolution of sexual dimorphism in secondary sexual traits. While some researchers have studied sex-specific patterns in herbivory and pollination, less attention has been paid to pathogens/parasites and a limited number of studies have revised sex-specific patterns in mycorrhizal symbiosis. In this article, we explore sex-specific interactions in dioecious and gynodioecious plants, examining the interrelationships among the incidence and/or frequency of herbivory, pathogen/parasite infestation, pollination and mycorrhizal symbioses. We review how multiple interactions (both above and belowground) act synergistically or antagonistically to shape the ecological and evolutionary results of pairwise interactions. Finally, we identify gaps in the knowledge of sex-specific patterns in multiple interactions in dioecious and gynodioecious plants, as well as future and promising lines of research.

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## Introduction

In natural ecosystems, plants live in complex environments in which they interact with other organisms above and belowground. In terms of fitness, some of these interactions, e.g., pollination, are evidently beneficial to the plants (Ayasse and Arroyo, 2011) others, such as herbivory or interactions with pathogens, are clearly detrimental (van Dam, 2009). However, certain biotic interactions may vary along a continuum from mutualism to parasitism (e.g., mycorrhizas; Johnson et al., 1997), while other interactions lead to neither positive nor negative effects (e.g., commensalism; van Dam, 2009). Belowground interactions between plants and other organisms can influence, and can be influenced by interactions that take place aboveground (Heil, 2011; van Dam and Heil, 2011). Normally, plant responses to a diversity of stresses and environmental cues have an effect on other species that depends directly or indirectly upon the plant as a source of nutrients and/or energy (Kiers et al., 2010). In this way, plants mediate interactions between above and belowground organisms. Therefore, understanding how multiple biotic interactions can act synergistically or antagonistically is a major goal in ecology and evolutionary biology that is reflected in the recent increase in investigations on this topic (Strauss and Irwin, 2004; Larimer et al., 2010; Heil, 2011; van Dam and Heil, 2011; Eisenhauer, 2012).

Most flowering plants are hermaphroditic, i.e., produce female and male sexual organs in the same flower, but unisexuality where the female and the male sexual functions are placed on separate individuals (dioecy) has evolved several times during the course of evolution in different plant lineages (Renner and Ricklefs, 1995; Charlesworth, 2002). Dioecy is relatively uncommon in flowering plants; only ca. 6% of flowering plants have dioecious populations, although it is represented in over 38% of all angiosperm families (Renner and Ricklefs, 1995). On the other hand, few flowering plants (~7%) feature other breeding systems, where combinations of female, male or hermaphrodite flowers at the plant and population levels are involved (e.g., gynodioecy; populations composed of female and hermaphroditic plants), which may represent intermediate steps toward the evolution of full unisexuality, or stable terminal breeding systems (Ainsworth, 2000). Several pathways for the transition from hermaphroditism to dioecy have been proposed (see Barrett, 2002), but current evidence suggests that the gynodioecy pathway is particularly common (Charlesworth and Charlesworth, 1978; Weiblen et al., 2000; Barrett, 2002; Spigler and Ashman, 2012). Male-sterility genes (caused by mutations in nuclear genes or in mitochondrial loci) spread within hermaphrodite populations, leading to an intermediate stage involving females and hermaphrodites. Genetic modifiers of female fertility subsequently convert hermaphrodites to males, gradually resulting in dioecy. In gynodioecious plants, the hermaphrodites are generally “less female” relative to the females, i.e., the hermaphrodites could be functionally more male if high frequencies of females exist in the population (Spigler and Ashman, 2012). The type of mutation (nuclear or cytoplasmic) and the ecological environment may affect the transition to dioecy (Ashman, 2006; Spigler and Ashman, 2012). Dioecy can be considered the most extreme mechanism for avoiding the effects of fixation of deleterious genes and inbreeding depression, although self-pollination (autogamy) has evolved in some angiosperm species (20%) as a mechanism of reproductive assurance (Schoen et al., 1996; Eckert et al., 2006). Regardless of the pathway, evolution of separate sexes in plants seems to have been (and is being) influenced by above and belowground interactions (see e.g., Ashman, 2002, 2006). The biotic interactions along with life-history trade-offs are pivotal elements of the

theory of the evolution of dioecy (Geber et al., 1999; Ashman, 2000, 2002) and thus, understanding the evolutionary consequences of sex-specific preferences in these interactions and how sexual morphs deal with such biotic interactions is of primary importance.

Life-history trade-offs (Gleeson and Tilman, 1992; Seger and Eckhart, 1996) can be used to predict sex-specific resource allocation patterns between sexual morphs. Plant resources are limited, and therefore resource allocation trade-offs between plant functions normally exist. These trade-offs manifest themselves so that allocation to one function reduces allocation to other functions. Classically, plant functions such as growth, reproduction, maintenance and defense are considered to be constrained by shared resource pool. In dioecious and gynodioecious plants, females generally allocate more resources to reproduction and defense than to growth, while males or hermaphrodites allocate more to growth than reproduction (Delph, 1999; Obeso, 2002). As a result, secondary sexual dimorphism (of traits not related directly to gamete production, Sakai and Weller, 1999) between sexual morphs has been documented (Geber et al., 1999), including those observed in the incidence and strength of above and belowground biotic interactions such as herbivory (e.g., Cornelissen and Stiling, 2005), parasitism (e.g., Williams et al., 2011), pollination (e.g., Munguía-Rosas et al., 2011) and, more recently, the interaction with arbuscular mycorrhizal fungi (e.g., Varga and Kytöviita, 2008; Vega-Frutis et al., 2012). Only if there are no sexual differences in resource allocation or if resources are not compromised (trade-offs), we would expect a lack of differences in biotic interactions between sexes.

