

— Review —

PLANT-POLLINATOR INTERACTIONS IN EAST ASIA: A REVIEW

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Abstract—Pollination studies in East Asia have been developing rapidly in recent decades. East Asia may provide important information on many aspects of plant-pollinator interactions because of the rich fauna and flora and highly heterogeneous environments that occur there. In this review, plant-pollinator interactions in East Asia were summarized. Bumblebees are important pollinators of many plant species in East Asia, as well as in Europe and North America. Native honeybees may also have important roles in pollination in East Asia. Bird pollination and hawkmoth pollination may be less common in East Asia than in North America. Geographic variation in pollination interactions is expected because several types of pollinators are rare or absent in some habitats or geographic regions. For example, specialized nectar-feeding vertebrates like sunbirds and pteropodid bats are absent from most of East Asia except for some areas in its southern part. Opportunistic nectar-feeding vertebrates may have important roles in pollination where specialized nectar-feeding vertebrates are absent. Human impacts on plant-pollinator interactions are understudied in this region. However, climate change, habitat degradation, and invasive species may have negative impacts on plant-pollinator interactions and thus plant reproductive success there. The information available on the plant-pollinator interactions in East Asia is still limited because many plant and pollinator taxa and many types of habitats are understudied.

Keywords: plant-animal interaction, flower visitor, conservation, invasive species, plant reproduction, island

INTRODUCTION

Animal pollinators play significant roles in the sexual reproduction of many flowering plants (Ollerton et al. 2011; Ratto et al. 2018). The ecological and evolutionary consequences of plant-pollinator interactions are geographically variable (Hiraiwa & Ushimaru 2017; Johnson et al. 2017; Ollerton 2017; Zanata et al. 2017). However, the worldwide variation in plant-pollinator interactions is still poorly explored (Ollerton 2012). For example, some global-level studies of plant-pollinator interactions and plant reproductive ecology included no or very few East Asian examples due to the lack of available data (Ollerton et al. 2009; Ollerton 2012; Schleuning et al. 2012; Rech et al. 2016; Johnson et al. 2017; Zanata et al. 2017). Additionally, pollinators like hawkmoths and nectar-feeding birds have been poorly studied in East Asia (Johnson et al. 2017; Ren et al. 2018; Liu & Sun 2019).

Geographically, East Asia comprises China, the Korean peninsula, the Japanese archipelago, and Taiwan (Prescott 2015). The northern part of the region (central and northern China, the Korean Peninsula, and the main islands of Japan) is Palearctic, the southern part of the region (southern China, Taiwan, and the Ryukyu Islands) is Oriental, and the Bonin Islands are part of the northern limits of Oceania (Udvardy

1975; Corlett 2004). For several reasons, East Asia could be an important temperate region of the Northern Hemisphere for use in comparative studies with North America and Europe, wherein the field of pollination biology is better-developed. First, East Asia has remarkably rich and highly endemic flora and fauna (Zhu 2016; Tojo et al. 2017; Lu et al. 2018; Tang et al. 2018). For example, more than 30000 species of vascular plants have been recorded in China, and more than half of these species are endemic (Blackmore et al. 2015). East Asia acted as a refugium for many plant taxa because it has historically been covered by glaciers less than North America and Europe (Tang et al. 2018). Second, the environment of East Asia is highly heterogeneous. For example, the Qinghai-Tibet Plateau is the largest and highest plateau in the world, and the species richness of both plants and pollinators on the plateau and in the surrounding region is very high (Williams et al. 2009; Sun et al. 2014). East Asia is physiographically more heterogeneous than eastern North America (Qian & Ricklefs 2000). The complex combinations of different geographic, climatic, and ecological factors that occur in East Asia may be associated with the high diversification of plants and animals there (Qian & Ricklefs 2000; Tojo et al. 2017). The heterogeneous environment in East Asia provide opportunities to study how plant-pollinator interactions differ across environmental gradients and among habitats. For example, islands in East Asia like Hainan Island, the Japanese archipelago, and Taiwan are good models to study how plant-pollinator interactions and plant reproductive characteristics can differ between islands and the mainland (Inoue 1993; Ling et al. 2017). Third, some plant

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genera have disjunctive distributions in East Asia and North America. These disjunctively distributed genera have more species in East Asia than in North America, and this component of the East Asian temperate flora is thus a good model system to understand the diversification of plants in temperate regions (Qian & Ricklefs 2000). Therefore, such genera provide opportunities to study how plant-pollinator interactions and the evolution of pollination systems differ among continents (Ren et al. 2019).

The study of plant-pollinator interactions and plant reproductive ecology in East Asia has been developing rapidly in recent decades (Barrett 2015; Ren et al. 2018). Ren et al. (2018) summarized the pollination research done so far in China, and suggested future directions it could take. However, a comprehensive review focused on the characteristics of plant-pollinator interactions across the entire region of East Asia has not yet been published. Some reviews have been published that were concerned with specific areas of East Asia, including the Oriental Region in East Asia (Corlett 2004) and the Qinghai–Tibet Plateau (Sun et al. 2014). Some reviews of the pollination systems of East Asian Orchidaceae and Chinese Gesneriaceae were also previously published (Van Der Cingel 2001; Tang et al. 2014; Ling et al. 2017).

The present review aims to provide a general overview of the plant-pollinator interactions involving wild plants in East Asia. This review specifically highlights the diversity of pollinators and the plants with which they interact in this region. Although this review focuses on biotic pollination, the occurrence of mixed pollination systems involving pollination by both animals and the wind, called ambophily, is also noted. Additionally, the potential impacts of human activities on the plant-pollinator interactions in East Asia are discussed. Finally, I discuss future prospects for research on plant-pollinator interactions in East Asia.

This review was not a formal systematic review or meta-analysis. Thus, the literature survey conducted herein was not very systematic. I selected representative papers published on East Asian pollination from 1956 to 2019. This time frame largely covered the development of research on plant-pollinator interactions in East Asia (Tanaka 1996; Ren et al. 2018). Published studies were located using Google Scholar searches for keywords representing the regions (e.g., China), plant taxa (e.g., *Rhododendron*), and pollinator groups (e.g., hawkmoth) in East Asia. I also located additional studies by checking the references lists of the published East Asian pollination studies obtained. The studies citing the East Asian pollination studies obtained were also examined. Additionally, I located local publications that are not easily accessible. Studies focused on individual plant species were mostly referred to so that the pollination systems of particular plant taxa could be described. Some community-level studies of plant-pollinator interactions and books on floral ecology suggested the existence of many specialized pollination systems (e.g., Kato 2000; Corlett 2001; Tanaka 2009). However, these studies were generally not cited herein to describe the pollination systems of particular plant taxa because detailed studies are needed to predict the most effective pollinators of particular flowers (King et al. 2013; Funamoto & Ohashi 2017). The community-level pollination

studies examined were thus mostly cited to describe trends in the flower-visiting habits of particular animal taxa and plant-pollinator interactions in specific habitats.

I searched within various community-level studies to evaluate the relative abundances of different types of pollinators in various habitat types (Fig. 2). Studies providing the number of visits by different types of pollinators were selected. The number of visits by the different types of pollinators were then obtained from the published literature. Data were extracted from the tables, figures, and supporting information in published studies. When a study encompassed multiple years and sites, its data were pooled across these to find a value for each study. I categorized pollinators into 9 functional groups: Bee, Wasp/Sawfly, Diptera, Syrphidae, Non-syrphid Diptera, Coleoptera, Lepidoptera, Hemiptera, and Others. The Others group included various groups of pollinators, such as Orthoptera, Blattodea, spiders, birds, and ants. These categories generally followed those used in other pollination studies (Fenster et al. 2004; Nikkeshi et al. 2015; Zhang & He 2017). However, some functional groups defined in these studies were combined or divided herein because all functional groups were not always distinguished in the selected community-level studies. For example, Diptera was used in a study by Inoue & Endo (2006b), wherein Syrphidae and Non-syrphid Diptera were not distinguished. Wasp and sawflies were lumped together herein because non-bee hymenopterans were combined in a study by Zhao et al. (2016). Although species of Hemiptera are not usually considered pollinators (Wardhaugh 2015), Hemiptera was treated as an independent category herein because hemipterans are frequently observed on flowers in many communities.

AMBOPHILY

Pollination mediated by both wind and insects is called ambophily, and has been reported in the Gnetaceae (e.g., *Gnetum* (Gong et al. 2016)), Araceae (e.g., *Lysichiton* (Tanaka 2004)), Euphorbiaceae (e.g., *Mallotus* (Yamasaki & Sakai 2013)), Ranunculaceae (e.g., *Aconitum* (Duan et al. 2009; L.-L. Wang et al. 2017)), and Salicaceae (e.g., *Salix* (Tamura & Kudo 2000)). Ambophilous flowers may be more common than previously expected in subtropical and alpine regions because ambophily can provide reproductive assurance when pollinator activity is limited by the harsh climate (Sun et al. 2014; Gong et al. 2016).

