

# Seasonal dynamics of floral composition and flower visitors in a subtropical alpine ecosystem in Taiwan

Gaku Kudo<sup>\*1</sup>, Tetsuo Kohyama<sup>2</sup>, Kai-Hsiu Chen<sup>3</sup>, Tsai-Wen Hsu<sup>4</sup>, and Chun-Neng Wang<sup>5</sup>

<sup>1</sup>Hokkaido University

<sup>2</sup>The University of Tokyo

<sup>3</sup>University of Lausanne

<sup>4</sup>Endemic Species Research Institute

<sup>5</sup>National Taiwan University

May 1, 2023

## Abstract

Flowering phenology of alpine plant communities and seasonal dynamics of flower visitors have been scarcely studied in the tropical/subtropical alpine regions. We report flowering phenology, flower production, and flower-visiting insects in the alpine site of central Taiwan. Throughout the research period (2017–2018), we recorded flowering phenology of 130 plant species, flower production of 81 species, and 15,127 insects visiting alpine flowers. Most of the alpine plants were visited by dipteran insects and/or hymenopteran insects. The seasonal patterns of flowering were more apparent in bee-visited plants compared to fly-visited plants in which the flowering of bee-visited plants clearly increased as the season progressed. About 63% of flower visitors were dipteran insects (syrphid and non-syrphid flies), and 30% were hymenopteran insects (mostly bumble-bee workers). Although the seasonal trend in fly abundance was less clear between years, bumble-bee abundance consistently increased in the middle to late seasons, reflecting colony development. There was a positive correlation between bee abundance and the number of flowering species of bee-visited plants, but there was no correlation between fly abundance and the number of flowering species of fly-visited plants throughout the season. These results suggest that the flowering phenology of subtropical alpine communities is influenced by the seasonal availability of pollinators. Bumble bees, syrphid flies, and non-syrphid flies had wide ranges of foraging flowers, but their niche overlap was relatively small. Because cold-adapted bumble bees are threatened by climate change in Taiwan, plant–pollinator interactions may be disturbed by global warming.

Article type: Biodiversity in Asia

## Seasonal dynamics of floral composition and flower visitors in a subtropical alpine ecosystem in Taiwan

Gaku Kudo<sup>1</sup>, Tetsuo Kohyama<sup>2</sup>, Kai-Hsiu Chen<sup>3</sup>, Tsai-Wen Hsu<sup>4</sup>, and Chun-Neng Wang<sup>5</sup>

<sup>1</sup> Faculty of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan

<sup>2</sup> Department of Ecosystem Studies, The University of Tokyo, Tokyo, 113-8657, Japan

<sup>3</sup> Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

<sup>4</sup> Department of Botany, Endemic Species Research Institute, Nantou 55244, Taiwan

<sup>5</sup> Department of Life Science, Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 10617, Taiwan

Corresponding author: G. Kudo, e-mail: [gaku@ees.hokudai.ac.jp](mailto:gaku@ees.hokudai.ac.jp)

## Abstract

Flowering phenology of alpine plant communities and seasonal dynamics of flower visitors have been scarcely studied in the tropical/subtropical alpine regions. We report flowering phenology, flower production, and flower-visiting insects in the alpine site of central Taiwan. Throughout the research period (2017–2018), we recorded flowering phenology of 130 plant species, flower production of 81 species, and 15,127 insects visiting alpine flowers. Most of the alpine plants were visited by dipteran insects and/or hymenopteran insects. The seasonal patterns of flowering were more apparent in bee-visited plants compared to fly-visited plants in which the flowering of bee-visited plants clearly increased as the season progressed. About 63% of flower visitors were dipteran insects (syrphid and non-syrphid flies), and 30% were hymenopteran insects (mostly bumble-bee workers). Although the seasonal trend in fly abundance was less clear between years, bumble-bee abundance consistently increased in the middle to late seasons, reflecting colony development. There was a positive correlation between bee abundance and the number of flowering species of bee-visited plants, but there was no correlation between fly abundance and the number of flowering species of fly-visited plants throughout the season. These results suggest that the flowering phenology of subtropical alpine communities is influenced by the seasonal availability of pollinators. Bumble bees, syrphid flies, and non-syrphid flies had wide ranges of foraging flowers, but their niche overlap was relatively small. Because cold-adapted bumble bees are threatened by climate change in Taiwan, plant–pollinator interactions may be disturbed by global warming.

Keywords: bumble bee, fly, flowering phenology, subtropical alpine, pollinator, Taiwan

## Introduction

Alpine ecosystems in higher latitudes are characterized by cool and short growing season, during which flowering of alpine plants progress rapidly. Many alpine plants depend on insects for pollination, and pollen limitation is a key factor affecting seed production of alpine plants (Kudo, 2022). Because temporal matching of flowering time and pollinator activity, and insect abundance are influenced by climate change, plant–pollinator interactions in alpine ecosystems are predicted to be disturbed by climate change (Inouye, 2015).

Bumble bees, syrphid flies, and non-syrphid flies are the most common and dominant pollinators in alpine ecosystems (Kearns, 1992; Pyke et al., 2011; Inouye, 2020). However, their frequencies and foraging activities vary among geographic regions and along elevational or latitudinal gradients. For instance, bumble bees are absent in New Zealand, where solitary bees and syrphid flies are important pollinators of alpine plants (Bischoff et al., 2013). The foraging range of floral resources of bumble bees becomes wider at higher elevations in the Colorado Rocky Mountains because of higher flowering overlaps among alpine plant species during a short summer (Miller-Struttman & Galen, 2014). Furthermore, the importance of fly pollinators commonly increases with elevation and latitude due to higher tolerance to cool conditions in dipteran insects compared to hymenopteran insects (Strathdee & Bale, 1998; McCabe & Cobb, 2021). Thus, relative importance of the two major flower-visiting insect groups, i.e., flies and bees, as pollinators of alpine plants may vary among mountain regions at a geographic scale.

Humid tropical/subtropical alpine regions are the most sensitive ecosystems to climate change, where plant communities are composed of many endemic species within isolated mountain areas (Buytaert et al., 2011). Alpine ecosystems in lower latitudes are characterized by longer growing periods and moderate seasonal fluctuations in temperature compared to the alpine ecosystems in higher latitudes. Thus, flowering phenology and seasonal dynamics of flower-visiting insects may be different from the alpine ecosystems in higher latitudes. However, phenological studies on the tropical/subtropical alpine ecosystems are limited (e.g., Kudo & Suzuki, 2004; Pelayo et al., 2019, 2021). To predict the climate change impacts on the tropical/subtropical alpine ecosystems, therefore, clarification of the basic features of flowering phenology at community scale and flower-visiting insects is crucial.