Given that the gynodioecy–dioecy pathway has been proposed as the principal route of evolution from hermaphroditism to dioecy, understanding how below and aboveground biotic interactions may impact the evolution of dioecy is a central topic in evolutionary biology (e.g., Barrett, 2002; Ashman, 2006). Our objective is to review and highlight the main research themes concerned with plant sex and multiple interactions. First, we summarize effects of antagonistic and mutualistic biotic interactions on some traits relevant to dioecious and gynodioecious species. Second, we review studies dealing with multiple biotic interactions. Third, we present a comprehensive list of studies of multiple interactions in both dioecious and gynodioecious plants, owing to the currently limited understanding of this topic, and the fact that below and aboveground interactions have traditionally been studied in isolation from one another. Some previous revisions have been conducted partially on this issue, especially regarding interactions with herbivores and pollinators (Ågren et al., 1999; Ashman, 2000, 2002; Cornelissen and Stiling, 2005) and these have been extremely valuable for understanding the role of biotic interactions in the evolutionary and ecological context between sexual morphs of dioecious and gynodioecious species. However, most studies were focused specifically on single interaction (e.g., herbivory) and on one plant host, and thus do not provide the full insight in an ecological context. Our review focuses mostly in dioecious and gynodioecious systems since information from other breeding systems is almost absent. Studies considering other breeding systems such as androdioecy (populations with male and hermaphrodite flowers in different individuals), trioecy (populations with female, male and hermaphrodite flowers in different individuals) and subdioecy (populations with female and male flowers in different individuals, but with males that usually produce hermaphrodite or female flowers) will expand our understanding of the role of mutualists and antagonists in the evolution of breeding systems, but these sexual systems are beyond the scope of our revision.

## Antagonistic interactions

### Herbivores

Interactions between plants and herbivores are among the most studied ecological interactions. Herbivores consume ca. 15% of plant biomass produced annually in temperate and tropical ecosystems (Cry and Pace, 1993), affecting both the ecology and evolution of plants; for instance, defending against herbivores may affect a plant's attractiveness to pollinators or other mutualists. The evolution of plant defenses against herbivores including resistance (constitutive or induced response of plants against herbivory to avoid or reduce damage), and tolerance (damage-induced response of plants to reduce the negative effect on fitness; Núñez-Farfán et al., 2007) have received increased attention over the past four decades, and herbivory has been proposed as an important factor in the evolution of separate sexes from hermaphroditism. Ashman (2002) has identified several ways by which herbivory facilitates the evolution of dioecy from hermaphroditism via gynodioecy (see details in Ashman, 2002 and references therein). Given that there are already some reviews of this topic (Ågren et al., 1999; Ashman, 2002; Cornelissen and Stiling, 2005), we briefly recapitulate the general results and highlight areas that require further attention. In short, the reviews and specific cases show that a sex-specific pattern of herbivory exists both in dioecious and gynodioecious breeding systems. In dioecious species male plants suffer more herbivore damage than females, and also present significantly less secondary defense compounds (tannins, total phenolics and phenolic glycosides) and structural defenses (such as leaf toughness, resins and trichomes) than females (see Boecklen and Hoffman, 1993; Ågren et al., 1999; Cornelissen and Stiling, 2005).

In gynodioecious species, although the available information is more limited, it seems that the sexual morph more specialized in seed production (females) suffers less damage than the hermaphrodites (e.g., Ashman, 2002; but see Alonso, 2003). In addition, some studies have shown that females tend to be more resistant to herbivores while males/hermaphrodites have more tolerance to herbivores (e.g., Ashman et al., 2004; but see Cole and Ashman, 2005).

A great deal of research on antagonistic interactions with herbivores in dioecious and gynodioecious plants have focused mainly on the defense of aboveground tissues, especially leaves and shoots; while the florivory (reviewed by McCall and Irwin, 2006) and defense against belowground herbivory has received little attention (Rasmann et al., 2011; Anderson et al., 2012). Therefore, our understanding of the ecology and evolution of defense in belowground plant structures is very limited. Sexual differences in reproductive schedules and resource allocation to growth or reproduction are generally associated with the presence of sex-specific patterns regarding the interaction between plant and herbivore. However, many studies have only evaluated the trade-offs between two functions; for example, growth vs. defense (Stevens and Esser, 2009). Research that simultaneously evaluates herbivory in terms of trade-offs among reproduction, defense and growth would provide a more complete and integrated view of resource allocation conflicts (see Cepeda-Cornejo and Dirzo, 2010). In addition, most studies have focused on the interaction between two species (host and herbivore); and the effects of multiple interactions as well as the interaction with abiotic factors in different populations have been virtually neglected. Differences at the level of populations are important; for example, in the dioecious *Baccharis concinna* G.M. Barroso, Carneiro et al. (2006) showed that rates of attack by species of galling insect varied between host-plant sexes and populations. In the gynodioecious *Geranium sylvaticum* L. Asikainen and

Mutikainen (2005) reported sex-differences in herbivore attack in two of six populations, whilst seed predators did not discriminate between sexes in any population. Therefore, studies that consider multiple populations and several generations including the abiotic and biotic context are necessary to fully understand the role of herbivores on sexual system evolution of plants.

### Pathogens and parasites

Pathogens and parasites are organisms (viruses, bacteria, fungi, animals or plants) that usually reduce host performance and fitness (e.g., growth and reproduction). In natural ecosystems, the effect of pathogens and parasites on plants can be remarkable; both may affect distribution and composition of plant species, plant succession (Castello et al., 1995), spatial and temporal density, genetic composition of plant populations and affect other trophic levels such as herbivores, pollinators and mycorrhizas (Clay and van der Putten, 1999; Press and Phoenix, 2005). Although the incidence of pathogens in dioecious species has been studied since several decades ago (Gikalov, 1935), these efforts have been mainly directed towards crops, with the result that intersexual patterns of pathogen incidence are less consistent than in the case of herbivory. A noteworthy exception is the anther-smut disease in the genus *Silene* (Hood et al., 2010). This fungus infests plant anthers and its spores replace the pollen (Alexander and Antonovics, 1988). In the stigma of females, a few infected pollen grains germinate and the ovaries abort shortly after (e.g., Alexander and Antonovics, 1988; Alexander, 1990a; Thrall et al., 1993; Marr, 1998). Some other studies have shown that anther-smut infection stimulates flower production and reduces bud size in males (Alexander, 1989; Alexander and Maltby, 1990). In *Silene dioica* (L.) Chairv., Lee (1981) observed that females exhibited greater infection by *Microbotryum violaceum* G. Deml and Oberw. than males. In the dioecious *Silene latifolia* Poir., a male-biased infection rate is typical in experimental and artificial conditions (reviewed by Williams et al., 2011), although in natural populations a female-bias in infection rates has been reported (Kaltz and Shykoff, 2001).

