

Weed-insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review

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Abstract The intensification of agricultural practices contributes to the decline of many taxa such as insects and wild plants. Weeds are serious competitors for crop production and are thus controlled. Nonetheless, weeds enhance floral diversity in agricultural landscapes. Weeds provide food for insects in exchange for pollination. The stability of mutualistic interactions in pollination networks depends on conservation of insect pollinator and weed communities. Some agricultural practices can destabilize interactions and thus modify the stability of pollination networks. Therefore, more knowledge on weed-insect networks is needed. Here, we review the interactions involved in insect visits to weed flowers in temperate arable lands. Our main findings are that (1) weed pollination

by insects has a key role in maintaining weed communities in arable lands; (2) weed-insect pollinator interactions are modulated by the flowers' features and their quality which are attracting insects; (3) most weeds are associated with generalist insect pollinators; and (4) even if weed-pollinator networks are largely mutualistic, some antagonist networks can be observed when deception occurs. We propose three weed-insect pollinator networks as potential bio-indicators to evaluate the ecological sustainability of arable land management strategies in temperate areas: (1) Geometridae and Bombyliidae species visiting Caryophyllaceae, (2) Papilionidae foraging on Apiaceae, and (3) Syrphidae visiting Asteraceae.

Keywords Arthropods · Biodiversity · Pollination · Weed management · Wildflowers

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References

1 Introduction

Agricultural ecosystems are the dominant landscapes throughout Western Europe and worldwide (Robinson and Sutherland 2002; Scheper et al. 2013). Due to the continuous increase of the world human population, “cropland”, “arable land”, “farmland” or “agricultural land” have considerably increased (Matson et al. 1997; Tschardt et al. 2005), by conversion of natural and semi-natural areas. These changes have accelerated especially in the post-war period characterized by increased external inputs such as fertilizers and pesticides (Tschardt et al. 2005). This agricultural intensification had led to a decline of landscape diversity and a loss of biodiversity observed in many taxa, especially for insects and plants (Sotherton 1998; Chamberlain et al. 2000; Benton et al. 2002; Kleijn and Sutherland 2003; Thomas et al. 2004; Tschardt et al. 2005; Flynn et al. 2009; Brückmann et al. 2010). Weeds are particularly affected due to their contentious relationship with crop production. Indeed, they are historically considered as a serious competitor for crop plants and therefore for crop production (Oerke 2006; Meiss et al. 2008; Fried et al. 2008). However, weeds are a significant part of the floral diversity in agricultural landscapes. They play major functional roles for agricultural ecosystems and their biodiversity and thus have several consequences on ecosystem services, especially pollination (Biesmeijer et al. 2006; Bretagnolle and Gaba 2015). Increasing weed abundance can (i) maintain pollinator populations, (ii) ensure pollination services, (iii) increase honey yields and therefore be a benefit for beekeepers, and (iv) improve the sociocultural value of landscape by ensuring the persistence and survival of wild flora (Bretagnolle and Gaba 2015). For instance, some studies have showed the importance of weeds as food resource for insect pollinators, especially bees (Rollin et al. 2013; Requier et al. 2014).

Weed-insect pollinator interactions are also very important to maintain weeds in agricultural landscapes. Even if weeds are predominantly self-pollinating (Sutherland 2004), wind- and insect-pollinated species are also typical of agricultural ecosystems (Petanidou and Lamborn 2005). The persistence dynamics of most weed species in arable land are largely driven by insect pollination; the frequency of flower visits by insects is a good parameter for classifying a weed's pollination strategy (Hoffmann 2005; Lunau 2006). There is a growing interest in the gene flow mechanisms among weed species in arable lands. This is due both to agronomic reasons (e.g., herbicide resistance) (Preston and Powles 2002) and to environmental concerns (e.g., pollen transfer between genetically modified crops and hybridizable weeds) (Conner et al.

2003). In addition, several concerns have been raised regarding the decreased plant and pollinator biodiversity in different ecosystems, focusing on the possible relation between the rarefaction of some plants and their dependence on particular insect pollinators (Benvenuti 2004; Gibson et al. 2006; Nicholls and Altieri 2012; Grass et al. 2013). The decline in wild bee diversity has been strongly correlated with the decline in wildflowers (Biesmeijer et al. 2006; Bretagnolle and Gaba 2015 for a recent review).

On this basis, the aims of this review are to (i) examine the key role of insects in the pollination strategies of weeds in temperate arable lands, (ii) highlight the mechanisms involved in insect visits to weed flowers in arable lands, (iii) provide a focus on the ecological importance of generalized interactions in insect pollinator-weed dynamics, (iv) highlight the diversity of weed-insect pollinator interactions and their potential as bio-indicators to evaluate the health of temperate arable lands, and (v) analyze sustainable farming practices designed to partly maintain weed-insect pollinator interactions.

2 Pollination strategies of weeds in temperate arable lands: the key role of insects

Not all flowering plants have the same pollination requirements. Plants can use different mechanisms to realize self-pollination, which is pollination of a flower by pollen from the same flower or flower on the same plant (Pesson and Louveaux 1984). In agreement with the time limitation hypothesis, self-pollination is crucial for rapid seed formation (Aarssen 2000). Due to this rapid seed set, arable land weeds can persist despite the vast range of agronomic disturbances (Sutherland 2004). For instance, *Amaranthus retroflexus* L. (Amaranthaceae) is characterized by unattractive flowers, almost total self-pollination (Brenner et al. 2000), and produces mature seeds just a few weeks after emergence (Costea et al. 2004). This reproductive strategy is an advantage if pollinators are in decline or absent (Barbier 1986). For instance, if cross-pollination by insects does not occur, dandelion (*Taraxacum* ssp.) and plants of the thistle family (*Carthamus* ssp.) ensure their reproduction by a mechanical self-pollination within the flower, through contact between the ripe stigma and pollen grains of anthers (Barbier 1986). Other weeds with flowers that are easily recognizable by insects are mainly self-pollinated, for example *Convolvulus arvensis* L. (Convolvulaceae) (Westwood et al. 1997), *Stellaria media* (L.) Vill. (Caryophyllaceae) (Verkleij et al. 1980), *Portulaca oleracea* L. (Portulacaceae) (Zimmerman 1977), and *Anagallis arvensis* L. (Primulaceae) (Gibbs and Talavera 2001).

However, to prevent self-pollination and inbreeding, many species use cross-pollination which promotes genetic diversity and permits the adaptation of plants to environmental

disturbances (Barbier 1986; Delaplane and Mayer 2000). The cross-pollination of angiosperms evolved in ancient natural ecosystems, from entomophily to anemophily (Thien 1980), which is likely to reduce the dependence on organisms that are strongly affected by erratic climatic conditions (Bawa 1995). This is supported by rudimentary and inefficient nectaries in wind-pollinated species (Culley et al. 2002). Ambophily is regarded as an intermediate transitional state between biotic and/or abiotic pollen movements (Culley et al. 2002) and generates gene flow, allowing the environmental plasticity needed for successful persistence in arable lands. This strategy enables a shift from predominant self-pollination to cross-pollination, as observed in many weeds (Holsinger 1991).

To promote cross-pollination, species have developed self-incompatibility mechanisms (e.g., *Papaver rhoeas* L. (Papaveraceae) and *Ranunculus repens* L. (Ranunculaceae)) (Lundqvist 1994; Thomas and Franklin-Tong 2004). Self-incompatible plants are receptive to each other's pollen and cannot develop seeds and fruit if pollen is transferred from anthers of a flower to the stigma of the same flower or different flower on the same plant (Fig. 1) (Barbier 1986). Absolute self-incompatibility is rare. A variable frequency of distribution between self- and cross-pollination is frequently observed, for example *Anthemis cotula* L. (Asteraceae) (Kay 1971), *Raphanus raphanistrum* L. (Sampson 1967), and *Sinapis arvensis* (L.) (Brassicaceae) (Stevens and Kay 1989). In the latter species, the white-yellowish flowers can favor or discourage insect visits. For instance, *Pieris rapae* L. (Lepidoptera: Pieridae) mainly visits yellow flowers, resulting in a predominance of cross-pollination in these populations (Stanton et al. 1989). In contrast, self-pollination dominates in varieties with white flowers. This phenomenon is not exclusive to Brassicaceae. It is also widespread in many weeds and could be a strategy for maintaining populations with diverse biological characteristics (Clegg and Durbin 2000).