The previous studies conducted in northern Japan (Kudo, 2016; Mizunaga & Kudo, 2017) reported that the abundance of bumble bees showed clear seasonality reflecting the colony development process in which only overwintered queens emerged in the early season and worker abundance increased abruptly in the middle

of the season. In contrast, the frequency of flower visitation by dipteran insects was positively related to ambient temperature, but often has no clear seasonality, and they showed outbreaks at unpredictable times. Responding to the seasonal pattern of bumble bees, the group of bee-visited plants tended to have a bimodal flowering pattern, that is composed of early-flowering species and late-flowering species, although actual flowering periods strongly depended on snowmelt time. On the other hand, the group of fly-visited plants showed a unimodal flowering pattern in which many species flowered in the middle of season when the ambient temperature was high. These results suggest that different selective forces may act on flowering behavior between bee-visited and fly-visited species even within the same alpine plant communities. To test this possibility, comparisons of flowering phenology and flower visitors across multiple alpine ecosystems are necessary.

In the present study, we recorded flowering phenologies of alpine plant communities and seasonal dynamics of flower-visiting insects in the Hehuanshan area of central Taiwan. Taiwan is a mountainous island located in the tropical/subtropical climate zone, where more than 200 mountains exist above 3000 m elevations. The mountain flora of Taiwan is characterized by a high proportion of endemic species (60%: Hsieh, 2002). A recent study reported that alpine vegetation in Taiwan has been altered by climate change (Chou et al., 2011), and it is expected that plant–pollinator interactions in the alpine ecosystems may also be influenced by climate change. Moreover, one recent study showing overdispersion in the flower color among closely related species in the alpine flora of Taiwan stresses the importance of plant-pollinator interaction at the community level (Tai et al., 2020). However, there is no information about the flowering patterns of alpine plant communities and the seasonal dynamics of flower-visiting insect communities. In order to clarify the interactions between flowering phenology and seasonal dynamics of flower visitors, we observed seasonal changes in the flower production of plants and the frequency of flower-visiting insects over two years. We expect that hymenopteran insects (mainly bumble bees) and dipteran insects are major flower visitors in the alpine ecosystem of Taiwan as well as mid-latitudinal alpine regions in the northern hemisphere. Our hypotheses are as follows:

- 1) Flowering of bee-visited plants may be concentrated during the active season of worker bees if bumble bees are major flower visitors in the alpine environment of Taiwan.
- 2) Flowering of fly-visited plants may vary among species if the seasonality of fly activity is less clear and unpredictable due to the stable temperature conditions during the flowering season.

## Methods

### Research site

This study was conducted in the alpine site of the Mt. Hehuanshan area (Nantou County) in central Taiwan in 2017 and 2018. The elevation of the research site was 2950–3230 m. Alpine regions in Taiwan are characterized by a humid subtropical oceanic climate. Annual mean air temperature at 3000 m elevation is 7.3 °C, ranging from 1.5 °C in January to 11.5 °C in July, and annual precipitation is 3630 mm, ranging from 155 mm in December to 520 mm in June (average of 2007–2018). In winter, daily minimum temperature is commonly below zero (–2.3 to –1.5 °C) from December to February. Major flowering periods of alpine plants last from late May to mid-September during which daily minimum and maximum temperatures are maintained around 6–7 °C and 17–19 °C, respectively.

### Field observation

Observations of plant phenology and flower-visiting insects were conducted five times each year; on 26–30 May (term 1), 21–23 June (term 2), 13–15 July (term 3), 7–9 August (term 4), and 28–30 August (term 5) in 2017; on 5–8 June (term 1), 29 June (term 2), 29–31 July (term 3), 13–14 August (term 4), and 3–5 September (term 5) in 2018. Air temperature was measured at 1-hr intervals at the height of 1 m above ground using a Tidbit V2 data logger (Hobo, Onset Co., USA) from May 31, 2017 to September 3, 2018 at 3060 m elevation.

For the survey of flowering occurrence and flower production, 21 fixed plots (named TW01-21; 2 × 10 m

in size) were established at various habitats (from dry ridge habitat to wet depression habitat) to cover the whole vegetation types in the study site (Fig. S1). In each plot, flowering occurrence and flower number of each species were recorded in the early (term 1), middle (term 3), and late seasons (term 5). Locations of individual plots were illustrated in Figure S1. In total, flower productions of 81 species were recorded across plots during two years. Furthermore, a phenological survey of flowering occurrence was conducted for all entomophilous plant species in this area. In each term (term 1–5), we walked around the whole area in which fixed plots were set (within a  $2.5 \times 1.0$  km area), and recorded flowering species. In total, flowering phenologies of 130 species were recorded throughout the survey periods.

For the survey of flower-visiting insects, we repeated 30-min censuses of flower visitors by walk throughout the season (five terms). The census period in each term was 1–3 continuous days during which 11–30 sets of census were conducted. Each census was conducted on calm days (wind speed was  $< 4$  m/s) during the daytime (8:00–17:00). In total, 106 censuses (53 hrs.) and 102 censuses (51 hrs.) were conducted in 2017 and 2018, respectively. At the beginning of each census, air temperature and relative humidity were measured. Flower-visiting insects were classified into following groups; (1) hymenopteran insects (subdivided into bumble bee, honey bee, solitary bee, wasp, and sawfly), (2) dipteran insects (syrphid fly, dagger fly, other fly), (3) lepidopteran insects (butterfly, skipper, moth), (4) coleopteran insects, (5) hemipteran insects, and (6) other insects. Ants and grasshoppers were excluded from the observation because their activity as pollinators seemed to be small. The number of insects visiting flowers and plant species of the flowers were recorded. In total, visits of 15,127 insects were recorded on the flowers of 105 plant species.

About 93% of observed insects were hymenopteran or dipteran insects (see Results). Based on the composition of visiting insects, the pollination type of individual plant species was classified into the following five groups: (1) bee specialist:  $> 75\%$  of visitors are hymenopteran insects, (2) fly specialist:  $> 75\%$  of visitors are dipteran insects, (3) bee generalist: 50–75% of visitors are hymenopteran insects, (4) fly generalist: 50–75% of visitors are dipteran insects, and (5) unclear type: very low visits ( $< 5$  visits) or mixture of several insect groups. In the present study, both bee-specialist and bee-generalist species are categorized as bee-visited species, and both fly-specialist and fly-generalist species are done as fly-visited species.

