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

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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 an 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, flowering phenology, fly, pollinator, subtropical alpine

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1 | INTRODUCTION

Alpine ecosystems in higher latitudes are characterized by cool and short growing seasons, 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 et al., 2015).

Bumble bees, syrphid flies, and non-syrphid flies are the most common and dominant pollinators in alpine ecosystems (Inouye, 2020; Kearns, 1992; Pyke et al., 2011). 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-Struttmann & 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 (McCabe & Cobb, 2021; Strathdee & Bale, 1998). Thus, relative importance of the two major flower-visiting insect groups, that is, 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 the lower limits of alpine zones are located at high elevations and plant communities are composed of many endemic species within small and isolated mountain areas (Buytaert et al., 2010). 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 the community scale and flower-visiting insects is crucial.

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 the 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 in elevation. 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 2 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.

2 | METHODS

2.1 | 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 and 17–19°C, respectively.

2.2 | Field observation

Observations of plant phenology and flower-visiting insects were conducted five times each year; on May 26–30 (Term 1), June 21–23 (Term 2), July 13–15 (Term 3), August 7–9 (Term 4), and August 28–30 (Term 5) in 2017; on June 5–8 (Term 1), June 29 (Term 2), July 29–31 (Term 3), August 13–14 (Term 4), and September 3–5 (Term 5) in 2018. Air temperature was measured at 1-h intervals at the height of 1 m above ground using a Tidvit 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 all of the vegetation types in the study site (Figure S1 and Table 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, and observation time in each plot was shown in Table S1. In total, flower productions of 81 species were recorded across plots during 2 years. Furthermore, a phenological survey of flowering occurrence was conducted for all entomophilous plant species in this area. In each term (Terms 1–5), we walked around the whole area in which fixed plots were set (within a 2.5 × 1.0 km area), and recorded flowering species. In total, flowering phenologies of 130 species were recorded throughout the survey periods (Table S2).

For the survey of flower-visiting insects, we repeated 30-min censuses of flower visitors by walking 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 to cover the whole area in which all fixed plots were included. 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 h) and 102 censuses (51 h) were conducted in 2017 and 2018, respectively. At the beginning of each census, air temperature and relative humidity were measured using a handy meteorological device (Kestrel 2000, Mistral Instruments, USA). Flower-visiting insects were classified into the 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, 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 at the width of 2 m along the census trails. Undetermined flower visitors that we failed to classify into specific groups were excluded from the analysis. 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 Section 3). 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.

2.3 | Analyses

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

2.3.1 | Comparison of flowering phenology between bee-visited and fly-visited species

Using the flowering records of two seasons, flowering patterns of bee-visited and fly-visited plants (excluding exotic species) were analyzed. Before the analysis, each survey period (Terms 1–5) in each year was replaced by the week number of the year, ranging from the 21st to 36th weeks (Table S3). Then, a generalized linear model (GLM) with a Poisson error distribution and a log-link function was conducted in which the number of blooming species at each census time was a responding variable, week number (both with a linear and quadratic term) and observation year (2017, 2018) were set as explanatory variables, and the total number of flowering species recorded in each year was set as an offset term after log-transformation. Interactions between week and year were also included in the GLM. The best-fit model was selected based on the Akaike's information criterion (AIC). In the GLM, bee-visited plants and fly-visited plants were separately analyzed.

Flowering duration of individual species in the study area were obtained as the period (week) from the first to the final record of flowering (Table S3). In the calculation of flowering duration, phenological records of 2017 and 2018 were pooled because the GLM results showed no yearly difference in flowering phenology (see Section 3). Flowering duration of individual species were classified into six ranks as follows; 1–3, 4–6, 7–9, 10–12, 13–15, and >15 weeks. To test the difference in flowering periods between bee-visited and fly-visited species, distributions of flowering ranks in bee-visited and fly-visited species were compared by a Kolomogorov–Smirnov test (K–S test).

2.3.2 | 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 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 bee-visited and fly-visited plant species because of the dominance of these types (see Section 3). 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.

