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REVIEW

Review on flower-visiting behaviour of orthopterans and setting priorities for further studies

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Abstract

The importance of pollination and pollinators is easy to underestimate and impossible to overstate, since its importance goes far beyond the crop production and even the maintenance of plant populations. Most terrestrial ecosystems ultimately depend on the plant–pollinator interactions formed by million years coevolution. This is essential for both the daily functioning of the ecosystems and the long-term development of biodiversity. At the same time, the loss of biodiversity caused by climate change and human activities will soon lead to an ecological crisis, a catastrophe, which could endanger our life: For example, through the decline and loss of various ecosystem services. Such may be the pollination crisis, resulted from a significant loss of pollinating insects' diversity and abundance. The discovery of a pollinator Orthoptera species has encouraged researchers in the densely populated region of Indo-Malaysia to explore the potential role of orthopterans as pollinators. Although the flower visitation of some species has been already known, the role of orthopterans in pollination is scarcely revealed. Here, we collected and reviewed the available data in order to point out some factors of their importance and set priorities that may serve as a basis for further investigations regarding ecological, evolutionary and practical points of view.

Keywords Ecosystem services · Evolution · Flower visitation · Pollination · Chemical ecology

Introduction

Pollination is essential mainly for the reproduction of angiosperm plants (angiospermatophyta), since 87.5% of them, about 300,000 species, depend on animal pollination. Pollinators fertilize about 70% of agricultural plants containing about 250 cultivated species of the European flora. We need pollinators during the production of about a third of our daily food. Animal pollination of flowering plants is an extremely important, critical ecosystem service from both economic point of view and considering our health and environment. Although its importance and endangering factors have been known for decades, its investigation and conservation become a hot topic only at the end of the last century. Pollination systems are under increasing threat, mainly caused by anthropogenic effects including habitat fragmentation, intensification and change of land use, use of pesticides and even the invasion of non-native plants and animals (Kearns et al. 1998; Levy 2011; Vieli et al. 2021).

The pollination is usually associated with bees, butterflies, bats and birds (Dyer et al. 2007; Levy 2011). Although other animals, especially other insect, taxa also contribute to pollination, we have very few data on it. Due to the ongoing global biodiversity crisis, the extinction rate of species is unprecedented. This decreases the potential value of biodiversity, even in the case of goods and services that have not been discovered yet but have potential benefit for us.

Ecosystem services such as pollination (Daily 1997; Ollerton 2017) can be efficiently managed if their evolutionary ecology background is better understood (Bronstein 2001). The pollination crisis (Ghazoul 2005; Potts et al. 2016) poses a major challenge to investigation of the ecological and economic aspects of pollination as an ecosystem service. The decline in the abundance and diversity of pollinators appears to be closely related to agricultural activities at both local and landscape levels (Carvell et al. 2017; Kovács-Hostyánszki et al. 2017). However, disturbances

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may not have a visible effect on flower-visiting species, whereas those may reduce the frequency of species–flower interactions, and consequently, the success of pollination (Carman and Jenkins 2016). Therefore, it is essential to understand the ecology of pollination and flower visitation by studying pollinators and even other flower-visiting communities, especially in case of some less known flower-visiting insect taxa (Kovács-Hostyánszki et al. 2019).

Here, we discuss our knowledge on Orthoptera flower visitation and pollination and provide additional data that highlights their potential but formerly unknown role in ecosystem services. Additionally, we set priorities for further investigations, which may help to sustain ecosystem services that directly affect our lives and biodiversity conservation.