Pollen self-incompatibility is one of the various strategies adopted by plant species to prevent the pollination of different flowers growing on the same plant, especially in the case of individuals with numerous blooms (Di Pasquale and Jacobi 1998). Such pollination, which is pointless in terms of gene flow, is known as geitonogamy. Geitonogamy avoidance

strategies include spatial and/or temporal separation of pollen and stigma (De Jong et al. 1993). Geitonogamy avoidance is advantageous in favoring adaptability to fast-changing environmental conditions (De Jong 2000; Torres et al. 2013). A trade-off between geitonogamy and xenogamy (i.e., cross-pollination) has been observed in andromonoecious and protandrous species, such as *Daucus carota* L. (Apiaceae) (Koul et al. 1989). In this case, the separation of the male and female phases is complete at the level of the flower and umbel; however, the two phases overlap at the level of the full plant, thus creating conditions for geitonogamy, though insect visits among the umbels of adjacent plants lead to xenogamy. Another interesting feature of this weed is the possible ecological role of the dark central floret of the inflorescence. This peculiar structure may act as a "fly catcher," although its real function is essentially unknown (Lamborn and Ollerton 2000). Other intermediate examples between self-pollination and cross-pollination include *Cynoglossum officinale* L., *Echium vulgare* L. (Boraginaceae) (De Jong 2000), and *Delphinium* spp. (Ranunculaceae) (Ishii and Harder 2006), in which the extremely variable number of flowers results in various levels of geitonogamy. The plants with a greater number of flowers tend to favor both self-pollination and insect-mediated cross-pollination, since the pollinators visit flowers of the same plant in sequence. A further diversification of breeding frequency is found in *E. vulgare* L. (Boraginaceae), in which the protandrous flowers produce more nectar and receive higher rates of visitation during their male than their female phases (Klinkhamer and de Jong 1990; Leiss and Klinkhamer 2005). Of the geitonogamy avoidance strategies, a drastic mechanism is displayed by the dioecious species, in which the separation of individuals into different sexes makes self-fertilization impossible. One example is *Silene dioica* (L.) Clairv. (Caryophyllaceae), which is visited by Apidae (mainly honey bees and bumblebees), Syrphidae, and Lepidoptera (particularly Pieridae species) (Kay et al. 1984). However, since the invasiveness of this species in arable lands is negligible, compared to monoecious *Silene* species, the cited strategy may be unsuccessful (Blair and Wolfe 2004). On this basis, dioecy is unlikely to be suitable for the persistence of insect-pollinated weeds in highly disturbed environments.

The predominance of self-fertilization is more widespread in the biotypes of agricultural environments, while outcrossing is widespread in biotypes of less disturbed environments. The disturbance factors of arable lands are likely to be favorable to predominantly self-pollinated biotypes (Hermanutz 1991). This is the case of *Datura stramonium* L. (Solanaceae), which is pollinated in its original environment by the hawkmoth, *Manduca quinquemaculata* Haworth (Lepidoptera: Sphingidae), Halictidae, and honey bees, while it is almost autogamous in arable lands (Motten and Antonovics 1992). However, the pollination strategy of some weed species depends on the extent of disturbance in

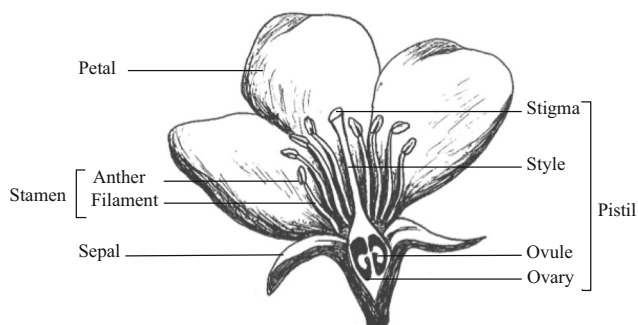


Fig. 1 General morphology of a flower

their environment. For instance, *Solanum ptycanthum* Dun. (Solanaceae) has predominantly insect-pollinated biotypes in natural ecosystems and predominantly self-pollinated biotypes in agro-ecosystems (Hermanutz 1991). These biological responses to agronomic disturbances have led to a decrease in nectary function, elongation of the androecium and gynoecium allowing contact between anthers and stigma, thus favoring self-pollination (Motten and Stone 2000). Agricultural disturbance such as soil fertilization tends to minimize the herkogamy of the original genotypes (i.e., different elongation of male and female apparatus), thus encouraging self-pollination. Thus, pollination strategy of weeds could be an indicator of the intensification of arable areas, with more insect-pollinated weeds in agricultural landscapes with less intensive practices.

3 Insect-pollinated plants: “attract and reward” mechanisms

Hymenoptera, Diptera, Lepidoptera, and Coleoptera are the majority of insects feeding on flowers in temperate regions. Each species feeds on the pollen and/or nectar of a plant species depending on its mouthparts, which have often evolved to enable the insect to feed on solid (e.g., pollen) or liquid (e.g., nectar) (Krenn et al. 2005). Among flower visitors, eusocial bees (e.g., the honey bees (*Apis mellifera* L.), bumblebees (*Bombus* spp.)) (Fig. 2) and solitary bees dominate. In Mediterranean arable lands, Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae are the main species of solitary bees (Bosch et al. 1997; Dicks et al. 2002; Petanidou and Lamborn 2005; Bretagnolle and Gaba 2015). However, some species of the Halictidae (*Halictus* and *Lasioglossum* particularly, e.g., *Lasioglossum malachurum* (Kirby), *Lasioglossum pauxillum* (Schenck), *Halictus rubicundus* (Christ)) are eusocial (Michener 2007) and can be locally dominant and abundant wild bee species (Rollin et al. 2015). The flower reward consists of nectar, pollen, or both (Table 1). Pollen grains have very different three-dimensional structure according to their botanical family (Fig. 3), which facilitates their adherence to various parts of the insect body, thus enabling transportation, and/or is packed in pollen baskets on the legs of several Apidae (e.g., the *corbiculae* of honey bees and bumblebees). However, workers of social species (e.g., honey bees and bumblebees) rarely collect pollen and nectar simultaneously. They usually direct their visits to flower species with a predominance of one or the other reward (Tepedino and Parker 1982; Rasheed and Harder 1997). Natural ecosystems have an abundance of wildflowers which frequently offer nectar production as a reward. On the other hand, agro-ecosystems such as arable lands often have a predominance of species that are poor in nectar, and insects are rewarded with pollen. For instance, the common

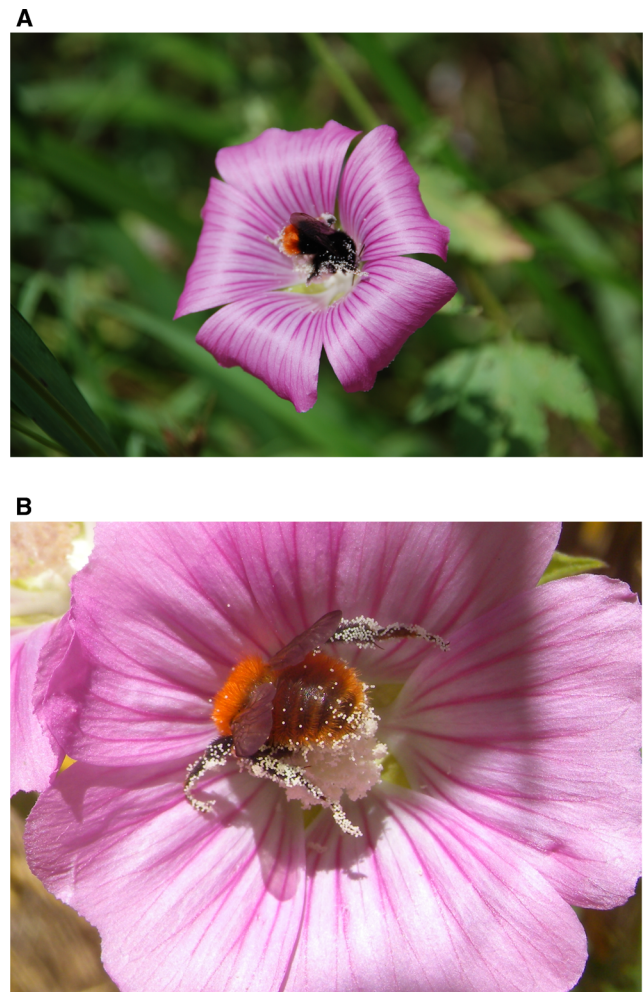


Fig. 2 Weeds such as the annual tree mallow, *Lavatera punctata* All. (Malvales: Malvaceae), are abundant sources of pollen and nectar for many insects, including bumblebees (Hymenoptera: Apidae), such as **a** the red-tailed bumblebee, *Bombus lapidarius* (L.), and **b** the common carder-bee, *Bombus pascuorum* (Scopoli)

poppy, *P. rhoeas* L. (Papaveraceae), a completely self-incompatible species, has no nectaries, and pollen is the only reward for visiting insects (Thomas and Franklin-Tong 2004). In intensive cereal landscape, poppies can account for up to 60 % of pollen resources for honey bees during late spring, in June (Odoux et al. 2012; Requier et al. 2014).