Regarding gynodioecious species, there are fewer studies on pathogen incidence than in dioecious species and from the scarce evidence currently available, we cannot discern a sexual pattern in pathogen infestation in these plants. López-Villavicencio and Branca (2005) observed reduced fitness and greater infestation of *Microbotryum violaceum* in hermaphrodites than in females in *Gypsophila repens* L. In *Silene acaulis* (L.) Jacq., however, neither seed production nor pathogen infection differed between females and hermaphrodites, and the sex ratios of healthy and diseased plants did not differ between study sites (Marr, 1997). Sites with high incidence of the disease, however, did tend to have more females than sites of low incidence (Marr, 2006). In *Fragaria virginiana* Duchesne (Cole and Ashman, 2005) and *Dianthus sylvestris* Boiss. (Collin et al., 2002), females presented higher rates of infection than hermaphrodites.

Pathogen/parasite incidence and permanence in a particular host depends on biotic and abiotic factors, but also on host physiology and life-history traits such as reproductive status or age at first reproduction. For instance, Lee (1981) observed that the female-biased infection by *M. violaceum* in *Silene dioica* varied widely between populations. Åhman (1997) showed that females *Salix viminalis* L. were more infested by *Melampsora* sp. rust than males; however, this difference disappeared during the reproductive season in some genetic families. In the same way, in *Juniperus monosperma* (Engelm.) Sarg., females had greater density of mistletoe (hemi-parasitic plants) infestation than males under stressful conditions; however, this difference was not observed under more benign conditions (Gehring and Whitham, 1992).

In terms of life-history trade-offs, one would expect greater allocation to pathogen defense in female than male/hermaphrodite plants. However, the lack of consistent sex-specific patterns in plant-pathogen/parasite interactions in dioecious and gynodioecious species can be explained by: (1) the limited number of plant species that have been evaluated to date, with most studies conducted on *Silene* species (Williams et al., 2011), (2) the density-dependent spread of diseases that occurs in some populations (Alexander, 1990b), (3) the fact that phenotypes and their offspring may differ in plastic traits that respond to local environmental conditions (environmental changes between generations), and (4) trade-offs between defense and reproduction (Biere and Antonovics, 1996). Relatively few studies have evaluated intersexual differences in foliar pathogens, relative to floral pathogens. Similarly, belowground pathogens have been largely neglected, probably because these are more difficult to investigate. Integrating the potentially interactive effect of above and belowground pathogens/parasites is likely to elucidate the issue further.

## Mutualistic interactions

### Pollinators

Since the publication of Darwin's book "The different forms of flowers on plants of the same species" in 1877, there has existed an interest in understanding the complex but fundamental process of sexual reproduction in plants and the mechanisms that lead to the evolution of separate sexes (Barrett, 2010). Species with unisexual flowers are incapable of producing seeds without a vector of pollen (with the exception of apomictic females, Bierzychudek, 1987; O'Connell and Eckert, 1999) and are therefore extremely sensitive to changes in abundance of pollen vectors. Some studies have shown that sexual dimorphism in floral characters may optimize pollinator attraction and directional pollen transfer (e.g., Bawa, 1980; Kay et al., 1984; Vaughton and Ramsey, 1998). Although there is some evidence to the contrary, most studies suggest that the morph that produce the pollen (males in dioecious or hermaphrodites in gynodioecious species) invests more in pollinator attractors (morphological and chemical), perhaps as a consequence of Bateman's principle of male-male competition for females (Burd, 1994). In general, males in dioecious species have larger perianth size particularly in temperate zones (see Delph et al., 1996), larger number of flowers (Eckhart, 1999) and are the most fragrant (Ashman, 2009) compared to females. These traits are, in turn, linked to a higher visiting rate of pollinators (e.g., Farwig et al., 2004; Ashman et al., 2005; Vamosi et al., 2006; Waelti et al., 2009). These results agree that the sex whose fitness depends more on mating success should invest more into attractants (Bell, 1985). In terms of nectar, there seems to be no general pattern of sexual dimorphism in nectar amounts (Renner and Feil, 1993; Delph et al., 1996; Eckhart, 1999). Nevertheless, nectar quality may differ between males and females: in *S. dioica* (Kay et al., 1984) and *Rubus chamaemorus* L. (Ågren et al., 1986), females produce greater quantities of more dilute nectar than males. Volatile production in sexually dimorphic species was recently reviewed by Ashman (2009): in general, male flowers of animal-pollinated species produced more volatiles per flower than females (see details in Ashman, 2009). However, very little is known regarding the specific organs in each gender responsible for volatile production (Dobson and Bergström, 2000) and the amount or timing of volatile emissions. Flamini et al. (2002) identified one exclusive compound emitted by pollen in the dioecious *Laurus nobilis* L., and Johnson et al. (2011) found that some compounds are emitted only by male flowers in the dioecious *Cytinus visseri* Burgoyne. Dufaj

et al. (2003) found three volatile compounds emitted only by leaves of males in *Chamaerops humilis* L. Interestingly, the specific pollinator of *C. humilis* selected more often male leaves than female ones, although no difference in the quantities of volatiles produced by the leaves of male and female plants were detected (Dufaj et al., 2003).

In gynodioecious species, the perianths of hermaphrodites are larger than those of females (18 of 19 species) and tend to produce more nectar than females (8 out of 9 cases) (Eckhart, 1999). Volatiles produced by anthers may play a role also in pollination attraction in gynodioecious species. Ashman et al. (2005) identified one compound emitted by the anthers only (not present in petals) in hermaphrodites of the gynodioecious *Fragaria virginiana*.