INSECTS

Generalist pollination

Many plants are visited by multiple types of pollinators (Fig. 1 A; Kato et al. 1993; Kato & Miura 1996; Kato 2000). The generalist species in East Asia include those in the genera *Corylopsis* (Hamamelidaceae) (Wong Sato & Kato 2017), *Ilex* (Aquifoliaceae) (Matsuhisa & Ushimaru 2015), *Psychotria* (Rubiaceae) (Watanabe et al. 2014), *Ranunculus* (Ranunculaceae) (Tian & Ren 2019), and *Rhus* (Anacardiaceae) (Matsuyama et al. 2009). These species generally have open-shaped flowers that make their nectar accessible to multiple types of flower visitors. Generalist pollination systems may be favored in harsh habits like those

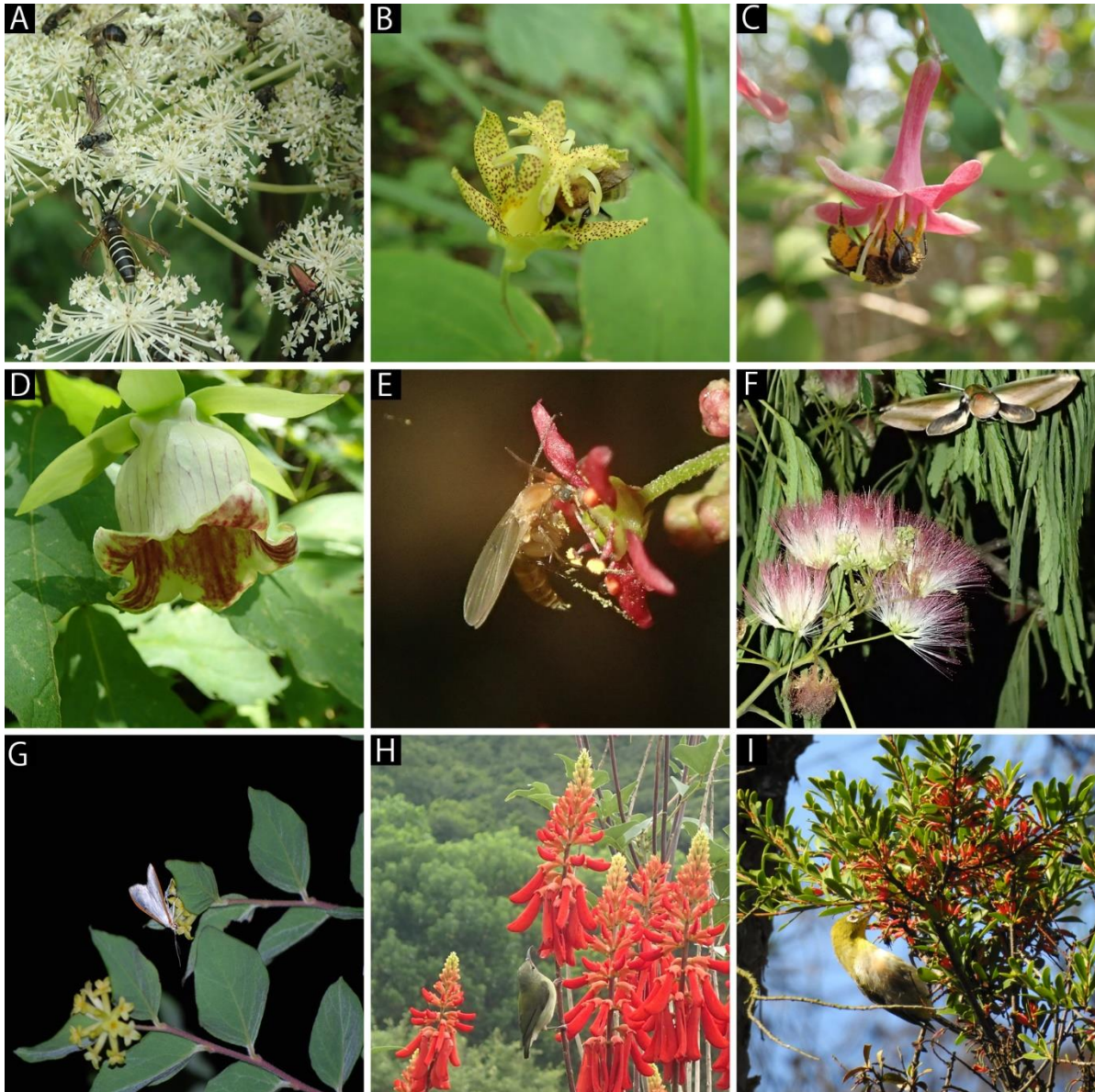


FIGURE 1. Representatives of flowers and pollinators in East Asia. (A) *Angelica pubescens* attracts a diverse assemblage of visitors, including hornets, sawflies, flies, and beetles. (B) A bumblebee, *Bombus honshuensis honshuensis*, visiting *Tricyrtis latifolia*. (C) *Andrena loniceræ* visiting *Lonicera gracilipes*. (D) A wasp-pollinated flower, *Codonopsis lanceolata*. (E) A fungus gnat visiting *Micranthes fusca*. (F) A hawkmoth, *Theretra* sp., approaching *Albizia julibrissin*. (G) A settling moth, *Palpita nigropunctalis*, visiting *Diplomorpha sikokiana*. (H) A fork-tailed sunbird, *Aethopyga christinae*, visiting a non-native South African tree, *Erythrina humeana*. (I) A Japanese white-eye, *Zosterops japonicus*, visiting *Taxillus kaempferi*. All photographs except (H) were taken in Japan, in natural habitats, while (H) was taken in a non-natural habitat, Fairy Lake Botanical Garden, in southern China. (A)–(H) were taken by Daichi Funamoto. (I) was modified from Sugiura (2018).

in alpine regions, where pollinators are rare or unpredictable (Peng et al. 2012).

Eusocial bees

The eusocial bees recorded from East Asia include bumblebees (*Bombus*), honeybees (*Apis*), and stingless bees (*Trigona*) (Michener 2007; Tadauchi et al. 2014). Bumblebees are distributed over most of East Asia (Michener 2007; Williams et al. 2009, 2010; Tadauchi et al. 2014), but they are absent on islands like the Izu Islands (except for Oshima Island), Bonin Islands, Ryukyu Islands (except for Yakushima Island), and the adjacent islands of Taiwan (Starr 1992; Inoue 1993; Tadauchi et al. 2014). Almost half of the world's bumblebee species are found in China (Williams et al.

2009, 2017). The edge of the eastern Tibetan Plateau is one of the greatest hotspots of bumblebee diversity in the world, where 56 species of bumblebees have been recorded (Williams et al. 2009). Native honeybees, such as *Apis cerana* and *Apis florea*, and managed honeybees (*Apis mellifera*) are distributed in the temperate and subtropical regions (Hepburn et al. 2005; Michener 2007; Tadauchi et al. 2014). Several species of native honeybees co-occur in southern China (Cui & Corlett 2016). Native honeybees are absent from the Bonin Islands and most of the Ryukyu Islands (Kato et al. 1999; Kato 2000; Tadauchi et al. 2014). Stingless bees have been recorded in southern China and Taiwan (Sakagami & Yamane 1984; Michener 2007).