Overview

Pollination is the propagation process of flowering plants (Spermatophyta), during which pollen (sometimes pollinarium: orchids) is sent directly to the seed in the case of open plants and first to the productive pistil in the flowers of closed plants (then it reaches the nucleus by growing a pollen tube). Though the delivery of pollen can happen in numerous ways, the role of animals, especially insects is notably (Real 2012). Among insects, their flower-feeding (florivore) species form a special group, which is less known or studied than the other related functional groups, for example pollinators (Breadmore and Kirk 1998; McCall and Irwin 2006). Nevertheless, they may have a direct and indirect effect on flower adaptation, species interactions and also on community dynamics (e.g. Krupnick and Weis 1999; Krupnick et al. 1999; Frame 2003; McCall and Irwin 2006). Although there is plenty of research on flower visitors, only a few taxa are recognized as pollinators (e.g. bees and butterflies are well-known pollinators), while other taxa, such as Orthoptera, are often considered to be more harmful than they really are. The importance and effect of pollinator (Bawa et al. 1985; Ollerton et al. 2011) and folivore (leaf-feeding) species (Ødegaard 2000; Novotny et al. 2006; Dyer et al. 2007) are well studied; however, the role of insects feeding on flowers and flower parts (Wardhaugh 2015) are mainly unknown. Many insects visit flowers, and some primarily feed on their parts (Rentz and Clyne 1983; Rentz 1993, 2010; Corlett 2016; Kondo et al. 2016) such as many Coleoptera, Blattodea, Hemiptera and Orthoptera species (Nagamitsu and Inoue 1997; Wardhaugh 2015).

About 27,000 Orthoptera species are known worldwide, with varying species richness in different geographical regions, for example in Southeast Asia with about 2,000 species (Myers et al. 2000; Cigliano et al. 2023; Tan et al. 2017a).

Due to the diversity of species and forms, they act a part of numerous ecosystem functions, such as herbivores including florivores, like *Phaneroptera brevis* Serville, 1838 (Tettigonoidea), *Nisitrus* species (Grylloidea), *Valanga nigricornis* (Burmeister, 1838) (Acridoidea) and *Conocephalus* (Tettigonoidea), *Xenocat* and *Atractomorpha* species (Acridoidea) (Tan and Tan 2017; Tan et al. 2017b), predators, such as *Hexacentrus unicolor* Serville, 1831 (Tettigonoidea) (Poo et al. 2016), and even pollinators, such as *Glomeremus orchidophilus* Hugel, 2010 (Acridoidea: Gryllacrididae) (Hugel et al. 2010; Micheneau et al. 2010; Lord et al. 2013). Nevertheless, there are relatively few reports about their flower visiting, on the whole (e.g. Schuster 1974; Rentz and Clyne 1983; Micheneau et al. 2010; Rentz 2010; Wardhaugh 2015; Krenn et al. 2016).

Until recently, orthopterans were not recognized as pollinators (e.g. Kevan 1999; Corlett 2004; Almeida-Soares et al. 2010; Edens-Meier and Bernhardt 2014; Subhakar and Sreedevi 2015; Symes 2017). Although the most recent reviews of Ollerton (2021), Micheneau et al. (2010) and Wardhaugh (2015) already referred to orthopterans as pollinators, do not discuss their role.

Flower-visiting orthopterans

The relationship between orthopteriod insects and flowering plants is quite old. It dates back to the late Jura and early Crete, when Ensifera evolved and diversified parallelly with gymnosperms and then angiosperms (Song et al. 2015). In the case of several Mesozoic lines of Prophalangopsid Tettigonoids were proven that they fed on pollen (Labandeira 2000, 2010; Labandeira et al. 2007). Since their conserved intestinal contents are rich in fossil pollen, they presumably already had some role in the pollination of preangiosperm plants (Krassilov et al. 1997). The divergence of Caelifera taxa occurred relatively early, sometime on the Permian–Triassic boundary, and at first, they did not follow the diversification of angiosperms. Since their adaptive radiation began in the Tercier period, about 55 million years ago, parallelly with the emergence and diversification of monocotyledons, including grasses (Song et al. 2015), thus the species of Caelifera, including Acridoidea, played a lesser role in the evolution of dicotyledons. Krenn et al. (2016) reported that obligate flower-visiting orthopterans are rare, and their results suggest that almost all of them belong to the order Ensifera. Tettigonoids and some Australian Orthoptera (e.g. Zaprochilinae) regularly visit flowers and feed on pollen and different parts of flowers (Kevan and Baker 1983), but unlikely pollinate them. Crickets belonging to several Neotropical lines (Schuster 1974) and wetas from Chatham Island, New Zealand (Lord et al. 2013), feed on flowers and are considered as potential pollinators since it was proven that they transport pollen on their body, between flowers.