### Mycorrhizas

Approximately 80% of terrestrial plant species grow in symbiosis with mycorrhizas in their root systems. Arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) are the most common and widespread group: about 74% of angiosperms live in symbiosis with AM fungi in their roots (Brundrett, 2009). The benefit for fungi in this symbiosis is primarily the direct gain of photosynthates (fungi can consume up to 4–30% of plant photosynthates) from the host plant (Jakobsen and Rosendahl, 1990; Finlay and Söderström, 1992). The benefit for the plant is more complex and includes facilitating soil nutrient uptake (especially in terms of phosphorus). Additionally, mycorrhizal plants are often more competitive and better able to cope with biotic (e.g., herbivory tolerance, soil-borne pathogen protection; Gehring and Bennett, 2009; Koricheva et al., 2009) and abiotic stresses (e.g., heavy metals, salinity, drought; Miransari, 2010). Given the fact that plants can detect, discriminate and reward the best fungal partners with more carbohydrates, and in turn, the fungal partners increase nutrient transfer (Kiers et al., 2011), and because of sex-specific resource allocation patterns, it is logical to predict that females and males/hermaphrodites could differ in terms of frequency of colonization by AM fungi in the roots, the effect of the AM fungi on growth and fitness, diversity of species of AM fungi that can colonize each sex, and the amount of photosynthates that each sex provides in order to maintain the symbiosis with the AM fungi (e.g., Varga, 2010).

To date, sex-specific interaction with mycorrhizal symbiosis has only been studied in five dioecious and two gynodioecious species, with contrasting results (Table 1). Varga (2010) reviewed the effect of AM fungi on dioecious species and there seems to be no clear pattern in terms of the frequency of mycorrhizal colonization within the roots (Table 1). Nevertheless, female and male plants may differ in their response to inoculation under experimental conditions with the same AM fungal species in terms of biomass, number of ramets, shoot phosphorus content and relative growth rate, with females exhibiting greater benefits than males (Varga and Kytöviita, 2008, 2010a), suggesting sex-specific benefits from the fungal symbionts. The AM fungal-plant relationship not only depends on the symbionts' identity, but also on abiotic factors such as nutrient availability in the soil (Vega-Frutis and Guevara, 2009) or plant phenology (Allen et al., 1998). In general, higher mycorrhizal colonization is observed during the stages of growth and reproduction and this may be linked to the larger need of nutrient uptake to support these plant functions. Under field conditions, female plants of *Distichlis spicata* (L.) Greene (Eppley et al., 2009) had higher frequencies of colonization during the growing season, whereas females in *Carica papaya* L. (Vega-Frutis and Guevara, 2009) and *Antennaria dioica* Gaertn. (Vega-Frutis et al., 2012) had higher frequencies of colonization than male plants during the reproductive season. In addition, a positive correlation between soil N:P ratio and hyphae length in the root was detected in females of *C.*

**Table 1**

Summary of publications that have investigated the arbuscular mycorrhizal (AM) fungi in dioecious and gynodioecious plants.

| Plant species        | Life form | Breeding system | Type of study  | Comparison <sup>a</sup> AM fungi | Reference                      |
|----------------------|-----------|-----------------|--|----------------------------------|--------------------------------|
| <i>J. monosperma</i> | Tree      | Dioecy          | Field + parasite   | F < M                            | Gehring and Whitham (1992)     |
| <i>A. dioica</i>     | Herb      | Dioecy          | Greenhouse ( <i>Glomus claroideum</i> ) + drought  | F = M                            | Varga and Kytöviita (2008)     |
| <i>C. papaya</i>     | Tree      | Dioecy          | Field + soil fertility   | F > M                            | Vega-Frutis and Guevara (2009) |
| <i>D. spicata</i>    | Herb      | Dioecy          | Field + soil fertility   | F > M                            | Eppley et al. (2009)           |
| <i>G. sylvaticum</i> | Herb      | Gynodioecy      | Field + defoliation  | F = H                            | Varga et al. (2009)            |
| <i>F. virginiana</i> | Herb      | Gynodioecy      | Greenhouse ( <i>Entrophospora columbina</i> + <i>G. intraradices</i> ) + selfed and outcrossed | 0                                | Botham et al. (2009)           |
| <i>F. virginiana</i> | Herb      | Gynodioecy      | Semi-natural + selfed and outcrossed   | 0                                | Collin and Ashman (2010)       |
| <i>A. dioica</i>     | Herb      | Dioecy          | Greenhouse ( <i>G. claroideum</i> ) + soil pH  | F > M                            | Varga and Kytöviita (2010a)    |
| <i>G. sylvaticum</i> | Herb      | Gynodioecy      | Greenhouse and field ( <i>G. claroideum</i> and <i>G. hoi</i> ) + floral visitors              | F = H                            | Varga and Kytöviita (2010b)    |
| <i>G. sylvaticum</i> | Herb      | Gynodioecy      | Greenhouse ( <i>G. claroideum</i> and <i>G. hoi</i> )  | F < H                            | Varga and Kytöviita (2010c)    |
| <i>A. dioica</i>     | Herb      | Dioecy          | Field  | F = M                            | Varga and Kytöviita (2011)     |
| <i>A. dioica</i>     | Herb      | Dioecy          | Field + soil fertility   | F > M                            | Vega-Frutis et al. (2012)      |

<sup>a</sup> F = M/H, no significant differences between female and male/hermaphrodite plants in terms of frequency of colonization by AM fungi; F > M, females have greater colonization by AM fungi than males; F < M/H, females have lower colonization by AM fungi than males/hermaphrodites; 0, no mention of the differences between sexes.

*papaya*, but only in the dry season (Vega-Frutis and Guevara, 2009). This suggests that females are sensitive to changes in soil fertility and that it is likely that females are able to adjust the frequency of AM colonization (Vega-Frutis and Guevara, 2009). In addition, AM fungi may increase intersexual, but not intrasexual competition, because differential mycorrhizal colonization in males and females may lead the sexes to obtain differential access to mineral nutrients (Eppley et al., 2009).