## Analyses

All statistical analyses were conducted using R version 4.2.2 (R Core Team, 2022).

### *Seasonal dynamics of flower production at a community scale*

First, seasonal dynamics of flower production in this area were analyzed using pooled data of all plots in each term. The number of flowering species and the species diversity of floral compositions by Shannon-Wiener's  $H'$  (based on the total flower number of individual species) were compared among observation periods (early, middle, late) and between years (2017, 2018). In the analyses, we conducted the comparisons of all species, bee-visited species, and fly-visited species, separately. In order to quantify the seasonal dynamics of flowering species, furthermore, dissimilarity of floral compositions was compared among seasons (early, middle, late) and between years (2017, 2018) by non-metric multi-dimensional scaling (NMDS), based on the Chao's similarity index. These analyses were performed using the Vegan package ver. 2.6-4 (Oksanen et al., 2022) and the MASS package in R. The effects of season and year on floral compositions were assessed by permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function.

Second, seasonal trends in the flower production of individual species were analyzed at plot base by a generalized linear mixed model (GLMM) with a Poisson error distribution and a log-link function, using the package glmmTMB in R. In this analysis, we specifically targeted for bee-visited and fly-visited plant species because of the dominance of these types (see Results). In the GLMM, flower number of each species in each plot was a responding variable, season, year, and pollination type (bee-visited or fly-visited) were fixed effect variables, and plot and species were set as random effect variables. In order to compare the seasonal patterns of flower production between bee-visited and fly-visited species, an interaction term between season and pollination type was included in the GLMM.

## Seasonal dynamics of flower visitors

Because hymenopteran and dipteran insects occupied > 90% of all flower visitors (see Results), factors affecting the visitation frequencies of bees and flies were separately analyzed by generalized linear models (GLMs). Visitation frequencies of bumble bees, syrphid flies, and non-syrphid flies in each census were used as responding variables, i.e., three GLMs were constructed. Other insect groups were excluded from the analysis due to low visitation frequencies (see Results). Explanatory variables were observation date (mean day of year in each census term), ambient temperature, relative moisture, and year. Interactions between observation date (both linear and quadratic terms) and year (2017 and 2018) were included in the model. For the GLMs, a zero-inflate Poisson distribution model (Brooks et al., 2002) was conducted because there were many zero values in some insect groups. Of 208 census data, three data for bumble bees and two data for non-syrphid flies were excluded from the analyses because of unusually excess counts of insects probably due to miscounts of insects in the field.

The network structure between flower-visiting insects and foraging plant species across seasons and years was visualized using package *bipartite* in R (Dormann et al., 2022). For obtained network structure, binary connectance (frequency-based connectance), niche overlap among insect visitors (based on Horn's index ranging from 0 with no common use to 1 with perfect niche overlap), mean number of shared plant species, and Shannon-Weaver's  $H'$  diversity index were calculated. In the network analysis, we constructed network structure of order-level comparison (Hymenoptera, Diptera, Coleoptera, Lepidoptera) and major taxonomic group comparison (bumble bees, syrphid flies, and non-syrphid flies). Furthermore, similarity of foraging flowers between major insect groups and Shannon-Weaver's  $H'$  diversity index of each insect group were calculated using the *Vegan* package.

Finally, the relationship between visitor frequency and the number of plant species at flowering was analysed for bee-visited plants and fly-visited plants, respectively. GLM postulating a Poisson error distribution was conducted in which the number of flowering species observed in each term (for bee-visited or fly-visited plants) was set as a responding variable and the average number of insects (for hymenopteran or dipteran insects) observed in each term as an explanatory variable.

## Results

### Ambient temperature

Transition of air temperature in the study site indicated relatively stable thermal conditions during the survey period (term 1–5) in both years (Fig. 1). Daily mean temperatures during the flowering season ranged between 10–15 °C, daily minimum temperatures were 6–10 °C, while daily maximum temperatures fluctuated between 10 and 23 °C. Thus, the seasonal gradient of thermal conditions was less clear during the flowering periods. During the winter time, from early December to mid-March, daily minimum temperatures were often below zero, but daily maximum temperatures mostly remained above zero.

### Flowering phenology

Throughout the survey, flowering of 130 species (42 families) was recorded, including four exotic species (*Hypochaeris radicata*, *Taraxacum officinale*, *Trifolium repens*, and *Veronica persica*). Major families were Asteraceae (18 sp.), Rosaceae (16 sp.), Ranunculaceae (10 sp.), and Orchidaceae (8 sp.). Based on the records of flower visitors, 19 plant species (14.6%) were categorized as bee specialists, 11 species (8.5%) as bee generalists, 54 species (41.5%) as fly specialists, 18 species (13.8%) as fly generalists, and 28 species (21.5%) as mixture or unclear (Table S1).

In the early season (late May), 49 species (39% of all species excluding exotic plants) had set flowers. The number of flowering species was maximum in mid- to late July in which 80–88 species (70–71%) were flowering. Then, the number of flowering species decreased gradually, but 57 species (51%) were still flowering in early September. Flowering patterns were different between fly-visited species (fly specialists and generalists) and bee-visited species (bee specialists and generalists) (Fig. 2). Fly-visited plants showed a higher proportion of flowering species throughout the season (> 50%) with a peak in late July (72%), indicating a

moderate seasonal change. In contrast, the flowering pattern of bee-visited plants showed a clear seasonality; only 21% of species were flowering in late May, but the number of flowering species increased rapidly with seasonal progress and attained a maximum level in mid-July (85%), then decreased gradually toward early September (58%).

### Flower production

In the permanent plots, flowering of 81 species (62% of all species) was recorded throughout the survey periods in which 21 species were categorized as bee-visited type, 53 species were fly-visited type, and 7 species were other type. Both the number of flowering species and diversity index ( $H'$ ) were small in the early season and large in the middle season (Table 1). This trend was more apparent in bee-visited species in which  $H'$  values ranged from 0.3–3.3, while seasonal changes in fly-visited species were moderate in which  $H'$  values ranged from 2.3–3.4. The NMDS result conducted for all species showed that variation in floral compositions across the survey periods was largely explained by seasonal difference (effect size,  $R^2 = 0.75$ ), while yearly variation was negligibly small (Fig. S2). Similar trends were detected when NMDS was performed for bee-visited species and fly-visited species separately, although the effect size of bee-visited species ( $R^2 = 0.86$ ) was larger than that of fly-visited species ( $R^2 = 0.68$ ). These results indicate that seasonal progress and species transition of flowering plants are more apparent in bee-visited plants than in fly-visited plants.