Although weeds with brightly colored flowers are frequently visited by insects, even species with duller flowers can provide key food floral sources, especially when few other plants are in flower (e.g., early spring) (Levin and Anderson 1970; Petanidou and Vokou 1993; Dafni 1996; Odoux et al. 2012; Rollin et al. 2013; Benelli et al. 2014; Canale et al. 2014; Requier et al. 2014). In late summer, insect pollinators can be observed on the most common weed species in semi-natural habitats, such as many Asteraceae (e.g., *Aster squamatus* (Sprengel) Hieron, *Conyza canadensis* (L.) Cronq., *Senecio vulgaris* L., *Sonchus* spp., and *Xanthium*

Table 1 Some examples of insects visiting weed flowers

Weed species	Reward	Visiting insect	Reference
<i>Abutilon theophrasti</i>	Pollen	solitary bees, Tachinidae	Benvenuti S., pers. observ.
<i>Agrostemma githago</i>	Pollen and nectar	Lepidoptera, solitary bees	Jürgens (2006)
<i>Anagallis arvensis</i>	Pollen and nectar	Bombyliidae	Benvenuti S., pers. observ.
<i>Anthemis cotula</i>	Pollen and nectar	Lepidoptera, solitary bees	Benvenuti S., pers. observ.
<i>Arum italicum</i>	Nectar	Diptera	Albrecht (2003)
<i>Asclepias syriaca</i>	Pollen and nectar	<i>Bombus</i> spp., Sphecidae, <i>Xylocopa</i> spp.	Kephart and Theiss (2004)
<i>Aster squamatus</i>	Pollen	<i>Apis mellifera</i>	Benvenuti S., pers. observ.
<i>Blackstonia perfoliata</i>	Pollen and nectar	Bombyliidae	Benvenuti S., pers. observ.
<i>Borago officinalis</i>	Pollen and nectar	<i>Apis mellifera</i>	Ricciardelli D'Albore and Intoppa (2000)
Brassicaceae	Pollen and nectar	Bombyliidae, <i>Apis mellifera</i> , solitary bees	Benvenuti S., pers. observ.
<i>Cabystegia saepium</i>	Pollen	Coleoptera solitary bees,	Benvenuti S., pers. observ.
Campanulaceae	Pollen and nectar	<i>Apis mellifera</i> , Syrphidae	Blonis and Vokou (2001)
<i>Centaurea cyanus</i>	Pollen and nectar	Diptera, solitary bees	Gange and Smith (2005)
<i>Centaurea nigra</i> , <i>Centaurea scabiosa</i>	Pollen and nectar	Solitary bees	Lack (1982)
<i>Centaureum erythraea</i>	Nectar	Bombyliidae	Benvenuti S., pers. observ.
<i>Cirsium arvense</i>	Pollen and nectar	Lepidoptera, solitary bees	Benvenuti S., pers. observ.
<i>Cichorium intybus</i>	Pollen and nectar	Diptera, solitary bees	Benvenuti S., pers. observ.
<i>Consolida regalis</i>	Nectar	<i>Bombus</i> spp.	Benvenuti S., pers. observ.
<i>Convolvulus arvensis</i>	Pollen	Coleoptera, solitary bees	Benvenuti S., pers. observ.
<i>Conyza canadensis</i>	Pollen	<i>Apis mellifera</i>	Benvenuti S., pers. observ.
<i>Cuscuta campestris</i>	Pollen	<i>Apis mellifera</i> , Sphecidae	Benvenuti S., pers. observ.
<i>Datura stramonium</i>	Pollen and nectar	<i>Bombus</i> spp.	Benvenuti S., pers. observ.
<i>Dianthus carthusianorum</i>	Nectar	Lepidoptera	Benvenuti S., pers. observ.
<i>Dipsacus fullonum</i>	Pollen and nectar	Lepidoptera, solitary bees	Bloch et al. (2006)
<i>Echium vulgare</i>	Pollen and nectar	Lepidoptera, solitary bees	Benvenuti S., pers. observ.
<i>Euphorbia esula</i>	Pollen	Halictidae	Klinkhamer and De Jong (1990)
<i>Euphorbia helioscopia</i>	Pollen and nectar	<i>Apis mellifera</i>	Larson et al. (2006)
<i>Jasione montana</i>	Nectar	Bombyliidae	Ricciardelli D'Albore and Intoppa (2000)
<i>Knautia arvensis</i>	Nectar	Lepidoptera	Benvenuti S., pers. observ.
<i>Lamium amplexicaule</i>	Pollen and nectar	Bombyliidae, solitary bees	Jennersten (1984)
<i>Lamium purpureum</i>	Pollen and nectar	Bombyliidae, solitary bees	Benvenuti S., pers. observ.
<i>Legostia speculum-veneris</i>	Pollen and nectar	Bombyliidae, solitary bees	Benvenuti S., pers. observ.
<i>Linaria vulgaris</i>	Pollen and nectar	<i>Bombus</i> spp.	Benvenuti S., pers. observ.
<i>Lychnis flos-cuculi</i>	Pollen and nectar	Solitary bees	Newman and Thomson (2005)
<i>Matricaria chamomilla</i>	Pollen and nectar	Solitary bees	Ricciardelli D'Albore and Intoppa (2000)
			Ricciardelli D'Albore and Intoppa (2000)

Table 1 (continued)

Weed species	Reward	Visiting insect	Reference
<i>Oenothera biennis</i>	Nectar	Lepidoptera	Kawaano et al. (1995)
<i>Ornithogalum</i> spp.	Pollen and nectar	Solitary bees	Ricciardelli D'Albore and Intoppa (2000)
<i>Papaver rhoeas</i>	Pollen	<i>Xylocopa</i> spp., other solitary bees	Benvenuti S., pers. observ.
<i>Polygonum lapathifolium</i>	Pollen and nectar	Solitary bees	Benvenuti S., pers. observ.
<i>Portulaca oleracea</i>	Pollen and nectar	<i>Apis mellifera</i> , Syrphidae	Benvenuti S., pers. observ.
<i>Senecio vulgaris</i>	Pollen	<i>Apis mellifera</i>	Benvenuti S., pers. observ.
<i>Silene alba</i>	Pollen and nectar	Apidae, Diptera, Lepidoptera, Vespidae	Young (2002)
<i>Silene dioica</i>	Pollen and nectar	<i>Apis mellifera</i> , <i>Bombus</i> spp., Lepidoptera, Syrphidae	Kay et al. (1984)
<i>Silene noctiflora</i>	Nectar	nocturnal Lepidoptera	Davis and Delph (2005)
<i>Solanum nigrum</i>	Pollen and nectar	<i>Apis mellifera</i> , solitary bees	Benvenuti S., pers. observ.
<i>Stachys arvensis</i>	Pollen and nectar	Solitary bees	Ricciardelli D'Albore and Intoppa, (2000)
<i>Stellaria media</i>	Nectar	<i>Apis mellifera</i>	Benvenuti S., pers. observ.
<i>Veronica persica</i>	Pollen and nectar	Formicidae, solitary bees	Benvenuti S., pers. observ.
<i>Viola</i> spp.	Pollen and nectar	Solitary bees	Beattie (1971)
<i>Xanthium strumarium</i>	Nectar	<i>Apis mellifera</i>	Benvenuti S., pers. observ.

strumarium L.) (Rollin 2013). Solitary bees and bumblebees can be observed also on other weeds with inconspicuous flowers, such as *Polygonum lapathifolium* L., *Polygonum aviculare* L. (Polygonaceae), *Cuscuta campestris* Yuncker (Convolvulaceae), *P. oleracea* L. (Portulacaceae), *S. media* (L.) Vill. (Caryophyllaceae), and *Abutilon theophrasti* Medik. (Malvaceae), or on weeds with gaudy but usually self-pollinated flowers, such as *C. arvensis* L., *Calystegia saepium* (L.) R. Br. (Convolvulaceae) (Westwood et al. 1997), and *D. stramonium* L. (Solanaceae) (Motten and Antonovics 1992).

Of the insects visiting weed flowers, an underestimated role is played by many Diptera, including Syrphidae, Bombyliidae, Tachinidae, and Sarcophagidae (Larson et al. 2001; Katzourakis et al. 2001; Howlett et al. 2009; Pisciotto et al. 2011). Although pollen feeding is widespread in Diptera, no species with mouthpart structures exclusively used for pollen feeding have been identified (Gilbert and Jarvis 1998). It is interesting to note that the only adaptations to pollen feeding are the labellar food furrows described for Syrphidae (Schuhmacher and Hoffmann 1982) but a clear adaptational value of the food furrows is questionable, since they are lacking in many pollen feeders (Krenn et al. 2005). Because of the long proboscis of Syrphinae and Eristalinae, adults of these Syrphidae are usually considered visitors of a wide range of flowers, where they feed mostly on nectar (Pesson 1984). These Diptera can also feed on pollen grains, especially of Gramineae and Oleaceae (Canale and Loni 2010), which must first be humidified with saliva (Gilbert 1985). Foraging visits by Bombyliidae have been noted on flowers that are difficult to reach for other insects due to their small and elongated floral calyx, such as Gentianaceae (e.g., *Centaurium erythraea* Rafn. and *Blackstonia perfoliata* (L.) Huds.), Campanulaceae (e.g., *Legousia speculum-veneris* (L.) Chaix and *Jasione montana* L.), Lamiaceae (e.g., *Lamium purpureum* L. and *Lamium amplexicaule* L.), and Primulaceae (e.g., *A. arvensis* L. and *Anagallis foemina* Mill.). The role of Bombyliidae as pollinators is likely to be minimal. Indeed, bee flies usually insert their proboscis into flowers, but their tongues are so long and slender that their heads are not inserted into the floral mouth, thus probably only a few pollen grains are removed (Krenn et al. 2005). The small role of bee flies as pollinators may also be due to their foraging behavior. Bee flies are rarely observed sitting or walking on top of inflorescences, instead they usually hover in close proximity to flowers, thus reducing the chances of pollen grains adhering to their bodies (Canale et al. 2014, 2015) (Fig. 4).

Lepidoptera also have a long proboscis that enables them to visit flowers with nectaries hidden in an elongated calyx (Table 2). Such insects include Lycaenidae, Pieridae and Sphingidae, Papilionidae, Nymphalidae, and Satyridae. Visits are frequent on flower species whose flowers have a particular shape, such as Dipsacaceae (*Knautia arvensis* (L.)