For gynodioecious species, Varga (2010) reported the effect of AM fungi on *Geranium sylvaticum* and found no differences between female and hermaphrodite plants in the frequency of colonization by AM fungi, although seed production was positively correlated with frequency of arbuscules (specific fungal structures to exchange of nutrients between fungi and plant) in females, but not in hermaphrodites (Varga et al., 2009). Moreover, AM fungi had a positive effect on flowering, but this difference depended on the species of fungi used, indicating that the cost–benefit ratio of mycorrhizal symbiosis is sex-specific. Also in the same species, sex-specific benefits from mycorrhizal fungi were detected and similarly to the study case with the dioecious *Antennaria dioica* (Varga and Kytöviita, 2008, 2010a), females benefited relatively more from the AM symbioses than hermaphrodites. Recently, Botham et al. (2009) and Collin and Ashman (2010) have begun to study the sex–AM fungal symbiosis in the gynodioecious *F. virginiana*. While these studies did not focus on differences in the frequency of colonization between the sexes, they do show the importance of inbreeding depression level of host plants (selfed vs. outcrossed). Selfed plants were less prone to interact with mycorrhizal fungi, and as a consequence obtained lower benefit of this interaction than outcrossed plants; therefore, AM fungi could influence the plant mating systems (Collin and Ashman, 2010).

## Multiple interactions

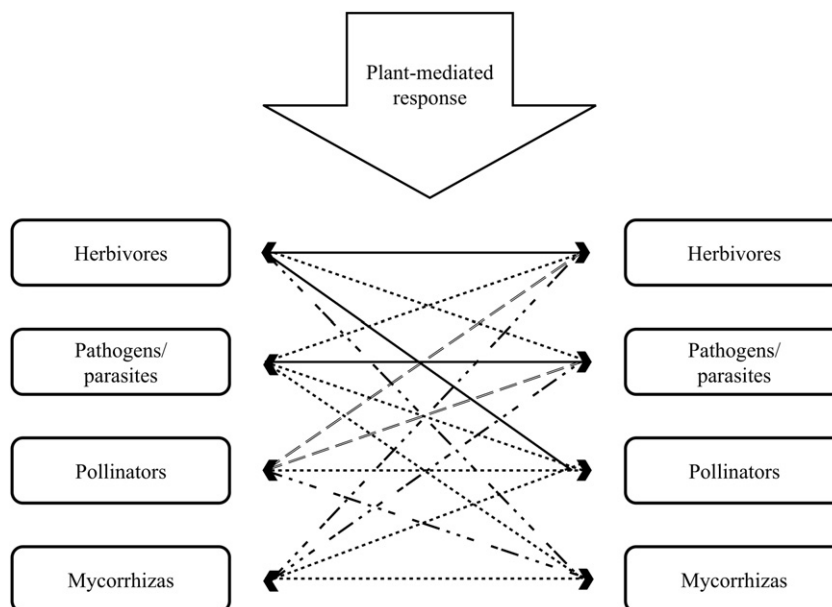
Recent studies in hermaphroditic plants have underlined the importance of achieving a comprehensive view of multitrophic interactions, including below and aboveground interactions under field and greenhouse conditions aimed at understanding the proximate and ultimate causes of these interactions on plant reproduction at population and community levels (Bardgett et al., 2005; Eisenhauer, 2012). Most studies have mainly focused on the interaction between two organisms. These have been valuable for assessing the mechanisms (ecological, chemical or molecular) that plants use to manage individual interactions. For example, van Dam and Heil (2011) and Larimer et al. (2010) showed how one biotic interaction can be affected by another biotic interaction

mediated by an inducible plant response. Species face multiple biotic interactions in nature and the ecological and evolutionary consequences of these multiple interactions on plant fitness cannot be predicted from the isolated study of single relationships. We suggest that the cost and benefit of interactions are dynamic, and that multiple interactions act synergistically and antagonistically and may differ from the outcomes produced by pair-wise interaction approaches. In addition, resources (mineral nutrients and light) and species identity play an important role in modifying the ecological and evolutionary outcomes of these interactions. In this sense, Strauss and Irwin (2004) reviewed the evidence for diffuse evolution (determined by interactions between many species) using examples of multi-species plant–animal interactions. They evaluated three criteria (see details in Strauss and Irwin, 2004): (1) the same trait could be affected, both positively and negatively, by different organisms, and trade-offs are often observed. For instance, in insect-pollinated plants, flowers must balance the benefits of attracting pollinators with the cost of attracting natural enemies, when these also respond to floral traits. (2) Interactions with one species affect the probability or intensity of interactions with other species. For instance, pathogen infection may facilitate subsequent attack by herbivores or other pathogens (Wolfe, 1997; Cole and Ashman, 2005). And (3), the effect of different organisms interacting on a focal species is not simply the sum of the effects of each organism. For instance, mycorrhizal colonization and defoliation have a positive and negative effect, respectively, on fitness (corolla mass and seed mass) of *Datura stramonium* L. (hermaphrodite plant); nevertheless, there was no significant effect on fitness when both interactions were evaluated simultaneously (Aguilar-Chama and Guevara, 2012).

In the case of dioecious or gynodioecious plants, multiple symbiotic interactions are even more complex because sexual morphs differ in primary and secondary sexual characteristics. In this case, selection pressures seem to be experienced differently by females and males/hermaphrodites (Geber et al., 1999). Below, we review plant responses to multiple above and belowground interactions in accordance with life-history trade-offs theory. We first review the interactions between plant sex and two biotic interactions, then between plant sex and three biotic interactions.

### Plant–herbivore–pathogen/parasite interactions

Herbivores and pathogens can strongly affect the performance, survival and distribution of other herbivores or pathogens simply through the shared consumption of plants and through inducing a number of defense mechanisms that affect the host-plant



**Fig. 1.** Schematic representation showing multiple interactions that are mediated by plant responses in a diverse spectrum of interactions among antagonistic and mutualistic organisms. These interactions can have positive, negative or no effects on the plant and can be antagonistic (continuous line), synergistic or antagonistic (dotted line), antagonistic or neutral (dashed line) and synergistic or neutral (double dashed line), relative to the other interacting organisms. This scheme is not comprehensive because only four biotic interactions are represented; however, it serves to illustrate the complexity and versatility of biotic interactions in nature.

quality for future consumers. Interspecific competition has been studied extensively for several decades (Hairston et al., 1960) and it is known that plant-induced responses elicited by one type of herbivores can affect the feeding behavior and development of other kind of herbivores (e.g., Anderson et al., 2012) (Fig. 1). However, the manner in which female or male responses affect herbivore–pathogen interaction remains a poorly studied topic. For instance, Cole and Ashman (2005) observed that the number of buds clipped by weevils (floral herbivore) in the hermaphrodite plants of the gynodioecious *F. virginiana* was reduced with increasing number of days that the plant was exposed to spittlebug (a xylem-feeding herbivore) (Table 2). Cole and Ashman (2005) also observed that spittlebug infestation in *F. virginiana* increased damage by fungal pathogens in females, but not in hermaphrodites (Table 2). The trade-offs caused by a xylem-feeding herbivore on the pathogen resistance and the resource demand of seed and fruit production is likely to be higher in females, because they were more susceptible to fungal infection. On the other hand, Wolfe (1997) showed in the dioecious *Neea psychotrioides* Donn. Sm. that male flowers had more galls than female flowers and that insect-induced galls facilitated the incidence of parasites and hyperparasites (parasite whose host is a parasite) within these structures (Table 2).