2.3.3 | Seasonal dynamics of flower visitors

Because hymenopteran and dipteran insects occupied >90% of all flower visitors (see Section 3), factors affecting the visitation frequencies of bees and flies were separately analyzed by GLMs. Visitation frequencies of bumble bees, syrphid flies, and non-syrphid flies in each census were used as responding variables, that is, three GLMs were constructed. Other insect groups were excluded from the analysis due to low visitation frequencies (see Section 3). 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 (Brook et al., 2022) 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

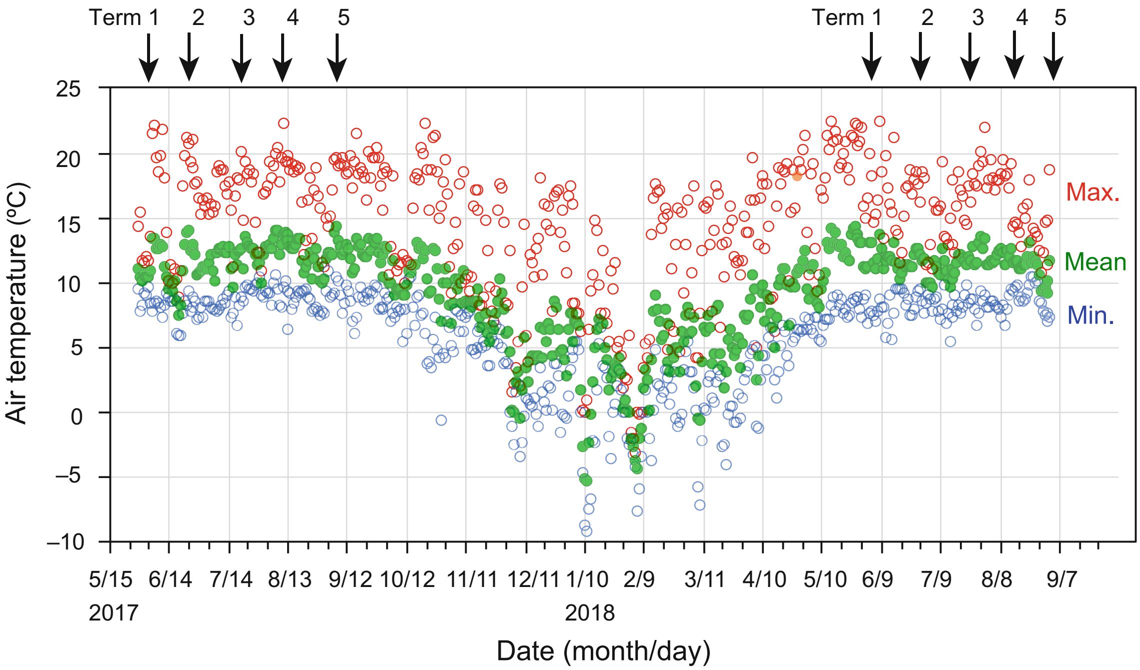


FIGURE 1 Seasonal transition of air temperature in the study site (at 3060 m elevation). Daily minimum, mean, and maximum temperatures are shown. Arrows indicate observation terms in 2017 and 2018.

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, dissimilarity 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 analyzed 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.

3 | RESULTS

3.1 | Ambient temperature

Transition of air temperature in the study site indicated relatively stable thermal conditions during the survey period (Terms 1–5) in both years (Figure 1). Daily mean temperatures during the flowering season ranged between 10 and 15°C, daily minimum temperatures were 6 and 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.

3.2 | Flowering phenology

Throughout the survey, flowering of 130 species (42 families) was recorded, including 4 exotic species (*Hypochaeris radicata*, *Taraxacum officinale*, *Trifolium repens*, and *Veronica persica*). Major families were Asteraceae (18 spp.), Rosaceae (16 spp.), Ranunculaceae (10 spp.), and Orchidaceae (8 spp.). 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 S2).