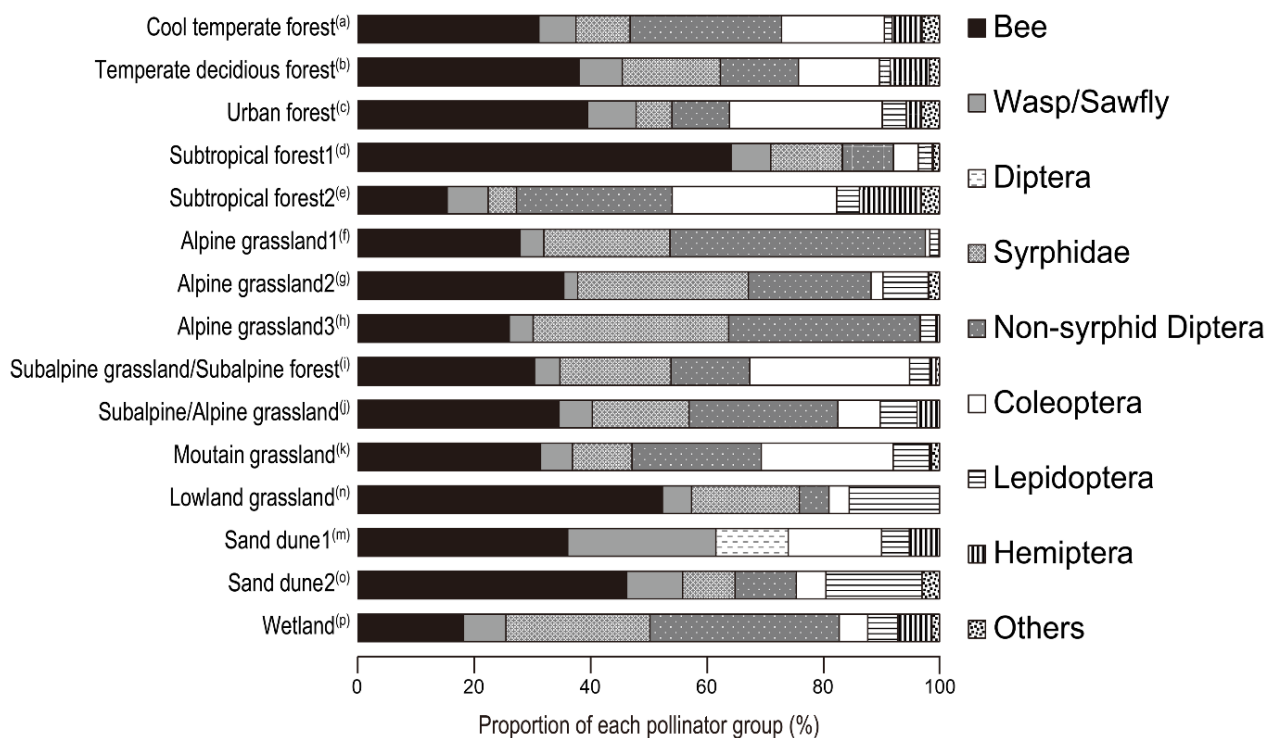


FIGURE 2. Relative abundance of different types flower visitors observed in various habitat types in East Asia. The study sites and references are as follows: (a) Ashu (Japan), Kato et al. (1990); (b) Kibune (Japan), Inoue et al. (1990); (c) Kyoto (Japan), Kakutani et al. (1990); (d) Heishiding Nature Reserve (China), Zhang & He (2017); (e) Amami Island (Japan), Kato (2000); (f) Mt. Tateyama (Japan), Ishii et al. (2019); (g) Hengduan Mountains (China), Fang & Huang (2012); (h) Taisetsu Mountains (Japan), Mizunaga & Kudo (2017); (i) Mt. Kushigata (Japan), Kato et al. (1993); (j) Mt. Yulong (China), Zhao et al. (2016); (k) Mt. Yufu (Japan), Yamazaki & Kato 2003; (l) Nishitani (Japan), Nikkeshi et al. (2015); (m) Hakoishi (Japan), Inoue & Endo (2006b); (n) Honshu and Izu Islands (Japan), Hiraiwa & Ushimaru (2017); (o) Nakaikemi marsh (Japan), Kato & Miura (1996). Notes: Syrphidae and Non-syrphid Diptera are not distinguished in Sand dune I, Hemiptera may be included in the Others category for Alpine grassland I, and ants may be included in the Wasp/Sawfly category in data for the Subalpine/Alpine grassland.

2003; Fang & Huang 2012; Mizunaga & Kudo 2017; Egawa & Ichino 2019). Bumblebees play an important role in pollination, especially in alpine habitats (Yumoto 1986; Mizunaga & Kudo 2017). Habitat and flower preferences differ among bumblebee species. For example, the short-tongued species *Bombus ardens* prefers shallow tree flowers and appears in forests, whereas the long-tongued species *Bombus diversus* prefers deep-tubed flowers and appears on both open-land habitats and in forests (Ushimaru et al. 2008). Species in the long-tongued subgenus *Megabombus* are more specialized foragers than short-tongued bumblebee species (JX. Huang et al. 2015). Bumblebees are important pollinators of numerous flowers (Suzuki et al. 2007), such as *Aconitum* (Ranunculaceae) (Liao et al. 2009; Lu et al. 2015), *Aquilegia* (Ranunculaceae) (Tang et al. 2007), *Clematis* (Ranunculaceae) (Dohzono & Suzuki 2002; Jiang et al. 2010), *Cirsium* (Asteraceae) (Ohashi & Yahara 1998), *Hosta* (Asparagaceae) (Suzuki et al. 2002), *Oreocharis* (Gesneriaceae) (Guo et al. 2013), *Pedicularis* (Orobanchaceae) (Macior 1988; Macior & Tang 1997; Wang & Li 2005; Huang & Shi 2013), *Rhododendron* (Ericaceae) (Ono et al. 2008; Kudo et al. 2011; Li et al. 2018), *Salvia* (Lamiaceae) (Ohashi 2002; YB. Huang et al. 2014, 2015; Z-H. Huang et al. 2015), *Tricyrtis* (Liliaceae) (Fig. 1B; Takahashi, 1987, 1993, 1994), and *Weigela* (Caprifoliaceae) (Ida & Kudo 2003; Inoue et al. 2007). Many

orchids, including *Calanthe* (Sakata et al. 2014), *Changnienia* (Sun et al. 2006), *Cremastra* (Sugiura 1996a), and *Cypripedium* (Li et al. 2006; Suetsugu & Fukushima 2014a; Sugiura & Takahashi 2015), are pollinated by bumblebees by nectar reward or various mimicry mechanism. Bumblebees can act as pollinators of flowers like heterotrophic plants and orchids in the dark understorey habitats (Tanaka 1978; Matsumura et al. 1997; Sugiura & Yamaguchi 1997). The drones of *Bombus ardens* act as important pollinators of *Meliosma tenuis* (Sabiaceae) (Wong Sato & Kato 2018).

Honeybees are presumed to be one of the most important pollinators in East Asia (Ren et al., 2018). However, the roles of honeybees as pollinators in natural ecosystems is still poorly known because majority of researches on Asian honeybees have been conducted in agricultural ecosystems (Cui & Corlett 2016). Honeybees tend to visit shallow flowers with exposed nectaries (Kato et al. 1990; Nagamitsu & Inoue 1999; Osada et al. 2003; Fang et al. 2012). The pollen resources used by *Apis cerana* and *A. mellifera* in a primary beech forest were generally similar (Nagamitsu & Inoue 1999). The honeybees collect pollen from flowers with exposed nectaries such as *Acer* (Sapindaceae), Araliaceae, Celastraceae, *Hovenia* (Rhamnaceae), *Hydrangea* (Hydrangeaceae), *Mallotus* (Euphorbiaceae), and *Zanthoxylum* (Rutaceae), as well as some wind-pollinated plants like *Carpinus* (Betulaceae) and *Quercus* (Fagaceae) (Nagamitsu & Inoue 1999). *Apis cerana*

tends to visit woody flowers with dioecious or monoecious greenish flowers with exposed nectaries at the canopy layer (Nagamitsu & Inoue 1999). In a mangrove area of Hainan Island, *Mimosa pudica* (Fabaceae) and *Sonneratia* (Lythraceae) species were reported to be the main nectar and pollen sources for *A. cerana* in October and November, respectively (Yao et al. 2006). *Apis cerana* can also pollinate winter-flowering plants (Tsuji & Kato 2010; Fang et al. 2012). Honeybees act as primary pollinators of flowers of Apocynaceae (e.g., *Cynanchum* (D-K. Wang et al. 2009)) and Orchidaceae (e.g., *Bulbophyllum* (Chen & Gao 2011) and *Cymbidium* (Sasaki et al. 1991; Yu et al. 2008; Tsuji & Kato 2010; Suetsugu 2014; Matsuda & Sugiura 2019)).

Stingless bees act as important pollinators of many plant species in Oriental Region (Corlett 2004). However, in East Asia, stingless bees are less frequently reported as flower visitors compared to the honeybees and bumblebees. They are reported as nectar and pollen robbers of several flowers (Zhang et al. 2005; Luo et al. 2008; Deng et al. 2015).

Solitary bees

Species in the long-tongued genera of Apidae, including *Anthophora*, *Amegilla*, *Eucera*, and *Tetralonia*, visit many flowers with long floral tubes (Miyamoto 1962; Kakutani et al. 1990; Kato 2000). In temperate regions, *Anthophora*, *Eucera*, and *Tetralonia* pollinate long-tubed flowers (Suzuki 1984; Luo & Chen 1999; Ma et al. 2014; Suetsugu & Fukushima 2014b; Sakata & Nakahama 2018). In warm temperate and subtropical forests, *Amegilla* species act as pollinators of understory and epiphytic flowers with concealed nectaries, such as members of the Gesneriaceae (e.g., *Lysionotus* (Yumoto 1987)), Liliaceae (e.g., *Tricyrtis* (Takahashi 1987)), Marantaceae (e.g., *Phrynium* (Duan & Li 2008)), Orchidaceae (e.g., *Doritis* (Jin et al. 2012)), and Zingiberaceae (e.g., *Alpinia* and *Zingiber* (Kato 2000; Fan et al. 2015)).