#### Plant–pollinator–mycorrhiza interactions

When the same resource is shared within a mutualistic relationship, competition can take place. For example, pollinators may reduce the visits of other pollinators by modifying floral attraction (e.g., flower color) after visitation has taken place (e.g., van Doorn, 1997). In contrast, floral visitation to some plant species stimulates the production of nectar (Ordano and Ornelas, 2004) that can lead to an increase in the total visitation of plants by the pollinator assemblage. When multiple symbionts simultaneously interact with a common host, positive interactive effects may occur if there is a benefit relative to the cost. This is more likely to occur if functionally distinct symbionts provide different benefits to the plant. Synergism is therefore often expected, especially between nutritionally complementary symbionts such as AM fungi that increase nutrient and water availability (Smith and Read, 2008; Larimer et al., 2010). For instance, Smith et al. (2000), showed that two different AM fungal species can be complementary even in terms of acquisition of the same resource (phosphorus acquisition close to roots in *Scutellospora calospora* Nicol. and Gerd. and far from roots in *Glo-mus caledonium* Nicol. and Gerd.), demonstrating that species can have different spatial abilities in terms of nutrient procurement.

**Table 2**  
 Summary of publications that have investigated the effect of two biotic interactions on the performance of dioecious and gynodioecious plants. All studies were conducted under field conditions.

| Type of multiple interaction | Plant species            | Life form | Breeding systems | Reference                       |
|------------------------------|--------------------------|-----------|------------------|---------------------------------|
| Herbivores + pathogens       | <i>F. virginiana</i>     | Herb      | Gynodioecy       | Cole and Ashman (2005)          |
|                              | <i>N. psychotrioides</i> | Tree      | Dioecy           | Wolfe (1997)                    |
| Mycorrhizas + pollinators    | <i>G. sylvaticum</i>     | Herb      | Gynodioecy       | Varga and Kytöviita (2010c)     |
|                              | <i>G. sylvaticum</i>     | Herb      | Gynodioecy       | Asikainen and Mutikainen (2005) |
| Herbivores + pollinators     | <i>N. menziesii</i>      | Herb      | Gynodioecy       | McCall (2008)                   |
| Pathogens + pollinators      | <i>S. alba</i>           | Herb      | Dioecy           | Shykoff and Bucheli (1995)      |
| Mycorrhizas + herbivores     | <i>G. sylvaticum</i>     | Herb      | Gynodioecy       | Varga et al. (2009)             |
|                              | <i>S. repens</i>         | shrub     | Dioecy           | Saravesi et al. (2011)          |
| Mycorrhizas + parasites      | <i>J. monosperma</i>     | Tree      | Dioecy           | Gehring and Whitham (1992)      |

Regarding the interactions that take place between sex, AM fungi and pollinators in sexually dimorphic species, we might expect that AM fungi have a positive effect on the plant and pollinators (Fig. 1). This is because AM fungi have generally positive effect on plant size, nutrient status and a variety of floral characteristics (see Koide, 2010), and because pollination-relevant traits affected by AM fungi include increase in the number of flowers, number of pollen grains, the quality and quantity of nectar and flower longevity (Koide, 2010). However, negative interactions or not effect between AM fungi and pollinators might also occur, through competition for shared resources (photosynthates) (Fig. 1). To date, only one study has explored this interaction in a gynodioecious species and no study exists in dioecious species. In the gynodioecious *G. sylvaticum*, Varga and Kytöviita (2010b) showed a sex-specific pattern of insect visitation by syrphid flies, where hermaphrodites had more visits than females, but only when these were inoculated with *Glomus claroideum* Schenck and Smith, while the behavior of bumble bees remained unaffected by mycorrhizal status or sex (Table 2). These findings suggest that sexes differ in their interaction with AM fungi and pollinators, and the positive or negative nature of this effect depends on the particular identity of the interacting organisms.

#### Plant–herbivore–pollinator interactions

As described above, herbivores have a direct negative effect on plants, but also on pollinators, especially in the case of floral herbivores, while pollinators have either no effect or a merely indirect positive effect on herbivores and pathogens (Fig. 1). In hermaphroditic species (e.g., Strauss et al., 1996), and monoecious species (Quesada et al., 1995; Parra-Tabla and Herrera, 2010; Barber et al., 2011) it is well known that plants damaged by florivores may be less attractive to pollinators as a result of changes in floral characteristics. As a consequence, the time spent by pollinators visiting flowers (Barber et al., 2011) and the proportion of pollen grains removed (Parra-Tabla and Herrera, 2010) are also affected by herbivory. Pollen-bearing flowers in dioecious and gynodioecious species tend to be larger and receive more visits from pollinators; therefore, larger flowers with larger displays can also attract more floral herbivores. For example, in *G. sylvaticum*, Asikainen and Mutikainen (2005) showed that, compared to females, hermaphrodites had a higher visiting rate of pollinators but also experienced higher floral herbivory (Table 2). In *Nemophila menziesii* Hook and Arn. (gynodioecious species), McCall (2008) showed that florivory in both sexual morphs had negative effects on female fitness (probability of setting fruit and seeds produced per fruit) and reduced pollinator visitation relative to undamaged flowers. In addition, the hermaphrodite plants with larger corollas and greater numbers of open flowers suffered more floral damage than females under field and experimental conditions (McCall and Barr, 2012; Table 2). In the same line, in the gynodioecious *F. virginiana* Ashman et al. (2000) also found hermaphrodites with larger floral size than females to be preferred both by pollinators and florivores. These studies suggest that corolla size is one trait that may be under selection from both pollinators and florivores (McCall and Irwin, 2006; Ashman and Penet, 2007).