These flower-visiting orthopterans consume different parts of the flower and pollen.

Orthopterans as pollinators

The real breakthrough was the work of Micheneau et al. (2010), in which they reported a special pollinator Orthoptera species. *Angraecum cadetii* Bosser, an endemic plant species of the islands of Mauritius and Reunion (Mascarene Islands, Indian Ocean), was studied, because its flowers show atypical morphology among its genus (greenish-white and medium-sized, with short, hollow spurs). Its potential natural pollinators were observed using cameras, and the characteristics of pollen associated with pollination (spur length, and volume, concentration and odour of nectar) were also examined. Pollination efficiency (pollen removal and deposition) and reproductive success (crop stock) under natural field conditions were quantified weekly during the flowering season (January to March) of three consecutive years (2003 to 2005).

Angraecum cadetii proved itself to be self-compatible, but it needs a pollinator for the successful fertilization. Only one pollinator was observed, a formerly unknown cricket *Glomeremus orchidophilus* (Orthoptera: Gryllacrididae) (Hugel et al. 2010). The cricket feeds on the nectar of *A. cadetii* at night, visiting the flowers by climbing on the leaves of the orchid or jumping from neighbouring plants, choosing the freshest flowers on each plant. Their flower visits were relatively long, in average, these took 16.5 s, with a maximum of 41.0 s. At the La Plaine-des-Palmistes (Pandanus Forest) site, 46.5% of the flowers were pollinated, and in the case of 27.5% of them, the pollen was deposited on the stigma. In the islands the ratio of fruit-bearing flowers ranged from 11.9% to 43.4%, depending on sampling sites.

Although orthopterans had been well known as herbivores, this was the first case when the role of an Orthoptera species in pollination was proven. Beyond that, *G. orchidophilus* is the only known Orthoptera that feeds on nectar with modified mouthparts (Hugel et al. 2010). Additionally, it is distributed only on the tropical island of La Reunion, and pollinates an also endemic orchid of the island, which unambiguously proves their coevolution.

Suetsugu and Tanaka (2014) draws attention also to this coevolutionary possibility. Investigating the species-rich genus of *Habenaria* (Orchidaceae) and its pollinators, they found that the diversification of orchids is closely linked to their diverse pollination system. They studied the diurnal flower visitors of *Habenaria sagittifera* Reichenbach f. and though orthopterans were not considered as regular flower visitors, larvae of *Ducetia japonica* (Thunberg, 1815) (Tettigonoidea) regularly visited and fed on pollen and antheridial capsules of the plant. Although the relationship between *H. sagittifera* and *D. japonica* cannot be seen as a close mutualism, regular visits and pollen consumption may show an evolutionary path towards the pollination interaction between them.

In another study, Lord et al. (2013) observed that some plant species on the sub-Antarctic islands of New Zealand have spectacular, highly pigmented inflorescences, but poor insect fauna apparently offer few opportunities for biotic pollination. Researchers documented reproductive systems and flower visitors of six plant species on Campbell Island. Pollen from all species tested was lipid-rich and low in starch and nectar. Among them, *Pleurophyllum hookeri* Buchanan appeared to be self-compatible, while *Pleurophyllum criniferum* Hook.f., *Veronica benthamii* Hook.f. and *Damnamenia vernicosa* (Hook. f.) were also able to implement self-pollination. The most common diurnal flower visitors were flightless flies (*Coenosia filipennis* Lamb, 1909) and other small Dipteras. Considering the nocturnal visitors, *Notoplectron campbellensis* Richards, 1964 (Orthoptera) visited the flowers of *V. benthamii* and transmitted pollen between the male and female flowers of *Anisotome latifolia* Hook.f. and *Bulbinella rossii* (Hook.f.). It may prove that biotic pollination can be more important in the subantarctic region than previously thought, and wetas are likely to be key flower visitors in this regard.