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-July 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) (Figure 2a). Fly-visited plants showed a higher proportion of flowering

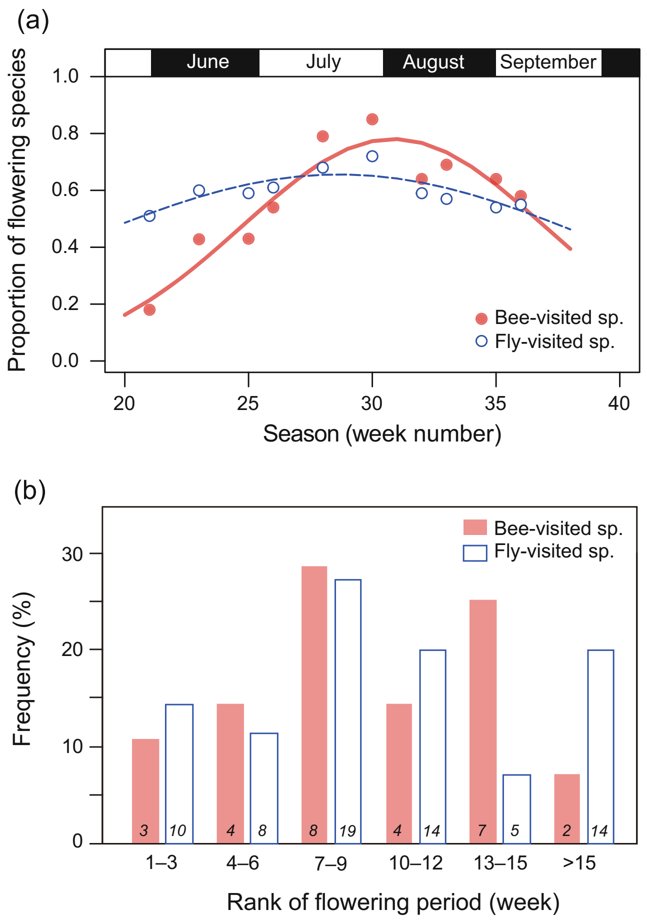


FIGURE 2 (a) Flowering patterns of bee-visited and fly-visited species, that is, seasonal changes in the proportion of flowering species in the study site. Fitting curves obtained from the GLMs are shown. Seasonal trend was significant for bee-visited plants ($p < 0.01$), while not significant for fly-visited plants ($p > 0.1$). (b) Frequency distributions (%) of flowering durations of bee-visited and fly-visited species in the study site. Flowering periods of individual species were ranked at 3-week intervals. Actual number of species included in each rank is shown in each bar. There was no significant difference between the pollination types ($p = 0.87$ by K–S test). GLMs, generalized linear models; K–S, Kolomogorov–Smirnov.

species throughout the season (≥50%) with a peak in late July (72%). The GLM result showed that both linear and quadratic terms of season, that is, week number, were not significant ($z = 1.57$, $p = 0.12$ and $z = -1.58$, $p = 0.11$, respectively), and year was excluded from the explanatory variable by AIC, suggesting a less clear seasonal trend. 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%). The GLM result showed significant effects of seasonal progress in both linear ($z = 3.09$, $p = 0.002$) and quadratic terms ($z = -2.94$, $p = 0.003$), while the effect of year was excluded by AIC. These results indicate that flowering patterns of bee-visited plants and fly-visited plants are significantly different even within the same communities.

Flowering durations of individual species within the site highly varied in both bee-visited and fly-visited plants (Figure 2b). Although several fly-visited species showed long flowering periods (>15 weeks), there was no significant difference in the distribution patterns of flowering durations between bee-visited and fly-visited plants ($D = 0.24$, $p = 0.87$ by K–S test).

3.3 | Flower production

In the fixed 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 to 3.3, while seasonal changes in fly-visited species were moderate in which H' values ranged from 2.3 to 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 (Figure 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 (Figure 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 (Figure 3).