#### Plant–pathogen/parasite–pollinator interactions

Since male plants are visited more often by pollinators than females because they generally have more flowers and rewards (Delph et al., 1996), males might be expected to have a higher likelihood of infestation by floral pathogens (Alexander and Antonovics, 1995). Jennersten (1988) noted that plants infected by *M. violaceum* bloomed earlier and remained open longer than healthy plants. As a

consequence, pollinators visited these flowers more often, and thus became vectors of the disease (Jennersten, 1988). This suggests that the interaction between the fungus and pollinator was comparable to pathogenicity in the sense that the fungus benefitted from the pollinators, but the pollinator was negatively affected by the fungus due to lack of pollen reward. Similarly, in the dioecious plant *Silene alba* (Mill.) E.H.L. Krause, pollinators visited more male than female flowers, and more healthy plants than those infected by *M. violaceum* (Table 2). Diseased and healthy plants did not differ in their nectar production; however, nectar concentration was lower in diseased plants and these plants received fewer visits from pollinators (Shykoff and Bucheli, 1995). In contrast, Lee (1981) observed that in 11 of 20 populations the females of *S. dioica* had greater infection by *M. violaceum* than males. Interestingly, infection was greater in males early in the flowering season and in females later during the flowering season (always coinciding with greater number of flowering shoots), suggesting that this maximizes the potential for the spread of the disease by insect pollinators (Lee, 1981). However, in cases of massive ovary infection by *M. violaceum*, females may even change their functional gender (Shykoff and Kaltz, 1997). Pathogens therefore may have a synergistic or antagonistic effect on pollinators, while pollinators in turn may have a synergistic effect or no effect at all on pathogens (Fig. 1).

#### Plant–mycorrhiza–herbivore interactions

Herbivores usually have a negative effect on mycorrhizas due to reduction in photosynthetic leaf area and plant fitness, while mycorrhizas may have positive, negative or neutral effect on herbivores (Fig. 1). Variation in response of AM fungi to herbivores in hermaphroditic species has been attributed to the age of the plant; the degree of defoliation and the timing of AM fungal colonization relative to herbivores (see Gehring and Bennett, 2009 and references therein). AM fungi have been shown to increase plant size and alter plant quality through changes in nutrient content (Smith and Read, 2008); the plant can therefore produce defenses and resist attack by herbivores (Gehring and Bennett, 2009). In this sense, Vannette and Hunter (2011) proposed the resource exchange model of plant defense to explain how plant root fungal colonization levels affect plant defense and growth. If the plants are sparsely colonized by fungi, growth and defense are both limited by mineral nutrients. In contrast, if the plants are intensively colonized by fungi, this represents fungal parasitism because the carbon cost exceeds the nutrient benefit. When the colonization scenario is optimal, both symbionts (host and fungus) benefit from the relationship (see details in Vannette and Hunter, 2011). This model was proposed to explain two opposite biotic interactions (herbivory and mycorrhizal symbiosis) when mineral nutrients are or are not available. In agreement, Garrido et al. (2010) found a negative interaction between tolerance to artificial defoliation and the inoculum concentration of a commercial AM strain in the hermaphrodite *Datura stramonium*, suggesting that both defoliation and AM fungi consume photosynthates from the host plant, decreasing the benefits of AM fungi colonization and the capacity for compensating damage (but see Aguilar-Chama and Guevara, 2012).

In dioecious and gynodioecious species, the sex morph that invests less in mycorrhizas could gain fewer benefits from this interaction and could be attacked more frequently or heavily by herbivores. AM fungal interaction has only been evaluated in one dioecious and one gynodioecious species under artificial defoliation. In *Salix repens* L. (dioecious plant), there was no effect of clipping on total ectomycorrhizal (another kind of mycorrhiza belonging to phylum Basidiomycota and Ascomycota) colonization in the roots of females and males, although soil fungal biomass

(measured as ergosterol) decreased in clipped male patches (Saravesi et al., 2011) (Table 2). In *G. sylvaticum* (gynodioecious species), Varga et al. (2009) showed that defoliation decreased total seed production in female and hermaphrodite plants, but did not affect AM fungal colonization frequency. Although no significant differences were observed between the frequencies of colonization by AM fungi between the sexes (Table 2), the seed set of female plants correlated positively with the frequency of arbuscules. These findings suggest a sex-specific relationship between fitness and AM fungi, and a cost–benefit balance among sex–AM fungi–herbivory that could depend of other factors not considered in these studies such as light and nutrients available in the soil.

#### Plant–mycorrhiza–pathogen/parasite interactions

Symbiosis with AM fungi results in systemic pathogen resistance in host plant that is called Mycorrhiza Induced Resistance (MIR, Pozo and Azcón-Aguilar, 2007). Plants colonized with AM fungi have been shown to be more resistant both against necrotrophic (Datnoff et al., 1995) and biotrophic pathogens (Pozo and Azcón-Aguilar, 2007) by stimulating a defense response or altering root exudates used by pathogens (Fig. 1). In addition to MIR, AM could reduce the incidence of pathogens through generally improved nutrient status, and through competition – in the case of root pathogens – for infection sites, or promoting growth of soil microbes that are antagonistic to pathogens (Azcón-Aguilar and Barea, 1996). In contrast, plants in symbiosis with AM have usually greater aboveground biomass than non-symbiotic plants, and because larger leaves have larger probability of receiving airborne spores of plant pathogens, AM could also increase pathogen incidence (Gernns et al., 2001) (Fig. 1).

A meta-analysis of the interaction between plants and pathogens showed that in general, AM fungi tended to reduce the detrimental effects of fungal pathogens on host plant (Borowicz, 2001). Notwithstanding the general trend, mycorrhizas tend to intensify the negative effects of nematodes on host plant, but this depended on type of nematodes (sedentary or migratory nematodes). The studies addressing plant–pathogens interactions have focused mainly on hermaphroditic plants, and are biased to agricultural systems or performed under artificial conditions (Borowicz, 2001). Press and Phoenix (2005) reviewed the impacts of parasitic plants on host plants, and how the parasitic plants impact other trophic levels such as herbivores, pollinators, seed dispersers, and soil microbes. In the case of mycorrhizas, the few studies showed positive and negative effects (see Press and Phoenix, 2005 and references therein).