Large carpenter bees (*Xylocopa*) prefer to visit the flowers of trees and shrubs, especially those belonging to the Fabaceae (Miyamoto 1961; Matsuura et al. 1974; Kato 2000). Carpenter bees act as major pollinators of relatively large-sized flowers, including those of Orchidaceae (e.g., *Calanthe* (Sugiura 2013)), Fabaceae (e.g., *Caesalpinia* (Li et al. 2004) and *Wisteria* (Miyamoto 1961; Kishi 2015)), Melastomataceae (e.g., *Melastoma* (Luo et al. 2008, 2009)), Iridaceae (e.g., *Iris* (Liu et al. 2011)), Zingiberaceae (e.g., *Alpinia* (Li et al. 2002)), and Capparaceae (e.g., *Capparis* (Zhang & Tan 2009)). Nectar robbing by *Xylocopa* bees is frequently observed on various plant species (Miyamoto 1961; Kato 1992; Naiki & Kato 1999; Sugiura 2008; He et al. 2018).

Megachilid bees visit flowers with short and medium-length floral tubes (Hiraiwa & Ushimaru 2017). These bees prefer to visit flowers of Fabaceae species (Matsuura et al. 1974; Kato et al. 1990). *Megachile* (*Callomegachile*) spp. collect floral resin from Chinese *Dalechampia* (Euphorbiaceae) to construct their nests (Armbruster et al. 2011). Flowers of one orchid species, *Sarcanthus scolopendrifolius*, are exclusively visited by *Megachile yasumatsui* (Son et al. 2017). Some of the megachilid bees are

specialized for particular species of flowers. *Lithurgus* is specialized to visit *Hibiscus* (Malvaceae) and *Ipomoea* (Convolvulaceae) (Kato 1992; Fukugawa & Denda 2018). *Megachile kobensis* is oligolectic to *Vitex rotundifolia* (Lamiaceae) (Maeta et al. 2004).

Ctenoplectra (Apidae) and *Macropis* (Melittidae) are specialized to visit oil-producing flowers. For example, *Ctenoplectra* visits flowers of cucurbit species like those in the genera *Momordica* and *Thladiantha* (Li 1997; Sung et al. 2009), and *Macropis dimidiata* visits those of *Lysimachia vulgaris* var. *davurica* (Myrsinaceae) (Yasumatsu & Hirashima 1956).

Bees of the Andrenidae, Colletidae, and Halictidae visit flowers with short-tubed and exposed nectaries (Osada et al. 2003; Matsuyama et al. 2009; Yamasaki et al. 2013; Tian & Ren 2019). Pollen-collecting small bees sometimes act as important pollinators of long-tubed flowers that lack long-tongued pollinators, suggesting their compensatory role as pollinators of such flowers (Zhang et al. 2011a; Guo & Wang 2014; Yamaji & Ohsawa 2015; Zhu et al. 2017). Small bees act as the main pollinators of some plants, including species of Liliaceae (e.g., *Fritillaria* (Naruhashi et al. 2006)), Berberidaceae (e.g., *Epimedium* (Suzuki 1984)), Orchidaceae (e.g., *Cypripedium* and *Gastrodia* (Bänziger et al. 2005, 2008; Li et al. 2008; Sugiura 2017)), and Theaceae (e.g., *Camellia* (Deng et al. 2010)). Some flowers provide shelter for male small bees as a reward (Pang et al. 2012; Zhu et al. 2013). Andrenid bees are often specialized for foraging on particular species of flowers (Miyamoto 1962; Tadauchi & Hirashima 1988; Shimizu et al. 2014). For example, two species of andrenid bees belonging to the subgenus *Stenomelissa* have much longer proboscises than those of other andrenid species, and each of them are specialized to visit *Lonicera gracilipes* or *Weigela hortensis* (both Caprifoliaceae), respectively (Fig. 1C; Tadauchi & Hirashima 1988; Hayashibara et al. 2011; Shimizu et al. 2014).

Wasps and sawflies

Wasps and sawflies visit many flowers with exposed nectaries (Fig. 1A; Kato, 2000; Corlett, 2001; Yamazaki & Kato, 2003; Inoue & Endo, 2006a; Ueno, 2015; Sugawara et al., 2016b). Specialized pollination systems including wasps are rarely recorded, but hornets like *Vespa*, *Vespula*, and *Dolichovespula* act as important pollinators of plants of Campanulaceae (e.g., *Codonopsis* (Fig. 1D; Yamazaki & Kato, 2003; Ren et al., 2014b)), Solanaceae (e.g., *Anisodus* (Y. Wang et al. 2009; Wang et al. 2010)), and Orchidaceae (e.g., *Coelogyne* and *Dendrobium* (Brodmann et al. 2009; Cheng et al. 2009)). Eumenid and scoliid wasps pollinate *Cynanchum wilfordii* (Apocynaceae) (Yamashiro et al. 2008). Scoliid wasps are one of the major groups of flower visitors in sand dune ecosystems (Fig. 2; Inoue & Endo, 2006a, 2006b). Vespid wasps may be important pollinators in cold seasons because they can visit flowers that bloom in late autumn and early winter, such as *Camellia sasanqua*, *Eriobotrya japonica* (Rosaceae), *Fatsia japonica* (Araliaceae), and *Mitrastemon yamamotoi* (Mitrastemonaceae) (Yumoto 1987; Wang et al. 2011; Ueno 2015; Suetsugu 2019).

East Asia includes the northern limit of the distribution of *Ficus* (Moraceae) (Azuma *et al.*, 2010; Y. Chen *et al.*, 2012). Each fig species is usually pollinated by a specific species of fig wasp (Yokoyama & Iwatsuki 1998; C. Chen *et al.* 2009; Azuma *et al.* 2010; Yang *et al.* 2015). However, some species of figs have more than one pollinator species (Azuma *et al.*, 2010; Y. Chen *et al.*, 2012; Yang *et al.*, 2015; Rodriguez *et al.*, 2017), and some fig species share the same pollinators (Yang *et al.* 2015; Wachi *et al.* 2016).

Sawflies can act as nectar robbers of long-tubed flowers (Zhu *et al.* 2017). *Nipponorhynchus* has a long proboscis and visits the flowers of *Chrysosplenium* (Saxifragaceae) (Smith & Naito 2015).

Ants

Ants have been considered to be ineffective pollinators, although they do sometimes act as pollinators (C-Q. Wang *et al.* 2008). For example, *Phyllanthus lepidocarpus* (Phyllanthaceae) is pollinated by ants (Kawakita & Kato 2009). Orchids like *Chenorchis*, *Epipactis*, and *Neottia* are primarily or partly pollinated by ants (Sugiura *et al.* 2006; C-Q. Wang *et al.* 2008; Liu *et al.* 2008). The weaver ant, *Oecophylla smaragdina*, may become involved in plant-pollinator interactions by consuming floral nectar and attacking flower visitors (Rodríguez-Gironés *et al.* 2013; González *et al.* 2015).

Large Diptera

Hoverflies can be pollinators of flowers with generalized morphologies (Jiang *et al.*, 2010; Song *et al.*, 2018; Wang *et al.*, 2018; Tian & Ren 2019). Hoverflies act as important pollinators in alpine communities and wetlands (Fig. 2; Yumoto, 1986; Kato & Miura, 1996; Mizunaga & Kudo, 2017). Specialized pollination by hoverflies is reported in orchids, such as *Epipactis* (Sugiura 1996b; Jin *et al.* 2014), *Paphiopedilum* (Shi *et al.* 2007, 2009), *Cypripedium* (Ren *et al.* 2011), and *Calanthe* (Ren *et al.* 2014a).