3.4 | Composition and foraging activity of flower-visiting insects

Throughout the 208 censuses (104 h) across 5 terms in 2017 and 2018, 15,127 insects were recorded on the

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

FIGURE 3 Seasonal changes in the flower number of bee-visited and fly-visited species per plot in 2017 (Y17) and 2018 (Y18). 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 2 for statistical results. Bee-visited plants: filled boxes and circles in red color; fly-visited plants: blue open boxes and circles in blue color.

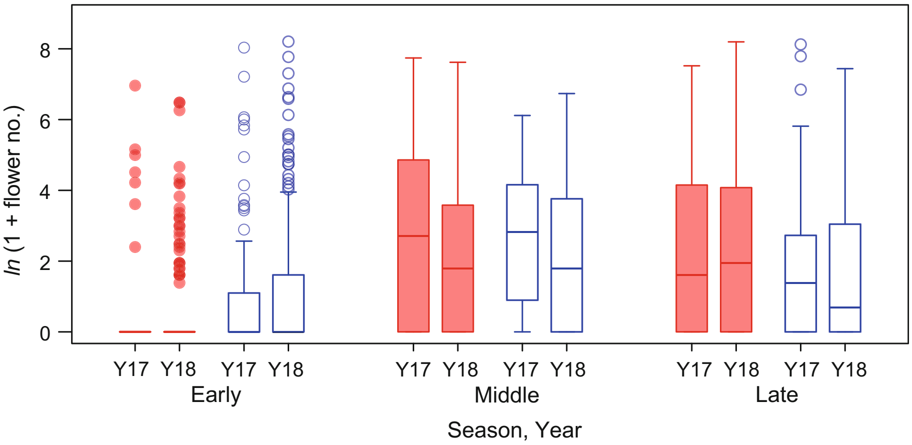


TABLE 2 Results of generalized linear mixed model (GLMM) conducted for the flower number of bee-visited and fly-visited species per plot in early, middle, and late seasons during 2017 and 2018.

Variable	Coefficient	SE	z-value	p-value
Intercept (Bee flower, Early, Y2017)	3.260	0.400	8.1	$<0.0001^{***}$
Fly flower	−0.759	0.440	−1.7	0.084
Middle season	0.540	0.014	38.2	$<0.0001^{***}$
Late season	0.909	0.013	67.4	$<0.0001^{***}$
Year 2018	−0.270	0.063	−42.9	$<0.0001^{***}$
Fly flower × middle season	−0.053	0.017	−3.1	0.0022^{**}
Fly flower × late season	−0.167	0.017	−10.1	$<0.0001^{***}$

$^{**}p < 0.01$, $^{***}p < 0.001$.

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 (Figure 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

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	*Bombus* spp.
	Honey bee	583	3.9	*Apis* spp.
	Solitary bee	229	1.5	Halictidae, Andrenidae, Megachilidae, etc.
	Wasp and other bee	26	0.2	Vaspidae, etc.
Diptera	Syrphid fly	3207	21.2	Syrphidae
	Dagger fly	166	1.1	Empididae
	Other fly	6117	40.4	Muscidae, Anthomyiidae, Tachinidae, Tephritidae, etc.
Lepidoptera	Butterfly	140	0.9	Pieridae, Nymphalinae, Satyrinae, Lycaenidae, Hesperiidae, etc.
	Moth	193	1.3	Unspecified
Coleoptera	Small beetle	571	3.8	Scarabaeidae, Mordellidae, Nitidulidae, Cantharidae, etc.
Hemiptera		119	0.8	Pentatomidae, Anthocoridae, etc.
Other		6	0.04	unspecified

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.

