



Ten years of progress in the study of *Hadena*-Caryophyllaceae nursery pollination. A review in light of new Mediterranean data[☆]



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ABSTRACT

Nursery pollination interactions are widespread between Caryophyllaceae species and the pollinating-seed predator *Hadena* moths (Noctuidae). A previous revision of this system was based mainly on widely distributed species in the north and center of Europe. However, there was no information from the Mediterranean region, one of the global diversification centers of both taxa. The aim of this work is to review the progress on the knowledge of this nursery pollination system since the first revision, providing unpublished data of Caryophyllaceae-*Hadena* associations from Spain. Furthermore, we conduct a preliminary network analysis to illustrate the advantages of this approach to explore nursery pollination systems.

In the last 10 years, most of studies have focused on selective forces exerted by *Hadena* on the plant reproductive traits through pollination and predation. *Hadena* moths are selectively attracted by flower scents, flower sizes and number of flowers per plant are also crucial for attraction of the moths. Caryophyllaceae species may have developed some phenological, chemical, morphological and physiological adaptations to avoid overexploitation by larvae. The evolution of sexual dimorphism in Caryophyllaceae may be a consequence of mutualistic and antagonistic interactions. Other pollinators as well as an anther smut fungus and larval parasitoids are important selective agents that can shift this interaction between mutualism and parasitism. Whereas most studies highlighted the parasitic nature of the *Hadena*-Caryophyllaceae interaction, we need further analyses on the pollinator effectiveness of *Hadena* and on the spatio-temporal variation of the interaction outcome. Based on our field surveys and bibliographic records we found evidence of nursery pollination between 22 noctuid species (mostly *Hadena*) and 70 Caryophyllaceae species from 11 genera (mostly *Silene* and *Dianthus*). From these interactions, 26 were new for the Iberian Peninsula and 18 were not described before. Results of our preliminary network analysis suggest that these interactions are constrained by phylogenetic, geographical and ecological filters.

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1. Introduction

Nursery pollinators, i.e., pollinating seed predators, are insects that use the reproductive structures of the plant they pollinate to feed their offspring (Dufay and Ansett, 2003). These interactions can be very specialized, reciprocally obligate, and mutualistic, including classical examples like yuccas and yucca moths in North America (Pellmyr, 2003), *Ficus* and Agaonidae wasps in tropical environments (Herre et al., 2008; Wiebes, 1979), and Phyllanthaceae

trees and *Epicephala* moths in Asia (Kato et al., 2003; Kawakita and Kato, 2004). However, in some nursery pollination systems other pollen vectors contribute to the pollination of the host plant, as in *Lithophragma* and *Greya* moths (Thompson and Pellmyr, 1992), and *Trollius* globeflowers and *Chiastocheta* flies (Suchan et al., 2015). In these facultative systems, the interaction between the nursery pollinator and its host plant may shift between being mutualistic and parasitic, depending on the pollination-predation net outcome and on the importance of co-pollinators (Dufay and Anstett, 2003). These non-obligate systems are very interesting for the study of the origin, evolution and maintenance of mutualisms (Thompson et al., 2013), and are widespread between *Hadena* moths (Noctuidae) and Caryophyllaceae species, especially *Silene* (Brantjes, 1976a,b,c; Giménez-Benavides et al., 2007; Kephart et al., 2006; Pettersson, 1991; Prieto-Benítez et al., 2016a; Reynolds et al., 2012).

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Both male and female *Hadena* moths visit and pollinate the flowers of Caryophyllaceae. Female additionally lays the eggs within or on the surface of the calyx of some flowers, and the larvae subsequently feed on the developing fruits (Bopp, 2003; Brantjes, 1976a). The review of this system by Kephart et al. (2006) found 58 interactions between 14 *Hadena* and 26 Caryophyllaceae species (14 *Silene* species). This work, though it is based on a small sample of documented cases, showed that the system has low specificity, with plant and moth species interacting with more than one partner suggesting a diffuse coevolutionary scenario. A special effort was made by these researchers to identify the selective forces that potentially operate on the plant and moth traits, independently or simultaneously.

The aim of this work is to review the current state of knowledge of the nursery pollination system between caryophyllaceous plants and *Hadena* moths ten years after the first review (Kephart et al., 2006). This is an excellent opportunity to assess the progress since then, identify major gaps, and discuss further directions for research. This model system has been a growing field of research over the last decade (Fig. 1). We conducted a search in the Web of Knowledge in 11 October 2016 with keywords “*Hadena*” and (“*Silene*” or “*Dianthus*” or “*Caryoph*”) that returned 54 matches. We also included several related publications by cross-reference, for a total of 59 works. Publications on this topic are only scattered from 1976 (Brantjes, 1976a,b,c) until the beginning of 2000s; and then got more frequent. However; most of the studies were conducted in Central Europe and North America (77%); and many of them exclusively centered on *Silene vulgaris*; *S. latifolia* and *H. bicruris* (83%); despite both plant and moth genera are highly diversified and widely distributed throughout the globe. To partially fill the gap we present new field data of Caryophyllaceae–*Hadena* associations from Spain; and conduct a preliminary analysis of complex networks to illustrate how this tool is a relevant framework to explore the structure and the degree of specialization of the nursery pollination systems.