Fig. 3 Scanning electron microscopy of pollen grains of **a** *Bellis perennis* L. (Asteraceae), **b** *Taraxacum* sp. (Asteraceae), **c** *Geranium molle* L. (Geraniaceae), **d** *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae), **e** *Papaver rhoeas* L. (Papaveraceae), and **f** *Trifolium pratense* L. (Fabaceae). © I. Bornard (Lab. Microscopie, Pathologie Végétale, INRA Avignon, France) and R. Chifflet and B. Vaissière (UMR Abeilles & Environnement, INRA Avignon & Univ. Avignon, France)

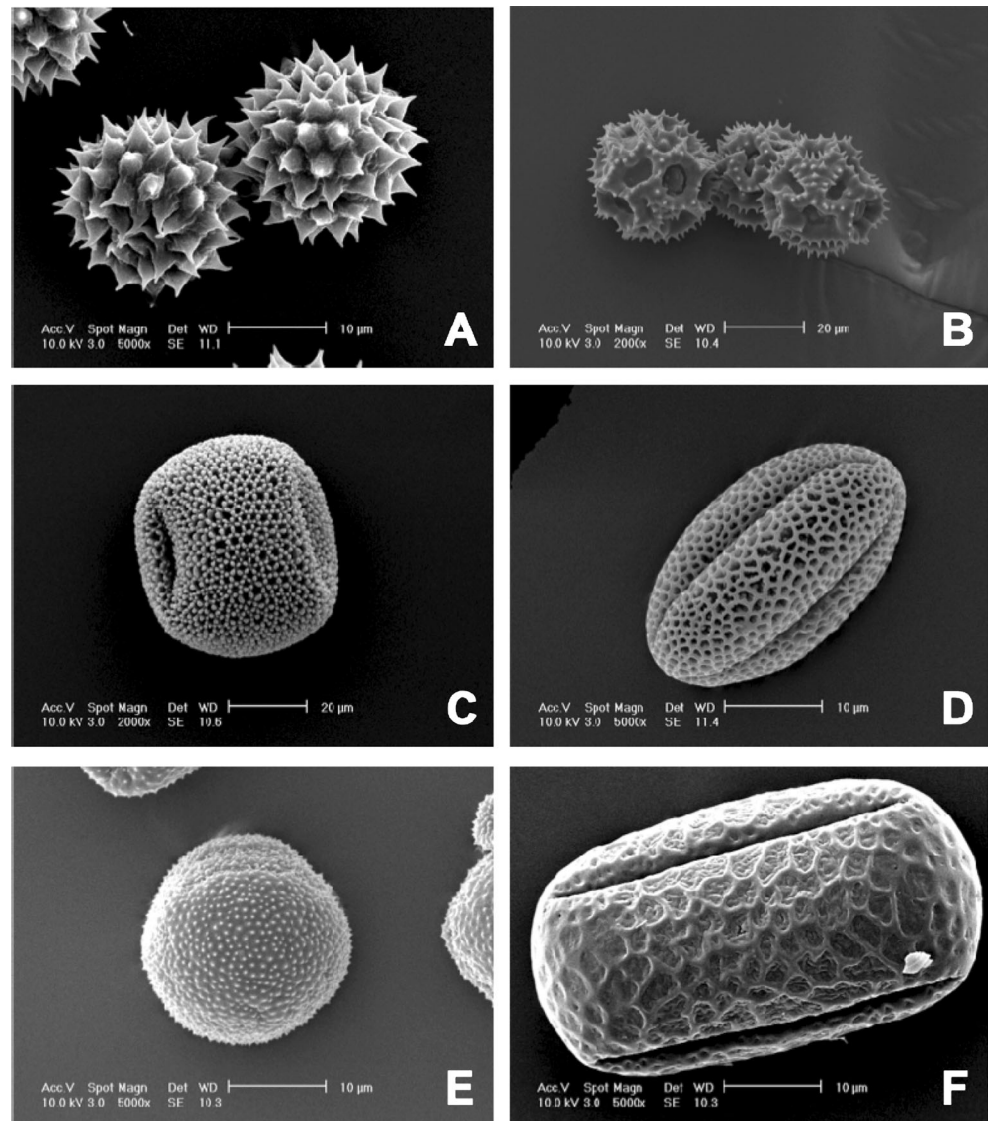


Fig. 4 Bee flies (Diptera: Bombyliidae) hover in close proximity to flowers, thus reducing the chances of pollen grains adhering to their bodies: here, a flower of *Agrostemma githago* L. (Caryophyllales: Caryophyllaceae) visited by *Bombylius fulvipes* Wiedemann

Coulter and *Dipsacus fullonum* L.) and Caryophyllaceae (*Agrostemma githago* L. and *Silene* spp.). Overall, the pollen transport by butterflies seems to be less efficient than by Hymenoptera (Jennersten 1984). Particular mechanisms may enhance it. For instance, some weeds (e.g., *Lychnis flos-cuculi* L. (Caryophyllales: Caryophyllaceae)) are slender with flowers at the apex. During foraging, the weight of the butterfly (e.g., Pieridae, such as *Gonepteryx rhamni* (L.)) bends the stem so that the flower opening points downwards (Fig. 5). The insect movements thus enable the pollen to be detached from the floral parts and to adhere to the insect's body (Benelli G., pers. observ.).

Coleoptera and Thysanoptera are visiting weed flowers but appear to act pollen predators rather than potential pollinators because their larvae exhibit parasitic behavior, feeding on pollen grains of fresh flowers which are still attached to the plant (Sakai 2002). Similarly, poor efficiency is seen in ants

Table 2 Some examples of Lepidoptera species foraging on weed flowers

Weed	Lepidoptera	Reference
<i>Amaranthus</i> spp., <i>Chenopodium</i> spp.	<i>Pholisora catullus</i>	Shapiro (2002)
Apiaceae	<i>Papilio machaon</i>	Wiklund (1981)
<i>Aristolochia</i> spp.	<i>Parnalius polyxena</i>	Novák and Severa (1980)
<i>Artemisia vulgaris</i>	<i>Pyrgus serratulae</i>	Novák and Severa (1980)
Asteraceae, Malvaceae	<i>Vanessa cardui</i>	Shapiro (2002)
<i>Avena fatua</i>	<i>Cercyonis pegala</i>	Shapiro (2002)
<i>Bidens pilosa</i>	<i>Nathalis iole</i>	Shapiro (2002)
<i>Brassica nigra</i>	<i>Pontia beckerii</i>	Shapiro (2002)
Brassicaceae	<i>Anthocharis sara</i>	Shapiro (2002)
	<i>Euchloe ausonides</i>	
	<i>Pieris rapae</i>	
	<i>Pontia protodice</i>	
<i>Cardamine</i> spp., <i>Nasturtium</i> spp.	<i>Anthocharis cardamines</i>	Novák and Severa (1980)
Caryophyllaceae	<i>Euphyia biangulata</i>	Novák and Severa (1980)
<i>Centaurea</i> spp., <i>Plantago</i> spp.	<i>Melitaea didyma</i>	Novák and Severa (1980)
<i>Chenopodium album</i>	<i>Brephidium exilis</i>	Shapiro (2002)
<i>Centaurea solstitialis</i> , <i>Cirsium</i> spp.	<i>Phycioides mylitta</i>	Shapiro (2002)
<i>Centaurea</i> spp., <i>Cirsium</i> spp.	<i>Thymelicus sylvestris</i>	Novák and Severa (1980)
<i>Echium vulgare</i>	<i>Ethmia terminella</i>	Novák and Severa (1980)
<i>Galium</i> spp.	<i>Ryparia purpurata</i>	Novák and Severa (1980)
	<i>Macroglossum stellatarum</i>	Novák and Severa (1980)
Graminaceae	<i>Brintesia circe</i>	Novák and Severa (1980)
	<i>Lerodea eufala</i>	Shapiro (2002)
<i>Hypericum</i> spp.	<i>Deilephila elpenor</i>	Novák and Severa (1980)
Lamiaceae	<i>Perizoma alchemillata</i>	Novák and Severa (1980)
<i>Lythrum</i> spp., <i>Epilobium</i> spp.	<i>Hyles vespertilio</i>	Novák and Severa (1980)
<i>Malva sylvestris</i> , <i>Alcea rosea</i>	<i>Heliopetes ericetorum</i>	Shapiro (2002)
Malvaceae, <i>Chenopodium album</i>	<i>Pyrgus communis</i>	Shapiro (2002)
Malvaceae, Papilionaceae	<i>Strymon melinus</i>	Shapiro (2002)
Malvaceae, Urticaceae	<i>Vanessa annabella</i>	Shapiro (2002)
<i>Melilotus officinalis</i> , <i>Melilotus alba</i>	<i>Colias eurytheme</i>	Shapiro (2002)
Papilionaceae	<i>Cyaniris semiargus</i>	Novák and Severa (1980)
<i>Plantago lanceolata</i> , <i>Plantago major</i>	<i>Euphydryas editha</i>	Shapiro (2002)
Polygonaceae	<i>Lycaena phlaeas</i>	Novák and Severa (1980)
<i>Polygonum persicaria</i>	<i>Lycaena helloides</i>	Shapiro (2002)
<i>Rumex crispus</i>	<i>Lycaena xanthoides</i>	Shapiro (2002)
<i>Rumex</i> spp.	<i>Lycaena cupreus</i>	Shapiro (2002)
Scrophulariaceae	<i>Junonia coenia</i>	Shapiro (2002)
<i>Silene</i> spp., <i>Lychnis</i> spp.	<i>Hadena rivularis</i>	Novák and Severa (1980)
<i>Sonchus oleraceus</i>	<i>Helicoverpa armigera</i>	Gu et al. (2001)
<i>Urtica</i> spp.	<i>Aglais urticae</i>	Novák and Severa (1980)
<i>Veronica</i> spp.	<i>Stenoptilia pterodactyla</i>	Novák and Severa (1980)
<i>Viola</i> spp.	<i>Argynnis paphia</i>	Novák and Severa (1980)

(Hymenoptera: Formicidae), despite their being flower visitors of many species (Bosch et al. 1997). This appears to be due to low pollen germination after ant contact (Beattie et al. 1984). In addition, their lack of hairs, potentially useful as

pollen carriers, and their limited plant-to-plant movement suggest that they are only occasional pollinators.