3.5 | 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 (Figure 5a). Dipteran insects visited the most diverse flowers ($H' = 4.81$) and showed the largest linkages with plant species among the 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. 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 (Figure 5b), syrphid flies, non-syrphid flies, and bumble bees linked to 62 (89%), 65 (93%), and 50 plant species (71%), respectively. The diversity index values for visiting flowers were similarly high ($H' = 4.31$–4.54). Dissimilarities of foraging flowers were relatively high between bumble bees and non-syrphid flies (0.72) and between bumble bees and syrphid flies (0.65), while the dissimilarity between non-syrphid and syrphid flies was at moderate level (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 ($z = 2.39$, $p = 0.017$; Figure 6a), whereas the number of fly-visited species at the flowering stage was independent of the abundance of dipteran insects ($z = -0.53$, $p = 0.60$; Figure 6b).

4 | 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

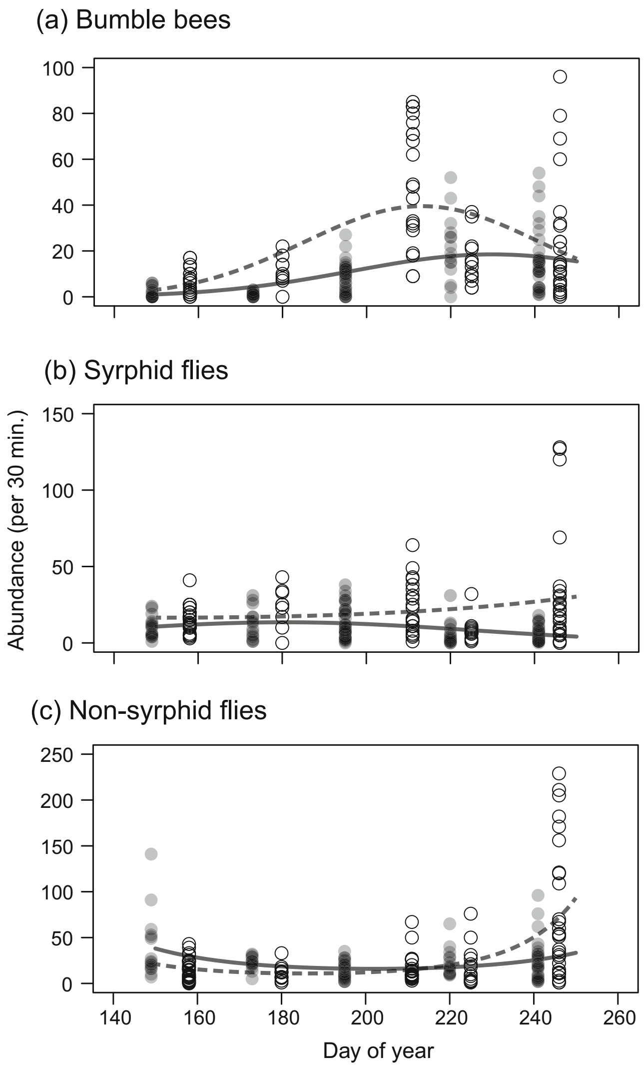


FIGURE 4 Seasonal changes in the abundance of major flower-visitors (a: bumble bees, b: syrphid flies, c: non-syrphid flies) in 2017 (filled circles and solid line) and 2018 (open circles and broken line).

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.

4.1 | 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 (Amsalem et al., 2015; Mizunaga & Kudo, 2017; Pyke et al., 2011). Thus, the availability of pollination service by bumble bees commonly increased with seasonal progress in alpine ecosystems although actual visitation frequency might vary depending on the availability of floral resources and weather conditions during the observation time (Kudo, 2022). In contrast, less clear seasonality in dipteran insects (including unpredictable outbreaks) is reported in the previous studies (Mizunaga & Kudo, 2017; Totland, 1994). 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 diverse species composition and species-specific lifecycle of anthophilous dipteran insects (Larson et al., 2001). For instance, the appearance time of syrphid flies highly varies among species and some species are known to have flexible lifecycle synchrony depending on climate and resource conditions that affect larval growth rate (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 (Bergman et al., 1996; Corbet et al., 1993). 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