The number of flowers per plot highly varied among plots across seasons in both bee-visited and fly-visited species (Fig. 3). The GLMM result showed that flower production in the early season was significantly smaller than that of the middle and late seasons (Table 2). Significant negative interactions were detected between fly-visited species and season, suggesting that the seasonal changes in flower production were moderate in fly-visited species compared to bee-visited species (Fig. 3).

### Composition and foraging activity of flower-visiting insects

Throughout the 208 censuses (104 hrs.) across five terms in 2017 and 2018, 15,127 insects were recorded on the flowers of 105 plant species. Hymenopteran insects occupied 30.4%, dipteran insects 62.7%, coleopteran insects 3.8%, lepidopteran insects 2.2%, and other insects 0.8% (Table 3). Major insect groups were non-syrphid flies (40.4%), bumble bees (24.9%), and syrphid flies (21.2%), while the frequencies of other insect groups were < 5%.

Seasonal patterns of visitation frequencies highly varied among major visitor groups (Fig. 4). The visitation frequency of bumble bees increased with seasonal progress in both years with a peak in the middle to late season (a positive coefficient of the linear term and a negative coefficient of the quadratic term of day number in the GLM; Table 4a). Worker bees occupied 98% (= 3710 / 3770) of all bumble bees. Thus, the seasonal trend of hymenopteran visitors reflected the population dynamics of bumble bee workers. In contrast, seasonal trends in the visitation frequency of dipteran insects highly varied between years. The abundance of syrphid flies was relatively high during the early half of the season and decreased in the later season in 2017, while it tended to increase with seasonal progress in 2018 (a negative and a positive quadratic term of day number in 2017 and 2018, respectively; Table 4b). The abundance of non-syrphid flies was large early in the season in 2017, while it was large late in the season in 2018 with lower values in the middle of season (positive quadratic values in both years; Table 4c). These results indicate that there is a clear seasonality in bee activity, while the seasonal trend of flies was unpredictable. The GLM results indicate that relative humidity was negatively related to the abundance of all insects (Table 4). The mean relative humidity during the censuses was 68%, ranging from 38 to 100 %. In contrast, the effects of ambient temperature varied among insect groups; bumble bees responded positively, syrphid flies responded negatively, and non-syrphid flies were less sensitive (Table 4). The mean ambient temperature during the visitor censuses was 17.9 °C, ranging from 11.5 to 24.9 °C.

### Insect-flower network

In the order-level network structure between flower-visiting insects and 73 flowering species, almost all plant species had linkages with dipteran and/or hymenopteran insects (Fig. 5a). Dipteran insects visited

most diverse flowers ( $H' = 4.81$ ) and showed the largest linkages with plant species among four orders. Hymenopteran insects also visited many flowers ( $H' = 4.45$ ) but the linkages with several plant species, that have strong linkages with dipteran insects, were limited. The diversity of foraging flowers of lepidopteran and coleopteran insects was moderate ( $H' = 4.12$  and  $3.20$ , respectively). Species compositions of foraging flowers of lepidopteran and coleopteran insects were highly overlapping with those of hymenopteran and dipteran insects (0.88–0.95 in similarity), but the similarity of foraging flowers between lepidopteran and coleopteran insects was moderate (0.69). When the foraging patterns of dipteran insects and hymenopteran insects were compared, the niche overlap was relatively low (0.34). Thus, the flowers targeted by dipteran and hymenopteran insects were considerably different.

In the network structure between three major insect groups and 70 flowering species (Fig. 5b), syrphid flies, non-syrphid flies, and bumble bees linked to 62 (89%), 65 (93%), and 50 plant species (71%), respectively. The values of diversity index for visiting flowers were similarly high ( $H' = 4.31$ – $4.54$ ). Similarities of foraging flowers were moderate between bumble bees and non-syrphid flies (0.72) and between bumble bees and syrphid flies (0.65), while the similarity between non-syrphid and syrphid flies was relatively low (0.57). Niche overlap among major insect groups was 0.303, suggesting that different insect groups tend to forage on different plant species irrespective of their wide foraging behavior.

GLM results conducted for the relationship between visitor frequency and the number of flowering species in each term revealed that the number of bee-visited species at the flowering stage was positively related to the abundance of hymenopteran insects ( $z = 2.39$ ,  $p = 0.017$ ) (Fig. 6a), whereas the number of fly-visited species at the flowering stage was independent of the abundance of dipteran insects ( $z = -0.53$ ,  $p = 0.60$ ) (Fig. 6b).

## Discussion

The present study revealed that dipteran insects (syrphid and non-syrphid flies) and hymenopteran insects (bumble bees) are the most common flower visitors in the alpine plant communities of Taiwan. On average, 23 and 56% of plant species were predominantly visited by bees and flies, respectively. In comparison with fly-visited plants, floral diversity and flower production of bee-visited plants increased with seasonal progress more apparently, corresponding to the seasonal dynamics of bumble bee workers. These results suggest a consistent linkage between the seasonal dynamics of social bees and the flowering phenology of bee-visited plants in the subtropical alpine ecosystem.

### Composition and seasonality of flower visitors

Percentages of dipteran insects (63%) and hymenopteran insects (30%) in the flower-visiting insect communities in the present study site (24.2° N, 2950–3230 m a.s.l.) were similar to the Japanese alpine ecosystems in the cool-temperate zone, where dipteran insects occupied 64 and 61%, and hymenopteran insects (mostly bumble bees) occupied 31 and 36% of all flower visitors in the Tateyama Mts. of central Japan (36.6° N, 2400–2800 m a.s.l.) and the Taisetsu Mts. of northern Japan (43.5° N, 1700–1900 m a.s.l.), respectively (Kudo 2016). Thus, bumble bees, syrphid flies, and non-syrphid flies are all dominant pollinators of alpine plants from subtropical to temperate zones in East Asia.