Lastly, ants may negatively affect plant fitness by reducing the intensity of pollinator visits (Junker et al. 2006). Ants'



Fig. 5 Some weeds, such as *Lychnis flos-cuculi* L. (Caryophyllales: Caryophyllaceae), are slender with flowers at the apex. During foraging, the weight of the butterfly (here, a Pieridae, *Gonepteryx rhamni* (L.)) bends the stem so that the flower opening points downwards. The insect movements thus enable the pollen to be detached from the floral parts and to adhere to the insect's body

activity decreased frequency and duration of pollinator visits by direct attacks or indirect effects due to presence of chemical signals. Nectar robbers that extract nectar through a pierced corolla tube, avoiding contact with anthers and stigmas, are also poor pollinators. A good example is *Bombus occidentalis* Greene (Hymenoptera: Apidae) which visit *Linaria vulgaris* Mill. (Scrophulariaceae) to collect nectar, poking holes in the corolla without penetrating inside (Malooof and Inouye 2000; Newman and Thomson 2005).

4 Do generalist insect pollinators serve weeds better? Not always

It is widely recognized that the lack of specialization regarding pollinator-plant relationship in common weeds is due to their persistence in time and space (Rodger et al. 2010). The evolutionary trend from generalization to specialization noted in natural ecosystems (Johnson and Steiner 2000) probably does not match the requirements of weeds that grow in arable lands. In these agro-ecosystems, de-specialization seems to be of pivotal importance for insects visiting weed flowers (Huang 2006). Indeed, de-specialization implies a lower risk of pollinator absence due to disturbance (Desneux et al. 2007). Thus, while specialization leads to optimal interaction in a particular ecological niche, it may be a disadvantage when climatic and agronomic conditions impair the appropriate functioning of the insect-weed relationships. Therefore, the specialization occurring among given weeds and insect pollinators could explain their rarity (Sutcliffe and Kay 2000). For instance, the extensive application of pesticides, which is a typical feature of conventional agricultural systems, strongly interferes with the fragile mechanisms that involve rigid insect-flora interactions.

Predominantly, insect-pollinated species have different degrees of specialization depending on the insects involved (Aigner 2001; Shuttleworth and Johnson 2008). Therefore, features such as floral color and symmetry play a key role in plant-pollinator systems (Giurfa et al. 1999; Cooley et al. 2008). Zygomorphic flowers, such as *Consolida regalis* Gray (Ranunculaceae), *E. vulgare* L. (Boraginaceae), *L. amplexicaule* L., and *Stachys arvensis* (Lamiaceae), are visited mainly by specialized long-tongued bees (e.g., Anthophoridae, Apidae, Melittidae and Megachilidae). This could be due to the particular position of the nectaries (Nilson 1998). A higher number of species visit actinomorphic flowers. For instance, many Asteraceae (e.g., *Centaurea cyanus* L., *Coleostephus myconis* (L.) Rchb. f., and *Cirsium arvense* (L.) Scop.) are visited by a huge number of unspecialized visitors, such as short-tongued bees (e.g., Andrenidae, Colletidae, and Halictidae) and Diptera. *R. raphanistrum* L. (Brassicaceae) also exhibits the typical floral traits of generalized pollination, such as upright, radially symmetric flowers and exposed reproductive organs (Fenster et al. 2004). Lastly, some insect visits appear limited to a restricted botanical group, as observed for some wild bees (referred to as monolectic or oligolectic (specialists)), which tend to visit a small number of plant families, or genera for pollen (Michener 2007). Polylectic bee species (honey bee, bumblebees) have a generalist foraging behavior, i.e they are, less selective in their choice of flower. In intensive cereal farming systems, a clear segregation pattern in the use of floral resources was found between honey bees and wild bees, with the former being tightly associated with mass-flowering crops (oilseed rape, sunflower) and the latter with semi-natural habitats, grasslands, and grassy strips (Rollin et al. 2013). Bumblebees had an intermediate strategy and were found in both oilseed and semi-natural habitats.

The most frequent insects on flowers of a given weed are not necessarily the most efficient pollinators. Indeed, the efficiency of insects as pollinators, especially bees, depends on many factors concerning pollen transport and deposit, such as the particular morphology of the insect body parts (e.g., pollen baskets or hairs), pollen moistening, flower structure or movement patterns of insect visitors (e.g., the speed of insects while handling flowers, species specificity) (Michener 2007). For bees, scopal hairs may show further modification in their density and plumosity in relation to the size and structure of the pollen grains. For example, bee species that frequently collect pollen from Boraginaceae (e.g., *Colletes nasutus*, *Andrena nasuta*) have hooked hairs to pull pollen away from anthers located deep in a small corolla (Michener 2007). The use of nectar or oil to moisten pollen loads (e.g., such as Panurginae and Mellitidae with sparse scopae, or Apidae with hind tibial corbiculae) permits considerable flexibility in sizes of pollen grains that may be collected (Thorpe 1979). However, moistened pollen is less available for pollination than uncompacted

dry pollen (Michener 2007) and decreases the pollination efficiency of bee species. The rapid visits performed by long-tongued bees may result in reduced pollen transport (Fenster et al. 2004). However, the electrostatic forces occurring on pollen can guarantee adhesion to the insect, even if it is lacking in hairy structures (Armbruster 2001). Some floral features enhance the pollen transfer during insect visits. A good example is the small hairs on the keel petal of the corolla (i.e., pollen traps): when the flower wilts, the stigma droops down and meets these hairs. Pollen morphology could also modify efficiency of pollen collection (Fig. 3). For example, the length of the spines on cotton pollen physically interfered with the pollen-aggregating process used by Apidae bees (e.g., honey bees, Vaissière and Vinson 1994). Foraging efficiency depends on matching between corolla depth and proboscis length. Foraging rates of bumblebee with long proboscis, even if they are able to utilize a wide variety of corolla depths, are less efficient on plants with short corollas than short-tongued bumblebees (Brian 1957; Ranta and Lundberg 1980; Graham and Jones 1996). This highlights the importance of the evolution of floral characters to facilitate insect landing and improve pollination efficiency (Nyman 1993). In addition, the relation between flower morphology and self- or cross-pollination has also been confirmed in other species (Kalisz et al. 1999). For instance, self-fertilization in *Mimulus guttatus* DC. (Scrophulariaceae) is affected by the morphology of the lower corolla lip (Arathi and Kelly 2004).

The foraging activity and the specialization are strongly linked to the relationship between the flowering phenology and the biological traits of visiting insects (Westrich 1989; Fenner 1998; Tylianakis et al. 2005; Michener 2007; Mader et al. 2011). Unlike social bees who are active foragers during many months, adults of many solitary bees are active only for a short season. Thus, they can be specialized on a plant which is in bloom at the same time as their adult flight activity period (Michener 2007; Kirk and Howes 2012). The earliest spring-flying species (e.g., many mining bees such as *Andrena chrysoceles*, *Anthophora plumipes*, *Osmia rufa* with adult flight activity from March to May–June) forage the earliest flowering plants (e.g., *Geranium* ssp., *Lamium* ssp.) (Kirk and Howes 2012). On the other hand, the ivy bee (*Colletes hederæ*) is active late in the year (from the end of August for males and from beginning September for females). His emergence coincides with flowering ivy (*Hedera helix* L.), his main food plant both for pollen and nectar (Michener 2007; Kirk and Howes 2012). For weeds flowering in cool periods, the potential pollinators are represented by insects that can function even at low temperatures, as in the case of early-flowering Amaryllidaceae which are pollinated by cold-tolerant Andrenidae (Herrera 1995). The role of temperature as a limiting factor is confirmed by Campanulaceae which receive fewer pollinator visits as the altitude increases (Blionis and Vokou 2001). In addition, insect pollinators tend

to favor peak or early flowerings, while pre-dispersal seed predators tend to favor off-peak or later flowerings (Elzinga et al. 2007). An interesting example of the mutualistic specialization of weed-insect pollinators is *Silene noctiflora* L. (Caryophyllaceae) with nocturnal moths (Lepidoptera). This gynomonoeious plant has hermaphroditic, pistillate flowers that only open during the night and are pollinated exclusively by nocturnal moths (Davis and Delph 2005). Similarly, *Silene alba* (Miller) Krause opens its flowers at the end of the day, thereby allowing pollination both by diurnal (e.g., Apidae, Vespidae, Diptera, Syrphidae, and Bombyliidae) and nocturnal visitors (e.g., Noctuidae and Sphingidae) (Young 2002). This “mixed” system is also characteristic of several weeds belonging to Caryophyllaceae (e.g., genera *Agrostemma*, *Saponaria*, *Dianthus*, and *Vaccaria*) (Jürgens 2006).