2. Literature survey

2.1. New evidence on the mutualism–parasitism dilemma and the evolutionary implications of plant–moth interactions

Most *Hadena* moths are major or common pollinators of its Caryophyllaceae hosts (Kephart et al., 2006; Kula et al., 2014). Both male and female moths visit flowers and provide pollination services, and the plant obtains only positive outcome from male moths, but positive and negative (due to larval predation) outcomes from female moths (Kephart et al., 2006; Labouche and Bernasconi, 2010). Nevertheless, the net effect of pollination vs. predation have been quantified in few cases because it depends on the pollination service provided by other pollinators, and may change with time and among populations (Thompson, 2005; Kula et al., 2014). Nevertheless, in the scarce studies it was found that *Hadena*–Caryophyllaceae interactions are mostly parasitic, with predatory activity exceeding pollination services (Pettersson, 1991; Giménez-Benavides et al., 2007; Reynolds et al., 2012; Kula et al., 2014; Prieto-Benítez et al., 2016a).

Whether mutualistic or parasitic, a recurrent topic on this system was to assess which functional traits of plants and moths are susceptible to coevolutionary adaptation. Kephart et al. (2006) suggested that some traits related to attraction of pollinators and efficient pollen transfer may have evolved in response to the moths. This is partially motivated by the traditional classification of *Silene* and sister taxa in two contrasting pollination syndromes, diurnal and nocturnal (Lindman, 1897; Greuter, 1995). Nocturnal species typically have white or pale petals and the beginning of flower

anthesis and scent emission are synchronic in the evening or night (Faegri and van der Pijl, 1979; Prieto-Benítez et al., 2016a). Diurnal species have pink or red corollas, the flowers remain open during day and night, and scent changes are imperceptible by the human nose (Greuter, 1995; Jürgens et al., 2002; Jürgens, 2006). Kephart et al. (2006) detected a significant association between these flower traits and nocturnal pollination, and we also know that female *Hadena* moths select by flower color, shape and scent when two host plants coexist (Castillo et al., 2014; Page et al., 2014). Kephart et al. (2006) showed a clear segregation of a few diurnal and nocturnal species by their scent composition. However, an inherent bias exists as most of the published scents of the European species reflected data captured only during day (species classified a-priori as diurnal) or night (species classified as nocturnal). Recent progress on the diel variation of flower scent in a larger sample of caryophyllaceous species have shown that most species emit volatile compounds with attractive potential to pollinators during both day and night (Castillo et al., 2014; Dötterl et al., 2012; Giménez-Benavides et al., 2007; Martinell et al., 2010; Waelti et al., 2008; Prieto-Benítez et al., 2015) with diurnal and nocturnal species having similar scent compositions at the respective times of the day (Prieto-Benítez et al., 2015). Interestingly, Prieto-Benítez et al. (2016b) found that flower scent in the tribe Sileneae is phylogenetically constrained to some extent, and the strength of phylogenetic signal is stronger in night than in day emissions, suggesting that the selective forces exerted by diurnal and nocturnal flower visitors on floral scents differ. Many species substantially change the amount and composition of scent from day to night, but sometimes in the opposite way as expected based on other flower traits, especially flower color (Prieto-Benítez et al., 2015, 2016a). These results help to explain why most caryophyllaceous species show a mixed suite of day and night flower visitors, including Hymenoptera, Diptera and Lepidoptera, and suggest the prevalence of a mixed pollination strategy (Dötterl et al., 2012; Prieto-Benítez et al., 2015, 2016a). For instance, in hybrids from *S. latifolia* (white petals) and *S. diclinis* (pink petals), the diurnal and nocturnal pollinators visited more frequently larger flowers, but they did not show clear preferences for flower color (Brother and Atwell, 2014). In any case, this is not in direct conflict with the pollination syndrome concept because floral specialization may reflect adaptations to the most effective pollinators, and pollination effectiveness may shift in space and time (Fenster et al., 2004; Ollerton et al., 2007). To understand the role of *Hadena* and any other pollinator as selective agents of caryophyllaceous floral traits, Kephart et al. (2006) encouraged the research community to gather detailed data on the pollination effectiveness of each functional group of flower visitors, in combination with phenotypic selection studies. Unfortunately, after ten years, the number of studies on this topic can be counted on one hand and results are not conclusive. *Silene sennenii* and *S. stellata* are white champions that produce higher rates of scent at night and have moth species as most effective pollinators (Martinell et al., 2010; Reynolds et al., 2009). *Silene ciliata* also has white flowers with crepuscular opening and dominance of night scent, but diurnal pollination provided greater female fitness in a pollination exclusion experiment, although pollination effectiveness was not really measured (Giménez-Benavides et al., 2007). In hybrids between *S. latifolia* (white petals) and *S. diclinis* (pink petals) nocturnal pollinators provided higher seed set than diurnal pollinators (Brother and Atwell, 2014). To our knowledge, there is only one published study quantifying the strength and direction of pollinator-mediated selection in *Silene*, but it was focused in *S. virginica*, a hummingbird-pollinated species (Reynolds et al., 2010).

Regarding the question whether or not *Hadena* fruit predation also shapes flower traits, some evidence supports moths as potential selective agents for traits minimizing the frequency and intensity of attacks. Some contributions in the last decade suggest

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