To date, the most comprehensive study has been carried out by a research team in Singapore on floriphagous orthopterans, which may also play an important role in pollination, providing valuable ecosystem services (Micheneau et al. 2010).

Study of Tan et al. (2017c) showed that not all orthopterans play a negative role in agriculture. To reveal the role of orthopterans in pollination, they made field studies in several habitats of Singapore, Malaysia, Thailand, Brunei Darussalam and Indonesia between 2015 and 2017. The nocturnal and diurnal flower visitations were recorded with cameras (both photos and videos). During the study, 140 records were made on Orthoptera flower visitation, in which totally 41 species (19 grasshopper, 13 locust and 9 cricket species) visited 35 different plant species. The two main types of flower-visiting orthopterans were also described: the first is the group of floriphilic grasshoppers, which prefer flowers more than other organs or parts (Tan and Tan 2017), and they feed on pollen and nectar. This group includes species of the subfamily Phaneropterinae (Rentz 2010; Suetsugu and Tanaka 2014). In Southeast Asia, *Phaneroptera brevis* is a very common orthoptera of shrubby habitats, which is often resting and feeding on various flowers. The other group of floriphilic orthopterans includes opportunistic polyphagous species. These species are mainly leaf-feeding insects but optionally they feed on available flowering parts (Burgess 1991; Bernays and Chapman 2007; Higginson et al. 2015). It has been recorded that these species feed on petals and/or petal-like organs (e.g. in the radii of a capitulum). *Valanga* *nigricornis* and *Xenocatantops humilis* (Serville, 1838), two locusts which were considered as pests, and the cone-headed katydids (*Conocephalus* species) and the Bukit timah cricket (*Tremellia timah* Gorochov & Tan, 2012) also belong to this type of flower-visiting orthopterans. A predatory bush cricket (Meconematinae) was also reported as flower visitor of *Dillenia suffriticosa* (Griff. ex Hook.f. and Thomson), which grows in an especially species-poor anthropogenic heath forest dominated by tiup-tiup tree (*Adinandra dumosa* Jack) where the pollen may provide a cheap and easily available source of protein for the bush cricket (Sim et al. 1992; Tan et al. 2017c).

The most known flower-visiting orthopterans are the adults of *Phaneroptera brevis*, which more frequent visit flowers than some common well-known flower visitors, such as hoverflies (Tan et al. 2019). To reveal how their feeding behaviour contributes to pollination, its feeding on the flowers of *Bidens pilosa* L. (Asteraceae) was studied with video recordings. Records proved that *P. brevis* adults consume pollen without damaging any parts of the visited flowers, while pollen grains attached to their antennae and legs enable pollination. The three times higher yield of the plants pollinated by *P. brevis* were also refers to the importance of this bush cricket in pollination, which needs further investigations (Tan and Tan 2018a).

The food preference and behaviour of *P. brevis* were also studied. The neural constraint hypothesis has been studied, which predicts the effect of resource availability on the efficiency of decision-making between flower and leaf as resources. Although the evidence of an obvious effect of floral density on the detection of resources by *P. brevis* adults was not provided, but increasing flower density generally decreased the efficiency and attentiveness of foraging bush crickets (Tan et al. 2017b). The preference between the flower and leaf also was not clear, even though bush crickets chose the flower more often, and preference of the higher flower source density was somewhat more common. In a later study, *P. brevis* was more frequent than other flower-visiting species, and its occurrence correlated positively with higher flower abundance (Tan et al. 2019), thus both the resource concentration and optimal nutritional hypotheses (maximizing the energy content of food per unit expenditure) (Krebs and Davies 1988) were supported.