The carrion flies belonging to the Muscidae and Calliphoridae visit many flowers with generalized morphologies (Fig. 1A; Kato *et al.* 1993; Corlett 2001; Mizunaga & Kudo 2017). Other flies also visit flowers, including species of Anthomyiidae, Bibionidae, Empididae, and Tachinidae (Kato *et al.* 1993; Yamazaki & Kato 2003; Mizunaga & Kudo 2017). In alpine regions, the importance of flies as pollinators increases (Fig. 2; Duan *et al.* 2007; Ye *et al.*, 2011; Zhao *et al.*, 2016; Mizunaga & Kudo, 2017). Flowers that bloom in the cold season are frequently visited by carrion flies (Corlett 2001; Wang *et al.* 2011; Du *et al.* 2012; Tsuji & Ohgushi 2018). Carrion flies act as important pollinators of rewarding flowers of Apocynaceae (e.g., *Vincetoxicum* (Yamashiro *et al.* 2008)), Euphorbiaceae (e.g., *Antidesma* (Li & Zhang 2007)), Phyllanthaceae (e.g., *Bridelia* and *Cleistanthus* (Luo *et al.* 2007; Y. Li *et al.* 2014)), and Tiliaceae (e.g., *Craigia* (ZR. Gao *et al.* 2012)). Carrion flies are attracted by some flowers that emit unpleasant scent such as Araceae (e.g., *Amorphophallus* (Chen *et al.* 2015b) and *Symplocarpus* (Uemura *et al.* 1993; Hong & Sohn 2003)), Berberidaceae (e.g., *Dysosma* (Gong *et al.* 2015)), Liliaceae (e.g., *Fritillaria* (Yashima *et al.* 1982)), Solanaceae (e.g.,

Anisodus (Duan *et al.* 2007)), Stemonaceae (e.g., *Stemona* (Chen *et al.* 2015a; Chen *et al.* 2017)), and Orchidaceae (e.g., *Cypripedium* (Zheng *et al.* 2011; Li *et al.* 2012)).

Long-tongued bee flies visit many flowers (Tanaka 1985; Osada *et al.* 2003; Abe 2007; Sugiura 2012; Yamamoto *et al.* 2018). *Bombylius major* is the most frequent visitor to flowers of *Rhododendron reticulatum* and *Viola rostrata* var. *japonica*. (Tanaka 1985; Sugiura 2012).

Microdiptera

The nematoceran microdiptera, including gall midges (Cecidomyiidae) and fungus gnats (mainly Mycetophilidae and Sciaridae), act as important pollinators of small, inconspicuous rewarding flowers, like those of Apocynaceae, Celastraceae, Garryaceae, Hamamelidaceae, and Saxifragaceae species (Fig. 1E; Okuyama *et al.* 2004, 2008; Yamashiro *et al.*, 2008; Kunitake *et al.*, 2010; Okuyama, 2012; Mochizuki & Kawakita, 2018). One species of sciarid fly visits a Japanese mycoheterotrophic plant *Sciaphila nana* (Triuridaceae) (Nemoto *et al.* 2018). Plants of these species typically grow in moist habitats like forest floors and stream sides where fungus gnats are abundant, but other types of pollinators are scarce (Okuyama *et al.* 2008; Yamashiro *et al.* 2008; Mochizuki & Kawakita 2018). Brood-site pollination by fungus gnats was reported in an alpine greenhouse plant, *Rheum nobile* (Polygonaceae) (Song *et al.* 2014). Non-rewarding pollination systems by nematoceran microdiptera has been reported for several plant families, including Aristolochiaceae, Asparagaceae, and Araceae. Flowers of *Heterotropa* (Aristolochiaceae) and *Aspidistra* (Asparagaceae) apparently mimic mushrooms, and are pollinated by fungus gnats (Sugawara 1988; Suetsugu & Sueyoshi 2018). Fungus gnats are frequently trapped by *Arisaema* (Araceae) flowers (Sasakawa 1993, 1994; Nishizawa *et al.* 2005; Tanaka *et al.* 2013). Flowers of *Thismia* (Burmanniaceae) are visited by fungus gnats and phorid flies (Li & Bi 2013; Mar & Saunders 2015). Specialized brood-site pollination systems by gall midges are reported in Schisandraceae, members of a basal family of angiosperms (Luo *et al.* 2010, 2017, 2018; Fan *et al.* 2011). Pollinating gall midges of the genus *Resseliella* oviposit their eggs in flowers, and their larvae feed on the resin secreted from wounded floral tissues (Luo *et al.* 2017, 2018). One plant species' flowers are usually pollinated by one species of gall midge (Luo *et al.* 2018).

Brachyceran microdipterans pollinate many flowers. Flowers of *Arisaema serratum* trap both brachyceran and nematoceran microdipterans, including species of Sciaridae, Phoridae, and Mycetophilidae (Nishizawa *et al.* 2005). *Aristolochia debilis* (Aristolochiaceae) and *Ceropegia dolichophylla* (Apocynaceae) trap kleptoparasitic fly pollinators belonging to the Milichiidae and Chloropidae (Heiduk *et al.* 2015; Sugawara *et al.* 2016a). Species of Sepsidae, Agromyzidae, and Drosophilidae pollinate the flowers of the orchid *Bulbophyllum orientale* (Chen *et al.* 2014). Non-rewarding specialized pollination systems involving Drosophilidae have been reported among the Orchidaceae (Liu *et al.* 2010; Li *et al.* 2012; Suetsugu 2018). Brood-site pollination by Drosophilidae was reported in Araceae (Miyake & Yafuso 2003; Takenaka *et al.* 2006;

Bröderbauer et al. 2014). Flowers of a water lily, *Nuphar subintegerrima* (Nymphaeaceae), are visited by ephydrid flies that mate and oviposit in the flowers (Nagasaki 2007). Agromyzid flies visit the heliotropic flowers of *Adonis ramose* (Ranunculaceae) for heat and pollen (Kudo 1995).

Butterflies

Butterflies visit flowers with a variety of different morphologies and colors (Kato 2000; Corlett 2001). However, few studies have documented the specialized pollination of specific plants by butterflies in East Asia. Butterflies, especially swallowtail butterflies (Papilionidae), act as important pollinators of Combretaceae (e.g., *Quisqualis* (Yan et al. 2016)), Ericaceae (e.g., *Rhododendron* (Yokogawa & Hotta 1995; Tagane et al. 2008; Takahashi & Itino 2017; Song et al. 2019)), Lamiaceae (e.g., *Clerodendrum* (Suzuki et al. 1987; Sakamoto et al. 2012; Mizusawa et al. 2014)), Liliaceae (e.g., *Lilium* (Morinaga et al. 2009; Sun & Yao 2013; Nakajima et al. 2018)), Rubiaceae (e.g., *Mussaenda* (Naiki & Kato 1999; Naiki 2008; Luo et al. 2015)), Xanthorrhoeaceae (e.g., *Hemerocallis* (Hirota et al. 2012)), and Zingiberaceae (e.g., *Hedychium* (JY. Gao et al. 2012, 2014)). *Habenaria radiata* (Orchidaceae) was reported to be pollinated by species of Hesperiiidae (Suetsugu & Tanaka 2014a; Ikeuchi et al. 2015). Two species of transplanted orchids, *Calanthe argenteo-striata*s and *Ludisia discolor*, were reported to be pollinated by *Pieris rapae* in a botanical garden (H. Zhang et al. 2010). An ecotype of *Cimicifuga simplex* (Ranunculaceae) was reported to be pollinated by nymphalid butterflies (Pellmyr 1986).

Hawkmoths

Nocturnal hawkmoth pollination has been reported in several species of flowers with long tubes and reproductive organs (Miyake et al. 1998). Hawkmoth pollination has been reported in flowers of Amaryllidaceae (e.g., *Crinum* (Miyake et al. 1998)), Caprifoliaceae (e.g., *Lonicera* (Miyake & Yahara 1998; Miyake et al. 1998)), Fabaceae (e.g., *Albizia* (Fig. 1F; Miyake et al. 1998)), Lamiaceae (e.g., *Clerodendrum* (Miyake et al. 1998; Miyake & Inoue 2003; Mizusawa et al. 2014)), Liliaceae (e.g., *Lilium* (Morinaga et al. 2009; Yokota & Yahara 2012; Liu & Sun 2019; Nakajima et al. 2018)), Orchidaceae (e.g., *Habenaria* (Xiong et al. 2015; Zhang & Gao 2017; Tao et al. 2018)), *Platanthera* (Inoue 1983, 1985, 1986), and *Vanda* (Suetsugu et al. 2015)), Rubiaceae (e.g., *Guettarda* (Xu et al. 2018)), Xanthorrhoeaceae (e.g., *Hemerocallis* (Hirota et al. 2012)), and Zingiberaceae (e.g., *Hedychium* (Gao et al. 2014)). Some hawkmoth-pollinated flowers are also visited by butterflies and settling moths (Miyake et al. 1998; Morinaga et al. 2009; Yokota & Yahara 2012; Gao et al. 2014; Mizusawa et al. 2014; Nakajima et al. 2018; Tao et al. 2018).

Day-flying hawkmoths, such as species of *Macroglossum*, act as pollinators of some long-tubed flowers (Naiki & Kato 1999; Tian et al. 2004; Mizusawa et al. 2014). *Melampyrum koreanum* (Orobanchaceae) is specialized to be pollinated by diurnal hawkmoths (Jo et al. 2014).