As expected, seasonal trends in foraging activity were different between dipteran and hymenopteran insects. The abundance of bumble bees was low early in the season, and increased in the middle to late season, reflecting the lifecycle of colony development (Pyke et al., 2011; Amsalem et al., 2015; Mizunaga & Kudo, 2017). Thus, the availability of pollination service by bumble bees commonly increased with seasonal progress in alpine ecosystems (Kudo, 2022). In contrast, less clear seasonality in dipteran insects (including unpredictable outbreaks) is reported in the previous studies (Totland, 1994; Mizunaga & Kudo, 2017). Also in the present study, seasonal dynamics of dipteran insects highly varied between years. The abundance of syrphid flies was larger in the early season in 2017, while it increased toward the later season in 2018. The outbreaks of non-syrphid flies were observed in the early season in 2017, but they occurred in the late season in 2018. These unpredictable patterns might reflect the species-specific lifecycle of dipteran insects (Larson et al., 2001; Rotheray & Gilbert, 2011). Dipteran insects are known as important pollinators early in the

season in European Alps (Bonelli et al., 2022) and high Arctic regions (Kevan, 1972; Tiusanen et al., 2016), indicating the importance of fly pollinators under harsh environmental conditions (Inouye et al., 2015).

Responses to weather conditions varied between bumble bees and dipteran insects. Foraging activity of bumble bees was positively correlated to ambient temperature as reported in previous studies (Corbet et al., 1992; Bergman et al., 1996). In contrast, the foraging activity of dipteran insects was weakly related to the ambient temperature. This unpredictable pattern in fly visitors may reflect the short lifecycle and diverse species composition in fly communities (Larson et al., 2001) rather than the temporal fluctuation of weather conditions. However, previous studies reported that the visitation frequency of dipteran insects often depended on the ambient temperature in alpine environments (McCall & Primack, 1992; Totland, 1994). For instance, a field survey of flower visitors in the alpine site of northern Japan reported that syrphid flies were most sensitive to ambient temperature, while foraging activity of non-syrphid flies was independent of temperatures (Mizunaga & Kudo, 2017), suggesting that syrphid flies are more sensitive to cool conditions than non-syrphid flies (Inouye et al., 2015). Thus, the temperature dependency of foraging activity of dipteran insects may vary among regions and between taxonomic groups. In the alpine site of this study, at least, sensitivity to weather conditions seemed to be small in dipteran insects. This is partly due to a low seasonal fluctuation of ambient temperature in the low latitudinal location. Mean monthly temperature during the major flowering season (June–September) was maintained between 10.7 and 11.5 °C, indicating a stable thermal condition (Fig. 1). In contrast, relative humidity was negatively related to the visitation frequencies of major insect groups. The alpine zone in Taiwan was characterized by wet conditions, and wet weather may restrict flight activity of small insects (Inouye et al., 2015).

### Flowering phenology and flower production of alpine plants

There are many studies on the flowering phenology in alpine plant communities (e.g., Holway & Ward, 1965; Thórhallsdóttir, 1998; Molau et al., 2005; Jabis et al., 2020), and some of them focused on the relationship between plants and flower visitors (e.g., Bosch et al., 1997; Makolaos et al., 2008; Iler et al., 2013; Pelayo et al., 2019, 2021). However, comparative studies of flowering patterns between different pollination types are limited as mentioned before (Kudo, 2016; Mizunaga & Kudo, 2017). In the present study, the number of blooming bee-visited species was positively related to the seasonal dynamics of bee abundance, but there was no correlation between the number of blooming fly-visited species and fly abundance. This difference may reflect the temporal availability of pollinators for bee-visited and fly-visited plants. A long-term study on the flowering phenology and pollination success of Japanese alpine plants (Kudo, 2022) demonstrated that the fruit-set rates of bee-visited plants increased as the season progressed, reflecting the increasing pollination service by worker bees. In contrast, the seasonal trend in the pollination success of fly-visited plants was less clear, where the variations in fruit-set success among species and between years were independent of flowering time. This result indicates a small seasonal restriction of pollination service by flies in alpine plant communities. Although the pollination efficiency of flies was generally lower than that of bees (Herrera, 1987), frequent visits of fly pollinators might compensate for the low efficiency per visit (Kearns & Inouye, 1994; Mizunaga & Kudo, 2017). Also in the present study, the visitation frequency of dipteran insects was 2.5 times larger than that of hymenopteran insects.

The seasonal patterns of flower production also differed between bee-visited plants and fly-visited plants. Similarly in the Japanese alpine communities, the seasonal pattern of flower production was moderate in fly-visited plants, whereas flower production of bee-visited plants tended to be maximum in the middle of the season although actual flower production of bee-visited plants highly fluctuated from year to year (Kudo, 2016; Mizunaga & Kudo, 2017). Interestingly, a recent dataset of flower color diversity among 727 species (ca. 20% of Taiwan flora) sampled along elevational gradient of Taiwan also found evidences that the majority of Taiwan flora evolved to match bee's innate color preference (Tai et al., 2020). In particular, the floral color diversities of bee-visiting plants in high altitude are over-dispersed among related species perhaps to facilitate their co-existence (Tai et al., 2020). Together, our data and the previous finding suggest the bee-visited plants in alpine Taiwan may have shifted their flowering times and colors to encourage bees' visiting. These results suggest that the flowering structure of alpine plant communities, i.e., temporal dynamics of floral diversity

and floral resources, may be influenced by the relative composition of bee-visited and fly-visited species.

### **Plant-pollinator network in the subtropical alpine ecosystem**

The network analysis between alpine plants and flower-visiting insects revealed that most alpine plant species in Taiwan depended on bumble bees, syrphid flies, and/or non-syrphid flies. Furthermore, niche overlap between these insect groups was relatively small (0.30), indicating that each insect group has its own linkage to the specific plant species. Interestingly, the similarity of foraging flowers between syrphid and non-syrphid flies was relatively low (0.57). This means that floral preference varies even within dipteran insects. As syrphid flies have relatively high floral constancy and high pollination efficiency (McGuire & Armbruster, 1991; Kearns, 1992; Fontaine et al., 2005), they will be important pollinators in the subtropical alpine ecosystems.

Bumble bees are the most important pollinators in alpine ecosystems due to their high pollination efficiency, floral constancy, and wide floral-use capacity (Bingham & Orthner, 1998; Fang & Huang, 2012). In the subtropical climate zone of Asia, species diversity and abundance of bumble bees increased with higher elevation, e.g., 3000–4000 m in the Himalayas (Saini et al., 2012). There are nine bumble bee species in Taiwan and most of them are seen in high mountain regions (Starr, 1992). Although we did not discriminate bumble bee species in the present study, the study of plant-bumble bee network conducted in the Himalaya-Hengduan Mountains in southern China reported that wide linkages between bumble bees and alpine plant species were formed by the intraspecific variation in floral choice (Liang et al., 2021). There are many studies demonstrating that the floral choice of bumble bees strongly depends on the body size and glossa length (e.g., Inouye, 1980; Harder, 1985; Pyke et al., 2011). To clarify how bee-visited plants share pollinators during the active period of worker bees, further studies are necessary.