Tan and Than (2019) also study the behaviour of *P. brevis* including personality and how they affect survival in a changing environment with ephemeral and dynamic availability of food sources. They studied inter-individual and inter-population differences in exploration and boldness and found evidence of population-level personality types for boldness, but not for exploration. Some individuals were consistently more exploratory and bolder than others, but the level of boldness was not significantly correlated with the individual propensity to discover, so a more exploratory individual is not necessarily willing to take risks and consume novel foods. The results suggested that boldness and discovery are ecologically important, but further studies are needed to understand population-level personalities and how and why natural selection can promote personality development in certain populations. All of these behavioural ecological studies suggest that the nutritional speciality of florivores has an evolutionary origin (Song et al. 2015).

Orthopterans as members of pollinating communities

Orthopterans are not individual pollinators, they are members of pollinating communities, in which each species has different contribution to successful pollination. Philipp et al. (2006) investigated a small and unique plant-pollinator network on the Galapagos Islands. Pollination visits of plants and pollen grains on insects were parallelly recorded. The dominant pollinator was the Galapagos carpenter bee (*Xylocopa darwini* (Cockerell, 1926)), but specimens of a fligthless locust (*Halmenus cuspidatus* Snodgrass, 1902) carriing pollen of five plant species were also detected. The pollination network showed an asymmetric pattern since some species had much more interactions, than many others. This pattern assumes a robust community, which may be quite sensitive to factors threaten the dominant species. The plant–pollinator interactions are crucial for survival of the species belonging to the community, thus the knowledge of the interactions is essential for their conservation and management.

Subhakar and Sreedevi (2015) investigated the pollinator insect assemblages considering their species richness on two pumpkin species in Tirupati region, southern Andhra Pradesh (India). On different pumpkin species, 10 and 11 pollinator species were registered including six butterflies (Lepidoptera) and one–one Hymenoptera, Coleoptera, Orthoptera and Dictyoptera species. Regarding the frequency of flower visits, lepidopterans were dominant (70.07% and 76.68%), followed by orthopterans (8.60 and 7.92%), while the other taxa had a marginal role.

Pedersen et al. (2018) studied *Epipactis flava* Seidenf. orchid in northwest Thailand and found that its flowers were visited by several insect species, and most of them served as pollinators. The most common pollen carrier was a cricket (*Homoeoxipha lycoides* Walker. 1869), followed by bees of the *Tetragonula testaceitarsis*/*hirashimai* complex, different species of Syrphinae subfamily, *Polybioides gracilis* Vecht, 1966 (Hymenoptera) and sweat bees of Halictinae subfamily.

Suetsugu (2019) investigated the parasitic plant *Mitrastemon yamamotoi* Makino, which is fully embedded in the tissue of the host, except in the reproductive stage, when it emerged from the host tissue. Though its extreme appearance drew the attention of botanists, very little is known about its reproductive system till now. *M. yamamotoi* were studied in southern Japan to determine self-compatibility, pollen production, and the role of diurnal and nocturnal flower visitors in its successful pollination. The plant is mainly pollinated by social wasps, but less known pollinators such as crickets and cockroaches also seem to be important, based on the frequency of visits and pollen load. The unusual composition of the pollinator assemblage of *M. yamamotoi* may be formed by several factors, including extremely modified flowers located close to the soil surface, dark environment, phenology with winter flowering period, and the geographical location of the study site (i.e. the northern boundary of the species range). Since *M. yamamotoi* is widespread in the subtropical and tropical forests of Asia, further studies are needed to reveal the different pollinator assemblages living in different parts of its range.

Preliminary data on temperate zone species

Flower-visiting habit of temperate zone orthopterans is mainly unknown, only some sporadic data can be found on it, for example Harz (1957) and Marini et al. (2009) reported that *Leptophyes albovittata* (Kollar, 1833) often feed on flowers of pungent or aromatic plants as mint (*Mentha* spp.), sage (*Salvia* spp.), nettle (*Urtica* spp.) and dead-nettle (*Lamium* spp.).