Settling moths

Settling moths visit flowers with a wide variety of morphologies and colors (Ikenoue & Kanai 2010). Settling moth pollination is usually reported for flowers with narrow tubes (e.g., Okamoto et al. 2008). Settling moth pollination has been reported for flowers of species of Apocynaceae (e.g., *Hoya* (Mochizuki et al. 2017), *Marsdenia* (Sakagami et al. 2019), and *Vincetoxicum* (Yamashiro et al. 2008; Nakahama et al. 2013)), Campanulaceae (e.g., *Adenophora* (Liu & Huang 2013; Funamoto & Ohashi 2017; Funamoto 2019)), Caprifoliaceae (e.g., *Lonicera* (Xuan et al. 2015)), Lecythidaceae (e.g., *Barringtonia* (Tanaka 2004)), Orchidaceae (e.g., *Platanthera* (Inoue 1983; Suetsugu & Hayamizu 2014) and *Habenaria* (Xiong et al. 2019)), Thymelaeaceae (e.g., *Aquilaria* (Chen et al. 2016), *Diplomorpha* (Fig. 1G; Okamoto et al. 2008), and *Stellera* (Zhang et al. 2011b)), and Rubiaceae (e.g., *Uncaria* (Funamoto & Sugiura 2016)). Several species of pyralid and crambid moths visit flowers of *Balanophora* species, and these moths oviposit their eggs on the flowers, after which the larvae of the moths consume the floral tissues (Kawakita & Kato 2002). A gymnosperm climber, *Gnetum luofuense*, is visited by nectar-feeding noctuid moths (Corlett 2001).

Microlepidoptera

Micropterigid moths like *Micropterix* and *Paramartyria* visit flowers, but their role as pollinators is unknown (Hashimoto 2006). Obligate pollination systems involving seed-predating *Epicephala* moths and plants of Pyllanthaceae are highly elaborated (Kato et al. 2003). Such obligate pollination mutualisms have been reported in plants of the genera *Breynia*, *Glochidion*, and *Phyllanthus* from southern China, southern Japan, and Taiwan (Kawakita & Kato 2017). Another obligate interaction between gelechiid moths and Pyllanthaceae from southern China was reported by Luo et al. (2011). The larvae of gelechiid moths feed on the leaves of their host plants, and the adults consume the nectar and pollen of the plants (Luo et al. 2011).

Coleoptera

Species of beetles belonging to the Cerambycidae, Elateridae, Oedemeridae, and Scarabaeidae visit many flowers with generalized morphologies (Fig. 1A; Kuboki 1980; Kato et al. 1993; Kato 2000; Osada et al. 2003; Yang et al. 2017). Beetles can be effective pollinators of flowers. For example, flower chafers act as important pollinators of *Magnolia obovata* because they carry a higher proportion of outcrossed pollen than bumblebees do (Matsuki et al. 2008). Beetles may also act as pollinators when the activity of other types of pollinators is low. For example, *Pidonia* (Cerambycidae), a genus of diverse and abundant coleopteran flower visitors in Japanese temperate forests, can visit flowers in shady conditions (Kuboki & Shimamoto 1979; Kuboki 1980; Sakakibara et al. 1996). Staphylinid beetles were observed among the flower visitors of *Symplocarpus renifolius*, the flowers of which apparently mimic dung or carrion (Uemura et al. 1993).

Specialized beetle-pollinated flowers are often reported. A cycad, *Cycas revoluta*, is pollinated by nitidulid

beetles (Kono & Tobe 2007). Beetles act as important pollinators of some basal families of angiosperms, such as Magnoliaceae and Schisandraceae (Ishida 1996; Matsuki et al. 2008; B. Wang et al. 2017; Luo et al. 2018). Nitidulid and curculid beetles act as specialized pollinators of Annonaceae (Pang et al. 2013; Pang & Saunders 2015; Lau et al. 2017). Some orchids are pollinated by beetles. Oedemerid beetles pollinate the short-spurred species *Platanthera chorisiana* (Inoue 1981). Flower chafers act as pollinators of several orchids, including *Holcoglossum* and *Luisia* (Jin et al. 2005; Tetsu & Suetsugu 2015; Arakaki et al. 2016). On Okinawa Island, flowers of *Luisia teres* are exclusively pollinated by male flower chafers that appear to attempt copulation on the flower, suggesting sexual deception of the beetles by the orchid (Arakaki et al. 2016).

Thysanoptera

Thrips are major flower visitors of plants of Chloranthaceae (e.g., *Chloranthus* (Luo & Li 1999)), Dioscoreaceae (e.g., *Dioscorea* (Mizuki et al. 2005; M-M. Li et al. 2014)), Juglandaceae (e.g., *Platycarya* (Fukuhara & Tokumaru 2014)), and Liliaceae (e.g., *Ophiopogon* (He et al. 2000)). The flowers of these species are typically enclosed and provide shelter for the thrips (Luo & Li 1999; Mizuki et al. 2005; Fukuhara & Tokumaru 2014; M-M. Li et al. 2014). Thrips provide supplementary pollination to a hoverfly-pollinated orchid *Epipactis thunbergii*, which has granular pollinia (Suetsugu et al. 2018).

Other insects

Flowers are also visited by members of many orders of insects that are not usually considered as pollinators (Inoue et al. 1990; Kato et al. 1990; Kato 2000; Yamazaki & Kato 2003), some of which may in fact act as pollinators. Anthocorid and mirid hemipterans act as important pollinators of *Macaranga tanarius* (Euphorbiaceae) (Ishida et al. 2009). Stoneflies may act as pollinators of *Corylopsis gotoana* (Wong Sato & Kato 2017). A katydid species consumes the pollinia of an orchid, *Habenaria sagittifera* (Suetsugu & Tanaka 2014b). On subtropical islands like the Ryukyu Islands and Bonin Islands, flower-visiting behavior by Blattodea and Orthoptera has been frequently observed (Kawakita & Kato 2002; Abe 2006; Tsujimura et al. 2016; Tsuda et al. 2018; Suetsugu 2019).

OTHER INVERTEBRATES

Many non-insect invertebrates also visit flowers. Terrestrial crustaceans, including amphipods, isopods, crabs, and hermit crabs, visit flowers on the Ryukyu Islands and in Taiwan (Kato 1995; Schubart et al. 2003; Higashi et al. 2013). Flowers of *Aspidistra elatior* are visited by amphipods and isopods (Kato 1995; Suetsugu & Sueyoshi 2018), but the most effective pollinators of these flowers are considered to be fungus gnats (Suetsugu & Sueyoshi 2018). Numerous amphipods were collected by yellow pan traps in a subtropical rainforest (Kodama & Shimizu 2017), suggesting a potential role of amphipods as flower visitors. Spiders and harvestmen occasionally visit flowers and consume floral resources (Suetsugu et al. 2014; Watanabe et al. 2014). A land snail, *Acusta despecta despecta*, visits the flowers of *Alpinia*

zerumbet and consumes their pollen on the Ryukyu Islands (Kobayashi et al. 2009; Denda et al. 2018).

VERTEBRATES

Mammals and reptiles

Flying foxes visit many species of flowers on the Ryukyu Islands and Bonin Islands (Abe 2006; Izawa et al. 2007; Lee et al. 2009; Nakamoto et al. 2009; Suzuki & Suzuki 2015). However, few studies have documented the importance of bats as pollinators in East Asia. Flying foxes act as important pollinators of *Mucuna macrocarpa* (Fabaceae) on Okinawa Island because they are the only pollinators that can pollinate the explosively opening flowers of this species on the island (Toyama et al. 2012; Kobayashi et al. 2018a). Leschenault's rousette fruit bat, *Rousettus leschenaultii*, visits the flowers of *M. birdwoodiana* in Hong Kong, but explosive opening of these flowers by the bats was not confirmed there (Lau 2004). Long-tongued fruit bats of the species *Macroglossus sobrinus* act as pollinators of *Musa itinerans* in southern China (Liu et al. 2002).

Flower-visiting behavior by non-flying mammals, including rodents, primates, and Carnivora, has also been observed. Squirrels usually act as nectar robbers (Deng et al. 2004, 2015; Georgian et al. 2015), but act as pollinators of some stiff flowers, like those of *Mucuna* species (G. Chen et al. 2012; Kobayashi et al. 2017, 2018a). The orchid *Cymbidium serratum* is pollinated by mice (Y. Wang et al. 2008). Flowers of *Mucuna macrocarpa* interact with many types of non-flying mammals, including squirrels, macaques, martens, and civets (Kobayashi et al. 2015, 2017, 2018b). The interactions between *M. macrocarpa* and mammals are geographically variable (Kobayashi et al. 2018b, 2018c). At the northern limit of the distribution of *M. macrocarpa* in Kyushu, Japan, where flying foxes are absent, the Japanese marten and Japanese macaque act as the main pollinators of its flowers (Kobayashi et al. 2015). On Okinawa Island, flying foxes act as pollinators of this species' flowers (Toyama et al. 2012; Kobayashi et al. 2018a). In Taiwan, where flying foxes are also absent, squirrels act as pollinators of this species' flowers (Kobayashi et al. 2017, 2018a). The masked palm civet, *Paguma larvata*, acts as a pollinator of *M. birdwoodiana* in Hong Kong (Lau 2012; Kobayashi et al. 2019).