Plant-pollinator networks may differ among subtropical/tropical alpine ecosystems located in different geographic regions. In the tropical alpine communities in the Venezuelan Andean paramo (3000–4200 m a.s.l.), for instance, flowering of most species occurred during the rainy season (May–November) although some species bloomed throughout the year (Pelayo et al., 2019). Major flower visitors were bumble bees (36.5%) and hummingbirds (43.5%), while dipteran insects were less common (4.1%). Bumble bees and hummingbirds were specialized to specific plants for foraging (low niche overlap), and flowering progressed continuously among plant species during the rainy season. Thus, the taxonomic composition of flower visitors and the flowering pattern of alpine plant communities in the Andean paramo were very different from the subtropical ecosystem in Taiwan. Dominance of dipteran insects (generalist pollinators), high humidity, and the existence of winter (December to April during which minimum temperature often decreases below zero) may characterize the plant-pollinator networks in the subtropical alpine ecosystem of Taiwan.

### **Conclusions**

The present study successfully draws a whole structure of flowering phenology and dynamics of major flower visitors in the subtropical alpine ecosystem. Because of the high proportion of endemic species and isolated alpine regions, the diversity of alpine vegetation in Taiwan is extremely sensitive to climate change. For instance, several plant species from the lower elevation have been reported to migrate upwards into the alpine regions, which may elevate the risk of extinction of several alpine species (Chou et al., 2011; Kuo et al., 2021). Furthermore, a higher risk of extinction is predicted for cold-adapted bumble bees under global warming in Taiwan (Lu & Huang, 2023). On the other hand, the symbiosis between dipteran insects and wild flowers is expected to be robust under climate change (Iler et al., 2013; Doyle et al., 2020). It implies that species compositions and plant-pollinator networks in the alpine ecosystems will likely be modified differently between bee-pollinated and fly-pollinated plants by climate change.

### **Acknowledgements**

We are grateful to M. T. Kimura, H. S. Ishii, A. Shibata, Y. Shiotani, Jing-Yi Lu, Xin-Ze Lu, Jun-Ho Wu, and Ing-Tse Chen for their assistance in the field surveys. This study is partly supported by JSPS KAKENHI (grant no. 15H02641, 22H02695) and National Science and Technology Council (grant no. 106WFA0151086,

106WFA0150943)

## References

- Amsalem, E., Grozinger, C. M., Padilla, M., & Hefetz, A. (2015). Bumble bee sociobiology: the physiological and genomic bases of bumble bee social behaviour. *Advances in Insect Physiology* , 48, 37–93.
- Bergman, P., Molau, U., & Holmgren, B. (1996). Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. *Arctic and Alpine Research* , 28, 196–202.
- Bingham, R. A., & Orthner, A. R. (1998). Efficient pollination of alpine plants. *Nature* , 391, 238–239.
- Bischoff, M., Campbell, D. R., Lord, J. M., & Robertson, A. W. (2013). The relative importance of solitary bees and syrphid flies as pollinators of two outcrossing plant species in the New Zealand alpine. *Austral Ecology* , 38, 169–176.
- Bosch, J., Retana, J., & Cerdá, X. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* , 109, 583–591.
- Bonelli, M., Eustacchio, E., Avesani, D., Michelsen, V., Falaschi, M., Caccianiga, M., Gobbi, M., & Casartelli, M. (2022). The early season community of flower-visiting arthropods in a high-altitude alpine environment. *Insects* , 13, 393.
- Buytaert, W., Cuesta-Camacho, F., & Tobón, C. (2010). Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Global Ecology and Biogeography* , 20, 19–33.
- Brook, S. M., et al. (2022). Package ‘*glmmTMB*’: Generalized linear mixed models using template model builder. R package version 1.1.6.
- Chou, C.-H., Huang, T.-J., Lee, Y.-P., Chen, C.-Y., Hsu, T.-W., & Chen, C.-H. (2011). Diversity of the alpine vegetation in central Taiwan is affected by climate change based on a century of floristic inventories. *Botanical Studies* , 52, 503–516.
- Corbet, S. A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., & Smith, K. (1993). Temperature and the pollinating activity of social bees. *Ecological Entomology* , 18, 17–30.
- Dormann, C. F. et al. (2022). Package ‘*bipartite*’: Visualising bipartite networks and calculating some (ecological) indices. R package version 2.18.
- Doyle, T., Hawkes, W. L. S., Massy, R., Powney, G. D., Menz, M. H. M., & Wotton, K. R. (2020). Pollination by hoverflies in the Anthropocene. *Proceedings of the Royal Society B* , 287, 20200508.
- Fang, Q., & Huang, S.-Q. (2012). Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. *PLoS ONE* , 7, e32663.
- Fontaine, C., Dajoz, I., Meriguet, J., & Loreau, M. (2005). Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* , 4, e1.
- Harder, L. D. (1985). Morphology as a predictor of flower choice by bumble bees. *Ecology* , 66, 198–210.
- Herrera, C. M. (1987). Components of pollinator “quality”: comparative analysis of a diverse insect assemblage. *Oikos* , 50, 79–90.
- Holway, J. G., & Ward, R. T. (1965). Phenology of alpine plants in northern Colorado. *Ecology* , 46, 73–83.
- Hsieh, C.-F. (2002). Composition, endemism and phytogeographical affinities of the Taiwan flora. *Taiwania* , 47, 298–310.
- Iler, A. M., Inouye, D. W., Høye, T. T., Miller-Rushing A. J., Burkle, L. A., & Johnston, E. B. (2013). Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Global Change Biology* , 19, 2348–2359.