Insect visitor-plant specializations do depend not only on flower traits and flowering phenology (Andersson 2008) but also on nectar composition, in terms of sugars and amino acids, viscosity, and the nectar secretion rate (Corbet 2003). It has been hypothesized that some specialist nectarivores can assimilate sucrose, whereas opportunistic nectar feeders digest only simple hexoses (Dupont et al. 2004). Sugar concentration is a key factor in nectar selection by nectar feeders. Indeed, insect pollinators using viscous dipping, such as solitary and social bees, obtain nectar containing higher sugar concentrations (52 %) than those using a suction method (33 %), like butterflies or hummingbirds (Kim et al. 2011). Moreover, honey bees show strong preferences for warmer and less viscous nectar due to faster ingestion and reduced thermoregulation costs, independently of changes in sugar concentration (Nicolson et al. 2013). Amino acids played a key role in attractiveness to insect pollinators. Different amino acids elicit different responses in insect gustative receptors (Gardener and Gillman 2002). For instance, the adult Lepidoptera’s diet is based exclusively on nectar. Thus, they are attracted to flowers rich with amino acids, especially female butterflies (Alm et al. 1990; Rusterholz and Erhardt 2000; Gardener and Gillman 2002). Honey bees can also alter their feeding selection in response to amino acids present in nectar. They prefer nectars enriched with some amino acids such as proline or glycine than other enriched with alanine and serine (Alm et al. 1990; Bertazzini et al. 2010). The predominance of phenylalanine and/or gamma-aminobutyric acid attracts long-tongued bees and hoverflies, whereas asparagine and tryptophan seem repellent to these insects (Petanidou et al. 2006). The amino acid concentration in nectar is not exclusively a function of the weed’s genotype. It can also be affected by agronomic techniques. For instance, nitrogen fertilization increases nectar amino acid concentration in *A. githago* L. (Caryophyllaceae) (Gardener and Gillman 2001). Arbuscular mycorrhizal fungi can likewise increase the number of flower visitors (mainly Diptera and Hymenoptera) in *C. cyanus* L. (Asteraceae) (Gange and Smith 2005). Lastly, the ecological significance

of the toxic nectar secreted for example by some weeds (e.g., *Cuscuta* spp. (Convolvulaceae), *Euphorbia* spp. (Euphorbiaceae), and *Solanum nigrum* L. (Solanaceae)) is poorly understood. Nectar alkaloids may be protective agents against generalized flower visitors like Lepidoptera, while favoring bees, which are both more oligotrophic and less susceptible to alkaloids than Lepidoptera (Rhoades and Bergdahl 1981; Baker and Baker 1983; Adler 2000). However, other hypotheses on the ecological context of toxic nectar have been discussed, which has been linked to the costs of plant defence in terms of pollination services (Gegear et al. 2007). Although the alkaloids in the floral nectar tend to reduce visitation by bumblebees, the magnitude of the effect is likely to depend on the availability and nectar properties of alternative flowers.

The attraction of visiting insects is also linked to the mechanisms involved in flower recognition. The recognition of appropriate flowers is crucial to prevent wasting energy (Fenster et al. 2004). Thus, flower shape and color play a key role in routing insect foraging flights (Menzel and Shmida 1993). Many Brassicaceae species reflect ultraviolet radiation to attract insect pollinators (Yoshioka et al. 2005). Some flower colors are correlated with particular pollinator species, although this cannot be generalized since data from different environments do not necessarily lead to the same conclusion (Petanidou and Lamborn 2005). Specialist bumblebees prefer purple flowers, which seems to confirm the “pollination syndrome” theory (Nakano and Washitani 2003). The “pollination syndrome” is the hypothetical correlative relationship between floral characters (e.g., shapes, structures, colors) and the forager traits of the animal groups serving as flower pollinators. Flower recognition by insects can be facilitated by color patterns. The “search images” system possessed by insects (Goulson 2000) can be aided by characteristic black spots at the base of the petal, functioning as a “nectar guide” (Johnson and Dafni 1998), as observed in *P. rhoeas* (Papaveraceae). Bright and gaudy colors are not always required to oligotrophic and less susceptible flower visitors. Some Euphorbiaceae have pale green flowers. However, they are frequently visited by insects (e.g., *Euphorbia esula* L. and *Euphorbia helioscopia* L. (Euphorbiaceae)) (Larson et al. 2006; Benvenuti S., pers. observ.). Recently, it has been noted that the pale color of flowers, often defined as a feature to attract pollinators, is not maintained by pollen-mediated selection but by another mechanisms. The value of combining experimental pollen supplementation and reductions can be correlated with variation of floral traits, especially in species where compatible pollen receipt is difficult to measure (Campbell and Bischoff 2013). With regard to olfactory and tactile cues, a mechanism for identification and recognition of flowers also consists in the production and emission of volatile compounds, mainly terpenoids and benzenoids (van Schie et al. 2006). The two dominant components of the fragrance of *Cirsium* species

(Asteraceae), benzaldehyde and phenylacetaldehyde, attract several orders of generalist insect pollinators (Theis 2006). Fragrance of their flowers is emitted in dynamic patterns that maximize pollinator attraction (Theis et al. 2007). For instance, generalist pollinators, such as oligolectic bees, often show innate sensory preferences for particular floral scent compounds of their host plant (Wright and Schiestl 2009; Dötterl et al. 2011; Burger et al. 2011). In addition an insect’s preferences for particular flower cues mean that it can actively identify new flower-borne physical and olfactory stimuli (Arak and Enquist 1993; Naug and Arathi 2007). Insects also have learning abilities to associate chemical signals to their food sources (Dukas 2008). Diptera, Lepidoptera, and Hymenoptera are the best examples of olfactory learning in insects (Wright and Schiestl 2009). Finally, using of olfactory signals provides more fitness advantages to both plant and pollinator than using of visual signals alone (Wright and Schiestl 2009).

5 Diversity and stability of weed-insect pollinator networks: a bio-indicator of the arable land health?

Plant-insect pollinator networks are largely mutualistic networks, providing benefits for both plants and insects (Waser and Ollerton 2006). Flowers offer rewards like nectar and/or pollen to their pollinators which in turn pollinate them. On their bodies, they transport pollen grains from one flower to another (of the same species). Insects can learn which flowers provide rewards and then search for more individuals of the same species to get more of it (Sauvion et al. 2013). However, there are antagonistic interactions between pollinators and wildflowers. Some flowers deceive the insect visitors by not providing any reward, while some insects exploit the plants’ resources without providing pollination (Waser and Ollerton 2006). Deceptive flowers can use olfactory, visual, or sexual cues to attract pollinators. This principle is especially common in orchids. One third of orchid species use deception to be pollinated, which represents 87 % of the known examples of deceptive pollination (Sauvion et al. 2013). For instance, *Cypripedium calceolus* L. emits a scent that attracts some honey bee species (e.g., *Andrena*, *Lasioglossum*, and *Halictus* genera; van der Cingel 2001). In a similar manner, *Anacamptis pyramidalis* L. does not produce nectar but their inflorescence resembles that of nectar-producing species very closely regarding size, shape, and color (Sauvion et al. 2013). Cases of sexual mimicry can be found in the genus *Ophrys*: Their labellum imitates female insects regarding size, shape, color, and sometimes even hairiness so well that it successfully attracts the respective males (e.g., *Ophrys sulcata* with *Andrena flavipes*, *Ophrys passionis* with *Andrena carbonaria*; Sauvion et al. 2013). Deceiving insect pollinators, on the other hand, can obtain nectar from flowers but

withhold pollination. A number of plants possess floral structures that only grant access to certain insect visitors. Hummingbirds, ants, wasps, and bees, however, may be able to collect the reward, which is usually nectar, without touching the plant's reproductive organs (Rust 1979; Roubik 1982; Galen 1983; Scott et al. 1993; Stout et al. 2000). Nectar production comes with a significant cost for plants: it may demand up to 37 % of their available energy (Southwick 1984). Moreover, if wildflowers are cheated out of their nectar, this may considerably impair their ability to produce seeds (*Blandfordia nobilis*; Pyke 1991). By lessening pollination success, nectar robbing could significantly reduce the fitness of wild plants.

Mutualistic pollination networks are key ecological processes in many terrestrial ecosystems. The stability of these networks depends on some structural properties, such as number of species, number of links between species, and specialization of the network (Vázquez et al. 2009). Plant-pollinator networks have a strong variability (on average four times more pollinator species than plant species; Vázquez et al. 2009). Interspecific interaction between a plant and a pollinator is called a link (Jordano 1987). Species are characterized by their degree, that is the number of links with other species (Jordano et al. 2003; Bascompte et al. 2006). Most of the species have a low degree: they are connected with few other species (Vázquez et al. 2009). For example, a pollinator is considered as specialized if it is connected to just one plant species. However, being a generalist is the more frequent behavior in plant-pollinator networks (Memmott 1999). The majority of plants is pollinated by several pollinators. In the same way, insect pollinators visit several plant species, even if they are from the same genus or family. Specialization can be measured as the specific or network level (Blüthgen et al. 2006). The second is used to study the stability of the network in the ecosystem which can be affected by many environmental factors.