Interactions between reptiles and flowers have been observed on subtropical islands, including the Bonin Islands and Ryukyu Islands. Flower-visiting behavior by the mourning gecko, *Lepidodactylus lugubris*, was observed on the Bonin Islands and Ryukyu Islands (Abe 2006; Jono 2008; Kobayashi et al. 2010; Tsujimura et al. 2016). Individual males of an invasive green anole, *Anolis carolinensis*, visited flowers of *Schima mertensiana* for nectar and carried the pollen of the flowers on their heads on the Bonin Islands (Okochi et al. 2006).

Birds

Sunbirds (Nectariniidae) are the only specialized nectar-feeding birds distributed in East Asia (Fig. 1H; Krauss et al. 2017). Sunbirds act as pollinators of plants belonging to many families, such as Musaceae (e.g., *Musa* (Liu et al. 2002)), Orchidaceae (e.g., *Coelogyne* (Liu et al. 2013)), Theaceae

(e.g., *Camellia* (Qiu et al. 2015; Sun et al. 2017)), Ericaceae (e.g., *Rhododendron* (Huang et al. 2017; Song et al. 2019)), Hamamelidaceae (e.g., *Rhodoleia* (Gu et al. 2010)), and Malvaceae (e.g., *Firmiana* (Huang et al. 2018)).

Many non-specialized, opportunistic nectar-feeding birds also visit flowers and consume floral resources (Chen & Chou 1999; Yoshikawa & Isagi 2014). White-eyes (Zosteropidae), bulbuls (Pycnonotidae), and leafbirds (Chloropseidae) frequently visit flowers (Chen & Chou 1999; Yoshikawa & Isagi 2014; Funamoto & Sugiura 2017; Sun et al. 2017; Song et al. 2019). In southern China, both opportunistic nectar-feeding birds and sunbirds act as the pollinators of bird-pollinated plants (Corlett 2001; Gu et al. 2010; Qiu et al. 2015; Huang et al. 2017; Song et al. 2019). Opportunistic nectar-feeding birds have increased importance as pollinators to bird-pollinated flowers in temperate Asia, where sunbirds are absent (Corlett 2004). Opportunistic nectar-feeding birds act as major pollinators of flowers of Ericaceae (e.g., *Rhododendron* (Yan et al. 2018)), Lamiaceae (e.g., *Leucosceptrum* (Zhang et al. 2012)), Loranthaceae (e.g., *Taxillus* (Fig. II; Yumoto 1987; Funamoto & Sugiura 2017)), Rhizophoraceae (e.g., *Bruguiera* (Kondo et al. 1991)), Rosaceae (e.g., *Cerasus* (Liu et al. 2018)), Scrophulariaceae (e.g., *Brandisia* (Qian et al. 2017) and *Pentacoelium* (Sugawara et al. 2019)), and Theaceae (e.g., *Camellia* (Yumoto 1987; Kunitake et al. 2004; Qiu et al. 2015)). Some plant species present mixed pollination systems including both insects and opportunistic nectar-feeding birds during the cold season in temperate regions and at high altitudes in the subtropics (Fang et al. 2012; Huang et al. 2017). Flower-visiting behavior by opportunistic nectar-feeding birds is mainly observed in the cold season (Yoshikawa & Isagi 2014). This may explain the seasonal tendency of flowers pollinated by opportunistic nectar-feeding birds to mostly bloom in the cold season (Yumoto 1987; Kunitake et al. 2004; Gu et al. 2010; Qian et al. 2017; but see Funamoto & Sugiura 2017).

DISCUSSION

Plant-pollinator interactions in East Asia

The available information on plant-pollinator interactions in East Asia is very scattered. Thus, any generalizations drawn at this point must be highly tentative. Further studies are needed to reveal the general trends in plant-pollinator interactions in East Asia. However, some generalizations can be made to allow East Asian plant-pollinator interactions to be compared with those in other temperate regions in the Northern Hemisphere, like those in Europe and North America.

Bumblebees are important pollinators of many plant species in East Asia, as in Europe and North America. Many plant species are visited by honeybees, which are sometimes considered one of the most important pollinators in East Asia (Ren et al. 2018). However, the roles of *Apis* species as pollinators in natural ecosystems are still poorly known. For example, only a few species with specialized honeybee-pollinated flowers have been reported, and only among the Orchidaceae and Apocynaceae, which have highly specialized

floral traits like pollinaria (e.g., D-K. Wang et al. 2009; Tsuji & Kato 2010). Few studies have documented the importance of *Trigona* species as pollinators in East Asia. Therefore, future studies are needed to elucidate the importance of *Apis* and *Trigona* as pollinators in East Asia. At least two approaches are required to determine the importance of eusocial bees as pollinators in natural ecosystems. First, the proportion of plant species in natural communities that depend on pollination by eusocial bees should be evaluated. Second, the effectiveness of pollination by eusocial bees and other pollinators should be compared among many plant species.

Some pollination systems may be less common in East Asia than in other regions. Vertebrate pollination is less common in East Asia than in North America. For example, numerous hummingbird-pollinated plants have been reported from North America (Grant 1994; Fleming & Muchhala 2008). Although sunbirds and pteropodid bats are present in the southern part of East Asia, specialized nectar-feeding birds and nectar-feeding bats are absent in Europe and the northern part of East Asia (J-S. Zhang et al. 2010; Vincenot et al. 2015; Krauss et al. 2017). In contrast, hummingbirds and nectar-feeding bats are present in North America (Fleming & Muchhala 2008). The lack of specialized vertebrate nectarivores in the northern part of East Asia may explain the limited diversity of the vertebrate-pollinated plants found there, as well as in Europe. However, East Asia has more vertebrate-pollinated plants than Europe. Vertebrate-pollinated flowers are extremely rare in continental Europe (Ortega-Olivencia et al. 2005). Unlike Europe, the northern part of East Asia has several relatively specialized nectar-feeding vertebrates, including white-eyes, callosiurine squirrels, and civets (Corlett 2004; Kobayashi et al. 2015, 2017, 2019; Funamoto & Sugiura 2017). Non-flying mammals and opportunistic nectar-feeding birds may partly fill the pollination niche of specialized nectarivores in the northern part of East Asia.

Nocturnal hawkmoth pollination is observed less in Asia than in Africa and the New World (Johnson et al. 2017), but the nocturnal activity of hawkmoths on flowers can be underestimated (Liu & Sun 2019). Europe also has only a few examples of nocturnal hawkmoth-pollinated plants, such as *Platanthera*, *Silene*, and *Lonicera* (Pettersson 1991; Proctor et al. 1996). However, fewer hawkmoth-pollinated flowers are observed in Europe than in East Asia, likely because Europe has fewer hawkmoth species than East Asia (Ballesteros-Mejia et al. 2017).

There is substantial geographic variation in the pollinator fauna across East Asia. Some regions lack particular groups of pollinators. Oceanic islands, such as the Izu Islands and Bonin Islands, typically lack long-tongued pollinators like bumblebees and butterflies (Inoue 1993; Mizusawa et al. 2014; Hiraiwa & Ushimaru 2017). Although the Ryukyu Islands are continental islands, bumblebees are also absent from most of these islands (Kato 2000; Tadauchi et al. 2014). Hawkmoths and solitary bees may thus act as important pollinators on these islands (Inoue 1993; Kato 2000; Yamada et al. 2010; Mizusawa et al. 2014; Yamada & Maki 2014; Hiraiwa & Ushimaru 2017; Nakajima et al. 2018).

Human impacts on plant-pollinator interactions

The distribution and phenology of organisms is expected to be affected by climate change, which may affect plant-pollinator interactions (Kudo & Ida 2013; Kudo 2014; Renner & Zohner 2018; Egawa & Itino 2019). For example, when flowering of *Corydalis ambigua* (Papaveraceae) occurs ahead of the emergence of bumblebees, it results in low seed production (Kudo & Ida 2013).