- Inouye, D. W. (1980). The effect of proboscis and corolla tube length on patterns and rates of flower visitation by bumblebees. *Oecologia* , 45, 197–201.
- Inouye, D. W. (2020). Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences* , 1469, 26–37.
- Inouye, D. W., Larson, B. M. H., Ssymank, A., & Kevan, P. G. (2015). Flies and flowers III: Ecology of foraging and pollination. *Journal of Pollination Ecology* , 16, 115–133.
- Jabis, M. D., Winkler, D. E., & Kueppers, L. M. (2020). Warming acts through earlier snowmelt to advance but not extend alpine community flowering. *Ecology* , 101, e03108.
- Kearns, C. A. (1992). Anthophilous fly distribution across an elevation gradient. *American Midland Naturalist* , 127, 172–182.
- Kearns, C. A., & Inouye, D. W. (1994). Fly pollination of *Linum lewisii* (Linaceae). *American Journal of Botany* , 81, 1091–1095.
- Kudo, G. (2016). Landscape structure of flowering phenology in alpine ecosystems: significance of plant–pollinator interactions and evolutionary aspects. In: Kudo, G. (ed) Structure and function of mountain ecosystems in Japan. Springer, Berlin, pp. 41–62.
- Kudo, G. (2022). Outcrossing syndrome in alpine plants: implications for flowering phenology and pollination success. *Ecological Research* , 37, 288–300.
- Kudo, G., & Suzuki, S. (2004). Flowering phenology of tropical-alpine dwarf trees on Mount Kinabalu, Borneo. *Journal of Tropical Ecology* , 20, 563–571.
- Kuo, C.-C., Su, Y., Liu, H.Y., & Lin, C.T. (2021). Assessment of climate change effects on alpine summit vegetation in the transition of tropical to subtropical humid climate. *Plant Ecology* , 222, 933–951.
- Larson, B. M. H., Kevan, P. G., & Inouye, D. W. (2001). Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Canadian Entomology* , 133, 439–465.
- Liang, H., Zhao, Y.-H., Rafferty, N. E., Ren, Z.-X., Zhong, L., Li, H.-D., Li, D.Z., & Wang, H. (2021). Evolutionary and ecological factors structure a plant–bumblebee network in a biodiversity hotspot, the Himalaya–Hengduan Mountains. *Functional Ecology* , 35, 2523–2535.
- Lu, M.-L., & Huang, J.-Y. (2023). Predicting negative effects of climate change on Taiwan’s endemic bumblebee *Bombus formosellus* . *Journal of Insect Conservation* , 27, 193–203.
- Makrodimos, N., Blionis, G., Krigas, N., & Vokou, D. (2008). Flower morphology, phenology and visitor patterns in an alpine community on Mt Olympos, Greece. *Flora* , 203, 449–468.
- McCabe, L. M., & Cobb, N. S. (2021). From bees to flies: global shift in pollinator communities along elevation gradient. *Frontiers in Ecology and Evolution* , 8, 626124.
- McCall, C., & Primack, R. B. (1992). Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. *American Journal of Botany* , 79, 434–442.
- McGuire, A. D., & Armbruster, W. S. (1991). An experimental test for reproductive interactions between two sequentially blooming *Saxifraga species* (Saxifragaceae). *American Journal of Botany* , 78, 214–219.
- Miller-Struttman, N. E., & Galen, C. (2014). High-altitude multi-taskers: bumble bee food plant use broadens along an altitudinal productivity gradient. *Oecologia* , 176, 1033–1045.
- Mizunaga, Y., & Kudo, G. (2017). A linkage between flowering phenology and fruit-set success of alpine plant communities with reference to the seasonality and pollination effectiveness of bees and flies. *Oecologia* , 185, 453–464.
- Oksanen, J. *et al.* (2022). *vegan* : Community Ecology Package. R package version 2.6-4.

- Pelayo, R. C., Soriano, P. J., Márquez, N. J., & Navarro, L. (2019). Phenological patterns and pollination network structure in a Venezuelan paramo: a community-scale perspective on plant-animal interactions. *Plant Ecology and Diversity* ,12, 6-7–618.
- Pelayo, R. C., Llambi, L. D., Gámez, L. E., Barrios, Y. C., Ramirez, L. A., Torres, J. E., & Cuesta, F. (2021). Plant phenology dynamics and pollination networks in summits of the high tropical Andes: a baseline for monitoring climate change impacts. *Frontiers in Ecology and Evolution* , 9, 679045.
- Pyke, G. H., Inouye, D. W., & Thomson, J. D. (2011). Activity and abundance of bumble bees near Crested Butte, Colorado: diel, season, and elevation effects. *Ecological Entomology* , 36, 511–521.
- R Core Team. (2022). R: A language and environment for statistical computing. R foundation for statistical computing.
- Rotheray, G., & Gilbert, F. (2011). The natural history of hoverflies. Forrester Text, London.
- Saini, M. S., Raina, R. H., & Khan, Z. H. (2012). Species diversity of bumblebees (Hymenoptera: Apidae) from different mountain regions of Kashmir Himalayas. *Journal of Scientific Research* , 4, 263–272.
- Starr, C. K. (1992). The bumble bees (Hymenoptera: Apidae) of Taiwan. *Bulletin of the National Museum of Natural Science* , 3, 139–157.
- Strathdee, A., & Bale, J. (1998). Life on the edge: insect ecology in arctic environments. *Annual Reviews in Entomology* , 43, 85–106.
- Tai, K.-C., Shrestha, M., Dyer, A. G., Yang, E.-C., Wang, C.-N. (2020). Floral color diversity: how are signals shaped by elevational gradient on the tropical–subtropical mountainous island of Taiwan? *Frontiers in Plant Science* , 11, 582784.
- Tiusanen, M., Hebert, P. D. N., Schmidt, N. M., & Roslin, T. (2016). One fly to rule them all—muscid flies are the key pollinators in the Arctic. *Proceedings of Royal Society B*, 283, 20161271.
- Totland, Ø. (1994). Influence of climate, time of day and season, and flower density on insect flower visitation in alpine Norway. *Arctic and Alpine Research* , 26, 66–71.
- Thórhallsdóttir, T. E. (1998). Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia* , 114, 43–49.

## Figure legends

**Figure 1.** Seasonal transition of air temperature in the study site (at 3060 m elevation). Daily minimum, mean, and maximum temperatures are shown. Arrows indicate observation terms in 2017 and 2018.

**Figure 2.** Seasonal changes in the number of plant species at flowering (only entomophilous species) in 2017 (pale colors) and 2018 (dark colors). Plant species were classified into bee-visited (red), fly-visited (blue), and other species (gray). The percentage of blooming species in each term is shown in each of the bee-visited and fly-visited species (excluding exotic species).

**Figure 3.** Seasonal changes in the flower number of bee-visited and fly-visited species per plot in 2017 and 2018. Throughout the 21 permanent plots, flowering of 21 bee-visited species and 53 fly-visited species was recorded. The box plots indicate the flower number of individual species in individual plots. See Table 3 for statistical results. Bee-visited plants: red box plots with closed circles; fly-visited plants: blue box plots with open circles.