In arable fields particularly, a large number of insect-pollinated weeds are rare or in decline. Some examples are *A. githago* L. (Caryophyllaceae), *C. cyanus* L. (Asteraceae), *Papaver argemone* L. (Papaveraceae), *Ranunculus arvensis* L. (Ranunculaceae) (Chancellor 1977), *Glebionis segetum* L. Fourr. (Asteraceae), *Legousia hybrid* (Campanulaceae), *Matricaria chamomilla* L. (Asteraceae), *S. alba*, *Viola arvensis* Murray (Violaceae) (Chancellor 1986), *C. regalis* L. (Ranunculaceae), *L. amplexicaule* L. (Lamiaceae), *S. noctiflora* L. (Caryophyllaceae), (Baessler and Klotz 2006), *Myosotis arvensis* (L.) Hill. (Boraginaceae), *Viola tricolor* L. (Violaceae) (Andreasen et al. 1996), *Anchusa arvensis* (L.) Bieb. (Boraginaceae), *L. speculum-veneris* L. (Campanulaceae) (Albrecht and Mattheis 1998), *Nigella arvensis* L. (Ranunculaceae), *Ornithogalum umbellatum* L. (Hyacinthaceae) (Dutoit et al. 2004), *Anthemis arvensis* L. (Asteraceae), and *Silene conica* L. (Caryophyllaceae)

(Sutcliffe and Kay 2000). In Europe, the number of weeds recognized as rare continues to grow, with the exception of species whose persistence dynamics have little reliance on biotic action for pollination (Sutcliffe and Kay 2000). Lists of declining species include many weeds, which are threatened because they depend on flower visitors for seed set (Motten 1986; Biesmeijer et al. 2006). Indeed, rare weed species have difficulties attracting insects and their interactions with pollinators are more fragile (Pontin et al. 2006). Thus, stability of weed-insect pollinator networks is essential to maintaining biodiversity in the arable landscapes.

Moreover, the risk of decline is greatest when pollinator mutualistic interaction is specialized (Gibson et al. 2006). For instance, species of the Caryophyllaceae family are often characterized by rigid mutualistic interactions that are initiated by Lepidoptera (Kephart 2006). This type of *interaction* is fragile, since many Lepidoptera and other pollinators depend on the plants in two ways: they require flowers with nectaries as a food source and certain host plants for oviposition and feeding of larval forms (Kremen et al. 2007; Nicholls and Altieri 2012; Benelli et al. 2014). Butterfly species frequently depend on restricted plant groups, often belonging to a single botanical family, a single genus or even a single species. A good example is the Old World swallowtail *Papilio machaon* L. (Lepidoptera: Papilionidae) which oviposits exclusively on Apiaceae (Wiklund 1981), as well as *Macroglossum stellatarum* L. which needs *Galium* spp. (Rubiaceae) as larval diet. On the other hand, in Nymphalidae, there is little specialization (e.g., the great-banded grayling, *Brintesia circe* (Fabr.)) as the pollinator-weed interaction is observed in many Gramineae species. If certain host plants have poor invasiveness within the various ecosystems, this inevitably leads to a scant presence of the related butterfly species (Dennis et al. 2004). Interestingly, while generalist pollinators (e.g., bees) promote weedy species and potentially create risks for weed populations, the specificity between butterflies and their host plants hinders weeds, as the butterflies are specific in their need for hosts. Therefore, Hymenoptera pollinators may inadvertently promote weeds while butterflies do not, and the risk of butterfly-plant host co-extinction has already been reported in some parts of the world (Koh et al. 2004). Consequently, more specialized weed species involved in mutualistic relationships could constitute the most reliable ecological assessment parameters since they are species whose presence is threatened by the disruption of the agro-ecosystem's biodiversity (Bàrberi et al. 2010).

The frequency of rare weeds in arable land plant communities represents an indicator of their ecological sustainability (Benvenuti and Macchia 2003; Albrecht 2003; Gabriel and Tschardt 2007). This is particularly true for insect-pollinated species, since their presence presupposes a level of biodiversity that extends to the animal kingdom (Levin 1971; Holzschuh et al. 2006; Nicholls and Altieri 2012).

Hyvönen and Huusela-Veistola (2008) propose some agrobiodiversity indicators based on the trophic networks between 25 common arable weeds and individual groups of farmland birds, pollinators (mainly wild bees), and insect pests. Interestingly, they note that, after high levels of agricultural intensity, the slowest recovery of values was for pollinators.

Overall, several rare weed-Lepidoptera visitors networks occur in arable lands (Jennersten 1988; Rundlöf and Smith 2006). For instance, (i) Geometridae (e.g., *Euphyia biangulata* Haworth) visiting Caryophyllaceae and (ii) Papilionidae (e.g., *P. machaon*) foraging on Apiaceae represent potential indicators of the biodiversity of arable lands (Novák and Severa 1980). Other butterflies, such as *P. rapae*, choose the same species both for pollinating and for oviposition. This exemplifies mutualism and parasitism simultaneously (Jones 1987) which may result in a “fitness conflict” for the organisms involved (Dufaÿ and Anstett 2003). Among Diptera, the widespread presence of Syrphidae (e.g., *Eristalis arbustorum* (L.)) has been considered as a good indicator of plant biodiversity (Hegland and Boeke 2006). Although they are able to successfully reproduce in a wide range of habitats, their presence has been frequently recorded in association with rare weed flowerings (e.g., *G. segetum* (L.) Fourr.). *G. segetum*-Syrphidae interactions could, thus, be potential bio-indicators of the health of arable land.

6 Agricultural practices affecting the stability of weed-insect pollinator networks

Many intensive agricultural practices negatively affect vegetal and animal biodiversity. The ecological consequences of changes in the intensity of arable land management can be explored with the aid of biodiversity indicators based on species interactions (Suárez et al. 2001; Osinski et al. 2003).

6.1 The spatiotemporal dynamic in agricultural landscapes: the importance of a heterogeneous mosaic

The spatiotemporal arrangement of agricultural landscapes affects significantly both weed and insect pollinator communities and consequently interactions between them and stability of pollination networks. The diversity of weeds in arable fields increases with the complexity of the landscape (Gabriel et al. 2005; Pinke et al. 2009). Landscape complexity is often defined by the rapport between quantity of arable land and quantity of non-arable lands (natural and semi-natural habitats such as grasslands, set-aside fields, hedges, and forests). Landscape complexity increases with percentage of non-arable lands in the landscape (Gabriel et al. 2005). Consequently, landscape planning is crucial for biodiversity (Rookwood 1995; Grass et al. 2013). Increased habitat diversity, structural heterogeneity, and reduced patch disturbance

can significantly promote species richness and genetic variability and reduce extinction rates of many species (Barbault 1995; Dover 1996; Potts et al. 2009; Bärberi et al. 2010). Thus, weed management is a key factor in the sustainability of agriculture (Gerowitt 2003; Bengtsson et al. 2005; Hole et al. 2005). Concerning weed pollinators, to avoid excessive energy consumption for foraging flights, distances between nesting sites and food sources must not be excessive. For instance, bees are central place foragers and cannot relocate their nest once it has been established (Kevan and Baker 1983). Abundance and diversity of bees increase with the connectivity between favorable habitat patches (Banaszak 1992; Steffan-Dewenter 2003; Williams et al. 2010), increasing the stability of pollination services (Garibaldi et al. 2011). Thus, they cannot persist and assure an effective pollination service to plants in homogeneous environments where nesting sites are too distant from foraging resources (Kluser and Peduzzi 2007; Williams et al. 2010).

It is also very important to consider the effect of temporal arrangement (inter- and intra-annual variations) of arable landscapes on the weed communities and their pollinators. Crop rotation is an major determinant of seed density in soil (Cardina et al. 2002). Longer crop rotations, combined with less intensive tillage, increase the diversity of emerged and seedbank weed species (Murphy et al. 2006). In addition, attractive long-term flowering crops, such as alfalfa *Medicago sativa* L. (Fabaceae), could be integrated in crop rotations, to promote insect pollinators and their pollination services (Rollin et al. 2013). Indeed, alfalfa was the most evenly used flowering crop among bees in an intensive agricultural landscape. It performed better for wild bee groups compared to semi-natural herbaceous habitats during summer, even if only 30 % of all wild bee genera reported were observed in alfalfa (*Andrena*, *Halictus*, *Hoplosmia*, *Lasioglossum*, *Megachile*, *Melitta*, *Xylocopa*) (Rollin et al. 2013). Moreover, annual mass flowering crops can change the floral resource availability in the landscape temporarily, which can transiently modify pollinator preferences and the stability of pollinator-wild flora networks, with functional consequences for the ecosystem (Tscharntke et al. 2012). For instance, the mass flowering of oilseed rape temporarily increases attractiveness of the crop and decreases pollination of the wild plant *Primula veris* L. by bees in adjacent natural areas (Holzschuh et al. 2011).

6.2 The key role of untilled areas for weed-insect pollinator networks

The spatiotemporal arrangement of arable lands should be complemented by untilled areas in the form of managed or natural conservation lands, or farm dams and scattered trees in fields, to ensure that insect-pollinated weeds are retained in the intensive agricultural landscape (Kremen et al. 2007; Lentini

et al. 2012). Intensive agricultural practices have increased the loss of natural and semi-natural areas (e.g., permanent grasslands, set-aside areas, gardens, hedges, woods, filed margins), with a significant negative effect on insects pollinators (Duelli and Obrist 2003; Le Féon et al. 2010). Yet, these areas are essential habitats for insect pollinators providing both appropriate foraging and nesting resources (Steffan-Dewenter and Tscharntke 2001; Potts et al. 2003; Vulliamy et al. 2006; Öckinger and Smith 2007; Goulson 2010; Rollin et al. 2013; Requier et al. 2014). For instance, woods represent a fundamental reserve of suitable sites for the survival and reproduction of pollinators (Potts et al. 2006), especially if they are located in a mosaic pattern within an agricultural setting (Banaszak 1992). Other areas offer a suitable environment for soil-nesting bee pollinators and Lepidoptera species that require particular weeds on which to oviposit (Graves and Shapiro 2003). For example, cattle grazing can exert beneficial effects on weed-insect pollinator networks, by promoting open mosaic areas with richer and more temporally heterogeneous habitats (e.g., grasslands) (Vázquez and Simberloff 2003; Zamora et al. 2007).