Habitat degradation, for example through urbanization, has been proposed to have negative impacts on biodiversity and plant-pollinator interactions (Harrison & Winfree 2015). However, few studies have explicitly examined the effects of habitat degradation on plant-pollinator interactions, and the studies that have been done found mixed results. For example, pollinator visitation and pollinator-related reproductive success were low in urbanized populations of *Commelina communis* (Ushimaru et al. 2014). In contrast, the visitation frequency of effective pollinators was similar or even higher in an urban population than that in the forest habitats of *Mucuna macrocarpa* (Kobayashi et al. 2018a).

Invasive pollinators can negatively affect plant-pollinator interactions and plant reproductive success (Dohzono & Yokoyama 2010). An invasive bumblebee, *Bombus terrestris*, can compete with native bumblebees for floral resources and nest sites (Matsumura et al. 2004). *Bombus terrestris* can disturb the reproduction of native bumblebees through interspecific mating (Kanbe et al. 2008; Kondo et al. 2009). Visitation by *B. terrestris* can decrease the reproductive success of flowers (Kenta et al. 2007; Dohzono et al. 2008). Domesticated European honeybees, *Apis mellifera*, can facilitate interspecific hybridization between two species of *Taraxacum* (Peng et al. 2018).

Island ecosystems are especially vulnerable to both habitat destruction and invasive species (Sugiura 2016). For example, plant-pollinator interactions are threatened on the Bonin Islands, a Japanese oceanic archipelago (Kato et al. 1999; Abe 2006). The pollinator fauna of the Bonin Islands is now dominated by invasive species like *Apis mellifera* that compete with native pollinators (Kato et al. 1999; Sugiura 2016). *A. mellifera* may facilitate the reproduction of alien flowers because these bees prefer to visit the flowers of alien species more than those of the islands' endemic species (Abe et al. 2011). *Anolis carolinensis* predated on endemic pollinators like bees, butterflies, flies, and beetles (Abe et al. 2008; Sugiura 2016). Predation by *A. carolinensis* is presumed to be the main factor responsible for the recent pollinator faunal decline seen on the Bonin Islands (Abe et al. 2008). These anoles are present on the main islands, but absent on the satellite islands (Abe et al. 2011). The number of species of pollinators present on flowers and the total number of visitations to endemic flowers on the main islands are lower than those on the satellite islands (Abe et al. 2011). The fruit set of a species endemic to the Bonin Islands, *Leptopetalum grayi*, was found to be lower on a main island where invasive species like honeybees and anoles were abundant than that on a satellite island where these invasive species were absent (Tsuda et al. 2018). The flower visitors of *L. grayi* on the main island were dominated by *A. mellifera*, whereas diverse native visitors were observed on this species' flowers on the

satellite islands (Tsuda et al. 2018). On the Bonin Islands, many plants present pollination syndromes toward particular types of pollinators, but virtually no candidate pollinators visit these flowers (Abe 2006; Watanabe et al. 2018). For example, some flowers present a hawkmoth pollination syndrome, but these flowers were observed to receive no or only very rare visits by moths (Abe 2006; Watanabe et al. 2018).

Extensive browsing and grazing by vertebrate herbivores like Sika deer and yak significantly reduce the abundance and diversity of insectary plants (Kato & Okuyama 2004; Xie et al. 2008; Sakata & Yamasaki 2015). In contrast, traditional light and moderate grazing increase the species richness of plants and the nectar production in the community (Mu et al. 2016). The decline in flowering plants caused by extensive browsing and grazing can reduce the abundance of bumblebees in the habitat (Kato & Okuyama 2004; Xie et al. 2008; Sakata & Yamasaki 2015), and thus reduce plant reproductive success (Sakata & Yamasaki 2015).

Future work

Research on plant-pollinator interactions in East Asia has been developing rapidly during recent decades. However, the available information on plant-pollinator interactions in East Asia is still limited. Both community- and species-level studies are required to understand the general trends in plant-pollinator interactions in East Asia. The accumulation of research carried out in these two directions on plant-pollinator interactions in East Asia would contribute to our understanding of global-level patterns in plant-pollinator interactions.

The available information on plant-pollinator interactions in East Asia is biased towards particular taxa of plants and pollinators. Although pollination studies have been conducted on 105 families of Chinese flora, in most of these families the pollination biology of less than ten species has been examined (Ren et al. 2018). Bumblebees and flowers specialized for pollination by bumblebees are frequently studied. However, few studies have examined the role of bumblebees as pollinators of flowers with more generalized pollination systems. Non-bee pollinators are clearly understudied. However, pollinators like butterflies, moths, wasps, flies, birds, and mammals can be important pollinators of many plants. Few studies have documented hawkmoth and bird pollination in East Asia (Johnson et al. 2017; Zanata et al. 2017; Ren et al. 2018). Nocturnal pollinators like bats, moths, and non-flying mammals are also understudied compared with diurnal pollinators. The importance of small pollinators, such as microdipterans, small beetles, and thrips, is also likely underestimated. More studies are required to reveal the importance of these understudied pollinators in East Asia. Experimental approaches could contribute to evaluations of the importance of these understudied pollinators. For example, the relative contribution of different types of pollinators to pollination success in particular plant species could be evaluated by selective exclusion experiments directed at particular pollinators, and also by comparing the single-visit pollination effectiveness among different types of pollinators (e.g., King et al. 2013; Kiepiel & Johnson 2014). Such studies have recently been conducted on many plant species in East

Asia (e.g., Huang et al. 2017; Funamoto & Ohashi 2017; Nakajima et al. 2018; Liu & Sun 2019; Tian & Ren 2019).

Studies carried out in a wide array of ecosystems and regions in East Asia are required because the research on plant-pollinator interactions done so far has not been evenly distributed geographically. The majority of pollination studies in China have been conducted in mountainous regions (Ren et al. 2018). In East Asia, relatively few studies have been conducted in the subtropics, coastal ecosystems, and wetland ecosystems. Although the Korean peninsula and Taiwan are biologically diverse and biogeographically important components of East Asia (Kong & Watts 1999; Choe et al. 2016; Zhu 2016; Tojo et al. 2017), very few studies on plant-pollinator interactions have been conducted in these regions.

The relationship between habitat type and the composition of pollinator fauna in East Asia is still unclear because few community-level studies that were comparable among habitat types have been conducted. However, some trends can be observed (Fig. 2). Although very few studies have been conducted in wetland habitats, dipteran pollinators are known to be abundant in wetland habitats (Kato & Miura 1996). Bees, especially bumblebees, and Diptera are dominant flower visitors in alpine regions (Yumoto 1986; Fang & Huang 2012; Mizunaga & Kudo 2017; Ishii et al. 2019). Wasps tend to be more abundant in coastal sand dunes than in other habitats (Inoue & Endo 2006b; Hiraiwa & Ushimaru 2017). More studies are needed to definitively elucidate the relationships between different habitat types and their pollinator fauna.

Comparing East Asian plant-pollinator interactions with plant-pollinator interactions in other regions, especially Europe and North America, can contribute to the improved understanding of the large-scale ecological and evolutionary consequences of plant-pollinator interactions (Ren et al. 2019). For example, taxa with disjunctive distributions across North America and East Asia provide opportunities to investigate how plant-pollinator interactions differ across continents (e.g., Fan et al. 2011; Ren et al. 2019).

Rapid economic growth in East Asia is considered to have had negative impacts on the East Asian ecosystem (Fang et al. 2018). The effects of human impacts on plant-pollinator interactions are still poorly investigated in East Asia. Observational and experimental studies are needed to understand these human impacts on plant-pollinator interactions because the effects of humans on plant-pollinator interactions can be case-specific (Ollerton 2017; Kobayashi et al. 2018a). For example, pollinator monitoring is required in East Asia. Although declines in the diversity and abundance of pollinators have been reported in North America and Europe (Ollerton 2017) and declines in Chinese bumblebee populations have been suggested (Williams & Osborne 2009), pollinator monitoring studies have still rarely been conducted in East Asia. In addition, the plant species richness and species richness of flower visitors found on the plants within a community are strongly and positively correlated across communities (Ollerton 2017). Evaluating the relationships among pollinator species/functional diversity, plant species diversity, and plant reproductive success can

provide valuable insights for conservation purposes (Hiraiwa & Ushimaru 2017; Ollerton 2017).

In conclusion, this review suggests that there is considerable variation in plant-pollinator interactions across the different regions and habitat types within East Asia. However, the available information on plant-pollinator interactions in East Asia is still limited. Many types of pollinators, habitats, and regions have received little attention. Pollination by nocturnal pollinators is particularly understudied. Community-level studies on many ecosystems across the entirety of East Asia are needed to understand general trends in plant-pollinator interactions in East Asia.

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APPENDICES

Additional supporting information may be found in the online version of this article:

APPENDIX I. A summary of pollinator groups in East Asia and the plant genera they visit/pollinate.

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