**Figure 4.** Seasonal changes in the abundance of major flower-visitors (a: bumble bees, b: syrphid flies, c: non-syrphid flies) in 2017 (filled circles and solid line) and 2018 (open circles and broken line).

**Figure 5.** Networks between flower-visiting insects and plants throughout the study periods. (a) A network between order-level insects and plant species; (b) a network between major groups of insects and plant

species. Shannon-Weaver’s  $H'$  diversity index of each insect group is shown. See Table S1 for the species code of major plant species.

**Figure 6.** Relationships between the mean abundance of flower-visiting insects and the number of blooming species observed in each term. (a) Bee-visited plants; (b) fly-visited plants.

**Table 1.** Species diversity of floral resources and the number of flowering species in the fixed plots in each census. As an index of species diversity, Shannon-Wiener’s  $H'$  values are shown. In total, flowering of 81 species was observed in the plots throughout the survey periods and was classified into bee-visited ( $N = 21$ ), fly-visited ( $N = 53$ ), and unclear ( $N = 7$ ) according to their floral visitors.

Plant species		2017	2017	2017	2018	2018	2018
		Early	Middle	Late	Early	Middle	Late
All species (81 spp.)	$H'$ index	2.61	3.71	3.73	2.81	4.39	3.34
	No. species	23	46	43	35	56	44
Bee-visited species (21 spp.)	$H'$ index	0.31	2.55	2.14	0.98	3.26	1.38
	No. species	3	13	14	7	18	16
Fly-visited species (53 spp.)	$H'$ index	2.38	2.75	3.15	2.32	3.44	3.01
	No. species	19	29	28	26	34	28

**Table 2.** Results of GLMM conducted for the flower number of bee-visited and fly-visited species per plot in early, middle,

Variable
Intercept (Bee flower, Early, Y2017)
Fly flower
Middle season
Late season
Year 2018
Fly flower × Middle season
Fly flower × Late season

**Table 3.** Frequencies of flower visitors observed throughout the censuses in 2017 and 2018.

Order	Taxonomic group	Count	%	Notes
Hymenoptera	bumble bee	3770	24.9	<i>Bombus</i> spp.
	honey bee	583	3.9	<i>Apis</i> spp.
	solitary bee	229	1.5	Halictidae, Andrenidae, Megachilidae, etc.
	wasp & other bee	26	0.2	Vaspididae, etc.
Diptera	syrphid fly	3207	21.2	Syrphidae
	dagger fly	166	1.1	Empididae
	other fly	6117	40.4	Muscidae, Anthomyiidae, Tachinidae, Tephritidae, etc.
	butterfly	75	0.5	Pieridae, Nymphalinae, Satyrinae, Lycaenidae, etc.
Lepidoptera	skipper	65	0.4	Hesperiidae

Coleoptera	moth	193	1.3	unspecified Scarabaeidae, Mordellidae, Nitidulidae, Cantharidae, etc.
	small beetle	571	3.8	
Hemiptera		119	0.8	Pentatomidae, Anthocoridae, etc.
Other		6	0.04	unspecified

**Table 4.** Results of zero-inflated GLMs conducted for the abundance of bumble bees (a), syrphid flies (b), and non-syrphid flies (c).

<b>(a) Bumble bee model</b>				
Variable	Coefficient	SE	z value	p value
Conditional model				
Intercept	-20.26	2.77	-7.3	<0.0001***
Day N	0.19	0.027	7.4	<0.0001***
Day N <sup>2</sup>	-4.29 × 10 <sup>-4</sup>	6.3 × 10 <sup>-5</sup>	-6.8	<0.0001***
Year (2018)	-2.35	3.11	-0.75	0.45
Temperature	0.037	0.008	4.6	<0.0001***
Relative humidity	-0.0058	0.0019	-3	0.0025 **
Day N × Year (2018)	0.043	0.030	1.5	0.15
Day N <sup>2</sup> × Year (2018)	-1.4 × 10 <sup>-4</sup>	7.0 × 10 <sup>-5</sup>	-1.8	0.059
Zero-inflate model				
Intercept	-2.56	0.29	-8.8	<0.0001***
<b>(b) Syrphid fly model</b>				
Conditional model				
Intercept	3.97	1.45	2.7	0.006 **
Day N	0.032	0.015	2.2	0.027 *
Day N <sup>2</sup>	-1.2 × 10 <sup>-4</sup>	3.7 × 10 <sup>-5</sup>	-3.2	0.0013 **
Year (2018)	10.38	1.74	6.0	<0.0001***
Temperature	-0.057	0.0078	-7.3	<0.0001***
Relative humidity	-0.036	0.0017	-21.3	<0.0001***
Day N × Year (2018)	-0.12	0.018	-6.7	<0.0001***
Day N <sup>2</sup> × Year (2018)	3.5 × 10 <sup>-4</sup>	4.4 × 10 <sup>-5</sup>	7.8	<0.0001***
Zero-inflate model				
Intercept	-3.67	0.47	-7.8	<0.0001***
<b>(c) Non-syrphid fly model</b>				
<b>(c) Non-syrphid fly model</b>				
Conditional model				
Intercept	19.3	0.91	21.1	<0.0001***
Day N	-0.16	0.0094	-16.7	<0.0001***
Day N <sup>2</sup>	3.8 × 10 <sup>-4</sup>	2.4 × 10 <sup>-5</sup>	16.2	<0.0001***
Year (2018)	4.62	1.38	3.4	0.0008***
Temperature	0.0092	0.0056	1.6	0.10
Relative humidity	-0.0092	0.0013	-7.3	<0.0001***
Day N × Year (2018)	-0.068	0.014	-4.8	<0.0001***
Day N <sup>2</sup> × Year (2018)	2.2 × 10 <sup>-4</sup>	3.5 × 10 <sup>-5</sup>	6.2	<0.0001***
Zero-inflate model				
Intercept	-5.3	1.00	-5.29	<0.0001***

figures/Fig1-Kudo-etal/Fig1-Kudo-etal-eps-converted-to.pdf

figures/Fig2-Kudo-etal/Fig2-Kudo-etal-eps-converted-to.pdf

figures/Fig3-Kudo-etal/Fig3-Kudo-etal-eps-converted-to.pdf

figures/Fig4-Kudo-etal/Fig4-Kudo-etal-eps-converted-to.pdf

figures/Fig5-Kudo-etal/Fig5-Kudo-etal-eps-converted-to.pdf

figures/Fig6-Kudo-etal/Fig6-Kudo-etal-eps-converted-to.pdf