The communities of weed-visiting insects can be enhanced by field margins, hedges (Marshall and Arnold 1995), other buffer zones (Ma et al. 2002), and set-aside fields (Corbet 1995; Steffan-Dewenter and Tscharntke 1997; Blaauw and Isaacs 2014). Weeds linked to mutualistic relations with pollinators can successfully grow in field margins. They provide suitable ecological niches for many pollinators. The introduction of wildflower strips favors a potentially stable community of cavity-nesting hymenoptera (Fabian et al. 2013), with particular reference to honey bees (Decourtye et al. 2010, 2011). But the efficiency of flowering areas managed for bees can be influenced by the presence of alternative flowers in the semi-natural habitats close by (Henry et al. 2012; Blaauw and Isaacs 2014). Furthermore, it leads to an increase in Lepidoptera searching host plants for oviposition and nectar as a food source (Saarinen 2002). Hoverflies are also attracted by certain flowering strips, such as alyssum (*Lobularia maritima* (L.) Desv., Brassicaceae) (Nicholls and Altieri 2012). The use of native weeds within or around intensely farmed landscapes helps to safeguard pollinator biodiversity, particularly the specialized pollinators linked to specific weeds (Carvell et al. 2007). It also has further benefits, such as pest population reductions, protects soil and water quality by mitigating runoff and soil erosion, and enhances rural aesthetics (Wratten et al. 2012). Despite the benefit to pollinators feeding, the presence of agri-environmental schemes based on weeds poses a risk of insecticide exposure to bees foraging when the area is treated (Girolami et al. 2012; Botias et al. 2015). Therefore, the enhancement of floral resources for bees in agrosystems through the establishment of habitats containing flowering weeds must

be accompanied by supplemental pesticide mitigation strategies.

6.3 Reduce external inputs to increase biodiversity

The decrease in some weeds may be due to the intensive use of external inputs (Marshall et al. 2003; Bretagnolle and Gaba 2015). This can be direct effects on weeds (e.g., herbicides, fertilizers) or indirect effects on their pollinators (e.g., insecticides). It is likely that the decline in pollinators is highly linked to weed decline (Kluser and Peduzzi 2007). Application of pesticides and inorganic fertilizers have considerably increased during the last few decades (Robinson and Sutherland 2002; Baessler and Klotz 2006) and cause significant modifications and decreases in the diversity of weed communities (Sutcliffe and Kay 2000; Hyvönen and Salonen 2002; Baessler and Klotz 2006; Storkey et al. 2009; Andreasen and Streibig 2011) and in weed seedbanks (Robinson and Sutherland 2002). However, herbicides affect species diversity and species composition more than nitrogen fertilization (Hyvönen and Salonen 2002). Nitrogen fertilizers promote nitrophilous species (e.g., *Chenopodium album* L. and *S. media* (L.) Vill.) and weed species with physiological shade tolerance (e.g., *Poa annua* L., *S. media*, and *V. arvensis* L.) because of enhancing the shading ability of crops (Andreasen and Streibig 2011). Moreover, herbicides significantly decrease weed density and plant height (Mavunganidze et al. 2014), while they are important factors for pollinator attractiveness. Insect visitors may show density-dependent preferences when different types of flowers are available within their environment, such as mass flowering crops (Rands and Whitney 2010). Even at low wildflower density compared to the mass flowering crop, insect pollinators can shift away from their preferred crop when wildflower density increases within filed margins. For instance, increasing tubular blossom density increases visit frequency by bumblebees and beetles (Hegland and Boeke 2006). Increasing number of flowers per plant (e.g., *E. vulgare* L.) can also promote bee attractiveness (Klinkhamer and Jong 1990).

Regarding insect pollinators of weeds, pesticides use in crops can be an additional source of chronic exposure for insect pollinators, due to the widespread contamination by pesticide residues of weeds growing in and near treated crops (Botias et al. 2015). Moreover, the herbicide resistance of some weed species (e.g., glyphosate) leads to increasing herbicide use in crops (Andreasen and Streibig 2011; Heap 2014; Labreuche et al. 2014; Fernandez et al. 2015) and thus increases the global risk of exposure for insect pollinators of weeds. The impact of agri-environmental schemes on insects is probably also an indirect result of the impact of the vegetation management (Kleijn et al. 2006). Field reduction of

fertilizer and herbicide applications significantly enhance plant species diversity (Hyvönen and Salonen 2002) and can promote bees through the increase of flowering weeds adjacent to crop areas (Kleijn et al. 2006). Organic farming systems have significant positive effects on pollination networks. For instance in Germany, a higher bee diversity, flower cover, and diversity of flowering plants have been recorded in organic compared with conventional fields (Holzschuh et al. 2006). These findings were confirmed by further research, highlighting that landscapes in Germany that comprise higher proportions of organic crop fields support more bee species, at greater abundances in fallow strips. An increase in organic cropping in the surrounding landscape, from 5 to 20 %, enhanced the richness of bee species in fallow strips by 50 %, the density of solitary bees by 60 %, and bumblebee density by 150 % (Holzschuh et al. 2008).

6.4 No tillage: an efficient practice to associate with other environmental strategies

Since 2000, weed management schemes have changed with an increase of crop areas not subjected to tillage. The main objective of conservation tillage is to minimize erosion and degradation of soils. It is a common practice in North and South America where in areas are characterized by intensive soil erosion (Holland 2004).

No tillage promotes weed communities, with an increase of both abundance and diversity of emerged and seedbank weeds (Cardina et al. 2002; Murphy et al. 2006; Labreuche et al. 2014). No tillage also changes the composition of the weed community, promoting annual grasses and perennial weeds with deeper plant roots (Labreuche et al. 2014). To nesting sites, numerous species of bees have their nests in the soil. Solitary mining bees (e.g., *Andrena* spp., *Halictus* spp., *Lasioglossum* spp.) directly excavate soil to construct their nests whereas bumblebees nest in pre-existing underground (e.g., old rodent nests) or aerial cavities or construct nests on the surface in tussocky grass (Michener 2007). It is important to adopt reduced, minimum, or non-tillage techniques, since less soil disturbance can favor the survival dynamics of these beneficial organisms (Kells and Goulson 2003; Nicholls and Altieri 2012). However, tillage should have a more significant effect on mining bees than on bumblebees whose nests are often located deeply below ground in hedgerow or woodland edges (Michener 2007).

However, no tillage is compensated by an increased use of herbicide, 30 % of which is glyphosate (Labreuche et al. 2014). These practices promote the development of herbicide tolerance for many weed species (Labreuche et al. 2014) and consequently increase the risk of insecticide exposure for weed-insect pollinators (Botias et al. 2015). To conclude, even

if no tillage has positive effects on weed communities and their pollinators, it must be supported by environmental schemes for the reduction of herbicides.

7 Conclusions

The preservation of biodiversity is an agronomic concern, since it involves the long-term enhancement of agricultural production (Bullock et al. 2007). This has led to a focus on the ecological interactions between the organisms involved in agricultural landscapes. The growing need to maintain and/or restore arable land biodiversity meant that we have focused on weed species that are becoming rare due to their dependence on pollinators (Paoletti 1995). Moreover, many insect pollinators are threatened by an increasing risk of extinction due to the gradual decrease in nectariferous plants that are food sources for adults, as well as by the decline of host plants that are essential for oviposition and larval development (e.g., butterflies species) (Kremen et al. 2007; Nicholls and Altieri 2012; Benelli et al. 2014).

In this review, we highlight the key role of insect pollinators, especially generalist species, in the pollination and the stability of weed communities in arable landscapes. Weed-insect pollinator interactions are modulated by flower traits, such as the flower's color, shape, and scent. These mutualistic interactions also depend on the quality of available pollen and nectar, particularly nectar composition in terms of sugars and amino acids, nectar viscosity, and secretion rate. We revealed that the stability of weed-insect pollinator interactions could be affected by some intensive agricultural practices (e.g., increasing external inputs, tillage, reduction of uncropped areas), with an increase of extinction risk for species with specialized interactions. Thus, it is important to work on alternative management strategies to combine crop production and biodiversity. For instance, reduced tillage in organic farming systems can preserve diversity of weeds in crops without compromising crop yield (Barberi et al. 2014).

Finally, we believe that the potential of rare weed-insect visitor networks we have proposed as bio-indicators of arable lands could be useful for a preliminary assessment of the sustainability of agronomic management. In particular, (i) the Geometridae (e.g., *E. biangulata*) and Bombyliidae species visiting Caryophyllaceae, (ii) the Papilionidae (e.g., *P. machaon*) foraging on Apiaceae, and (iii) the Syrphidae (e.g., *E. arbustorum*) visiting rare Asteraceae (e.g., *G. segetum*) could represent potential indicators of the biodiversity of arable lands. We therefore encourage research on this issue, highlighting the need for further data to confirm our hypotheses. Further knowledge in this area could also help to

build up an agenda to restore ecologically damaged arable lands.

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