To our knowledge, only one study has addressed the tritrophic interaction among host sex–AM fungi–parasites using *Juniperus monosperma* (a dioecious species, Table 2). In both sexes, high densities of mistletoe (parasitic plant) decreased AM fungal colonization, but females were more severely affected than males. Although the sexes did not differ significantly in the frequency of mycorrhizal colonization when parasite densities were low, females tended to have higher mycorrhizal colonization than males. It is likely under high parasite densities that the carbon available to maintain the fungal symbiosis could be reduced via direct carbon loss to parasite, or via photosynthetic losses. Alternatively, if the female trees also invest nutrients in reproduction, they may be less able to provide carbon to AM fungi than male trees (Gehring and Whitham, 1992). Although there are no host sex-specific studies to show that AM function differently in terms of pathogen protection of the host, it is tempting to speculate that the lower pathogen load in females compared to male plants could be related to the higher AM affinity in females and MIR.

#### Plant interactions between mycorrhizas, herbivores, pathogens/parasites and pollinators

The boundaries between mutualist and antagonist organisms are complex and commonly chemical and molecular pathways exist in the plants to respond to the diversity of organism interacting in the nature with them. Currently, there are no studies that take the host sex into account and have involved more than two interacting partners in addition to the host plant. Therefore, this chapter remains purely speculative. Nevertheless, some scenarios can be drafted. Plants employ sophisticated strategies to perceive and respond to the diversity of biotic multi-interactions, these strategies include plant hormones. For instance, when a root is colonized by mycorrhizas, simultaneous rise in root jasmonic acid (JA) levels has been shown (e.g., Herrera-Medina et al., 2008; Hause and Schaarschmidt, 2009). AM induced resistance during pathogen attack involves induction of higher JA levels in plant tissues (Pozo and Azcón-Aguilar, 2007). Jasmonates not only deter biotrophic pathogens but have been shown to be active against herbivores as well (Ryan and Moura, 2002). Therefore, higher JA levels effectuated by AM and the pathogens may have a negative effect on herbivores. Furthermore, JA is likely to affect pollinator activity as well, due to their effect on anther development (Avanci et al., 2010) and due to their ability to deter foliar herbivores (McCall and Karban, 2006). Therefore, AM effects on plant jasmonate status are likely to have cascading effects on interactions with pathogens, herbivores and pollinators. Since JA is involved also in determining the male identity of flowers (Browse, 2009; Cheng et al., 2009), it seems plausible that they could be involved in defining sexual differences in biotic interactions in sexually dimorphic species. In addition, systemic acquired resistance, which provides enhanced plant resistance to pathogen infection, has been shown to be induced by salicylic acid (SA). SA production may be partially suppressed by mycorrhizal symbiosis, (Hause et al., 2007; Pozo and Azcón-Aguilar, 2007), which could explain the susceptibility of some mycorrhizal plants to biotrophic pathogens such as migratory nematodes (Borowicz, 2001). However, both the SA and JA pathways induce a spectrum of gene products that show considerable overlap between them, and also interact with other plant growth regulators such as abscisic acid and ethylene, which are important in the responses to the abiotic environment (Genoud and Métraux, 1999; Paul et al., 2000). Elucidating between the roles of JA and SA in biotic interactions clearly will be a fascinating task in the future.

#### Future directions

Studies revised above highlight the importance of considering multi-species interactions in understanding the ecological context for the evolution of unisexuality. However, the complexity of these multiple interactions makes it difficult to predict the adaptive value of each component of the interaction (e.g., plant sex, mutualists or antagonists). In addition, interactions may become even more complex when we consider the abiotic factors (e.g., light, soil nutrients, temperature) or other biotic interactions not considered here (e.g., fungal endophytes, nitrogen fixers, seed predators, below-ground pathogens and herbivores, competitors and myrmecophily, to name just some examples).

Although we have gained considerable knowledge regarding the ecological and evolutionary mechanisms that dimorphic plants use to interact with antagonistic and mutualistic organisms, it is clear that some gaps remain. Herbivory, along with pollination, are perhaps the most well understood interactions. Nonetheless, our knowledge of these interactions comes from studies of pairs of



species, which is an inadequate scenario. In addition, our understanding is more limited about the strategies that plants use to cope with multiple biotic interactions. To date, studies have been to a large extent biased towards those interactions which human senses can perceive, but the interactions between roots and soil organisms, such as belowground pathogens, mycorrhizas, belowground herbivores, endophytic fungi, predation, all require more attention. It is possible that these more obscure interactions may modulate many of the visible aboveground interactions. In addition, responses to the abiotic and biotic environments have a strong influence upon one another, but abiotic and biotic factors have generally both been studied independently. However, in the light of climate change, habitat fragmentation, and invasive species, it is crucial to understand the crosstalk between abiotic and biotic multi-interactions. Studies should include species with contrasting life forms (annual and perennial species), growth forms (herbaceous and woody plants), ecological strategies (e.g., shade-tolerant and light-demanding, fast-growing and slow-growing species) and mating systems (selfing and outcrossing) in order to explore some ecological correlates of sex-specific patterns in biotic interactions. Broad scale spatial and temporal studies are also needed to explore geographical and seasonal patterns.

Finally, since the plants perceive and respond to environmental cues using sophisticated strategies that induce a cascade of biochemical complexes (Paul et al., 2000), studies integrating molecular biology and ecology could advance our understanding of how dioecious and gynodioecious species (including those featuring other breeding systems) manage multiple interactions. Overall, sexual differences in biotic interactions seem quantitative in nature rather than qualitative at this point. Females have more intensive relationship with fungal mutualists, are better defended against pathogens and herbivores and may generally invest less in pollinator attraction. How these quantitative differences cascade through the network of biotic interactions and whether subtle differences are damped rather than accentuated in the web of relations remain to be explored.

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