Studies with different volatiles including components of flower scents is a new and prosperous topic in chemical ecology and even plant protection zoology. These allelochemicals are widely used in monitoring (volatile traps) and protection (e.g. mass trapping, lure-and-kill methods, etc.) against different pest species (Tóth et al. 2019; Vuts et al. 2021; Nagy et al. 2022). Studies carried out to develop new volatile baits provide interesting and novel data on food source preferences of temperate zone orthopterans. Traps baited with different volatiles worked in Velyka Dobron' (West Ukraine: Transcarpathia) attracted a large number of seven Tettigonidae species, and five of them showed significant preferences to the tested volatiles: *Ruspolia nitidula* (Scopoli, 1786), *Phaneroptera falcata* (Poda, 1761), *Leptophyes albovittata* (Kollar, 1833), *Conocephalus discolor* (Thunberg, 1815) and *Meconema thallasinum* (De Geer, 1773). Since *P. falcata* and *L. albovittata* were attracted mainly to compounds included also in different flowers, such as *Cirsium, Eupatorium*, *Achilea*, *Helianthus* and *Senecio* species, thus it may refer to the host plant preference and flower-visiting habit of these species (Nagy et al. 2023). The results are supported by former results on flower-visiting and pollination of tropical *Phaneroptera brevis* (Tan et al. 2017b, 2019, 2018a; Tan and Tan 2017, b). The detailed results of the study, which draw attention to the unexpected importance of orthopterans as pollinators also in the temperate zone, will be published later somewhere else.

Summary and conclusions

Insects and plants represent the majority of the Earth's biodiversity. Interactions between plants and insects are complex, interesting, important and crucial parts of the ecosystems (Novotny et al. 2006; Lewinsohn and Roslin 2008; Novotny and Miller 2014). Researches on these interactions play an essential role (i) in the understanding ecology and coevolution (e.g. Crepet 1984; Grimaldi 1999; Novotny et al. 2006; Novotny and Miller 2014); (ii) in resource management (e.g. Lundberg and Moberg 2003; Cardel and Koptur 2010; Hudewenz et al. 2012) and also (iii) in conservation biology (e.g. Kearns et al. 1998; Bale et al. 2002; Tscharntke and Brandl 2004).

The study of pollinating orthopterans and the common pollinator communities, in general, shows a significant shortage, despite the efforts in the last decades (Ollerton 2011, 2021; Wardhaugh 2015; Ollerton et al. 2017; Kovács-Hostyánszki et al. 2019). Since former studies have mainly focused on the coevolution of a given pair of species (plant-Orthoptera), thus in general their role in pollination is still unknown (Micheneau et al. 2010; Lord et al. 2013; Suetsugu and Tanaka 2014). Beyond that, these studies were carried out mainly in tropical and subtropical zones, especially in the Indomalayan region (Tan et al. a, b, c; Tan and Tan 2018a, b, 2019).

The only exception is an indirect preliminary study, carried out with volatile traps of insect pests in West Ukraine (Transcarpathia) (unpublished data of Nagy A and Szanyi Sz), which proved significant attractivity of compounds of flower scents to temperate zone *Phaneroptera* and *Leptophyes* species. Although the species richness of flower-visiting orthopterans is probably lower than other widespread and well-known pollinator taxa (e.g. bees, lepidopterans and dipterans), their wide distribution and relatively high abundance may make them an important member of flower-visiting- and even pollinator assemblages.

Considering the numerous gaps in our knowledge, next priorities can be designated for further studies. First, the data on the food source preference of orthopterans should be reviewed and targeted studies should be made on food source preferences of the most abundant species of different habitats, including agricultural land. In the case of species that show clear preferences for flowering plants, and directly the generative parts, detailed investigations are needed to reveal the nature of their relation, considering chemical ecology aspects and physiology of both plant and orthoptera species.

Beyond the given plant–orthoptera interactions, investigations of the whole community may serve as a basis for the evaluation of the role and real importance of different taxa in forming and maintaining local ecosystems and in directing different evolutionary processes.

In the case of Central Europe, regarding published data and our preliminary results (Nagy et al. 2023), study on flower-visiting of Tettigonoidea and Grylloidea species, especially species belonging to genera of Phaneroptera, Leptophyes, Conocephalus, Meconema, Poecilimon and Isophya can be suggested.

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Declarations

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