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

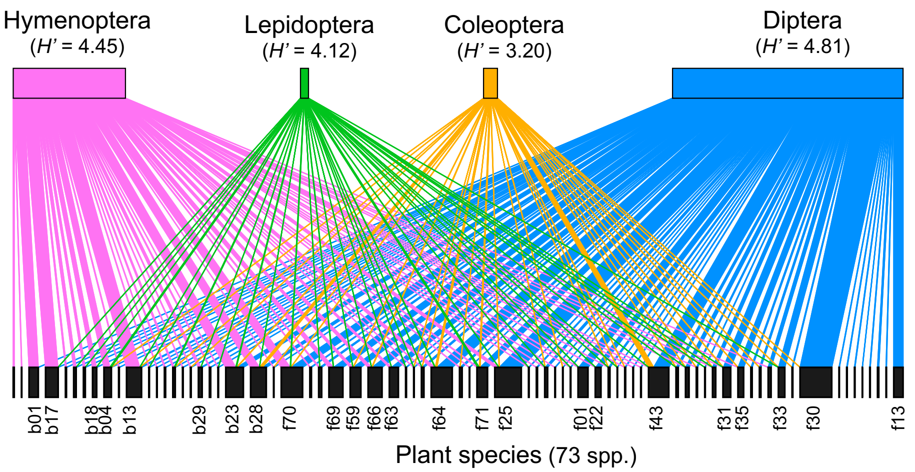
Variable	Coefficient	SE	z-value	p-value
(a) Bumble bee model				
Conditional model				
Intercept	−20.26	2.77	−7.3	<0.0001***
Day N	0.19	0.27×10^{-1}	7.4	<0.0001***
Day N^2	-4.29×10^{-4}	0.63×10^{-6}	−6.8	<0.0001***
Year (2018)	−2.35	3.11	−0.8	0.45
Temperature	0.37×10^{-1}	0.08×10^{-1}	4.6	<0.0001***
Relative humidity	-0.58×10^{-2}	0.19×10^{-2}	−3.0	0.0025**
Day N × year (2018)	0.43×10^{-1}	0.30×10^{-1}	1.5	0.15
Day N^2 × year (2018)	-0.14×10^{-3}	0.70×10^{-4}	−1.8	0.059
Zero-inflate model				
Intercept	−2.56	0.29	−8.8	<0.0001***
(b) Syrphid fly model				
Conditional model				
Intercept	3.97	1.45	2.7	0.006**
Day N	0.32×10^{-1}	0.15×10^{-1}	2.2	0.027*
Day N^2	-0.12×10^{-3}	0.37×10^{-4}	−3.2	0.0013**
Year (2018)	10.38	1.74	6.0	<0.0001***
Temperature	-0.57×10^{-1}	0.78×10^{-2}	−7.3	<0.0001***
Relative humidity	-0.36×10^{-1}	0.17×10^{-2}	−21.3	<0.0001***
Day N × year (2018)	−0.12	0.18×10^{-1}	−6.7	<0.0001***
Day N^2 × year (2018)	0.35×10^{-3}	0.44×10^{-4}	7.8	<0.0001***
Zero-inflate model				
Intercept	−3.67	0.47	−7.8	<0.0001***
(c) Non-syrphid fly model				
Conditional model				
Intercept	19.30	0.91	21.1	<0.0001***
Day N	−0.16	0.94×10^{-2}	−16.7	<0.0001***
Day N^2	0.38×10^{-3}	0.24×10^{-4}	16.2	<0.0001***
Year (2018)	4.62	1.38	3.4	0.0008***
Temperature	0.92×10^{-2}	0.56×10^{-2}	1.6	0.10
Relative humidity	-0.92×10^{-2}	0.13×10^{-2}	−7.3	<0.0001***
Day N × year (2018)	-0.68×10^{-1}	0.14×10^{-1}	−4.8	<0.0001***
Day N^2 × year (2018)	0.22×10^{-3}	0.35×10^{-4}	6.2	<0.0001***
Zero-inflate model				
Intercept	−5.30	1.00	−5.3	<0.0001***

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

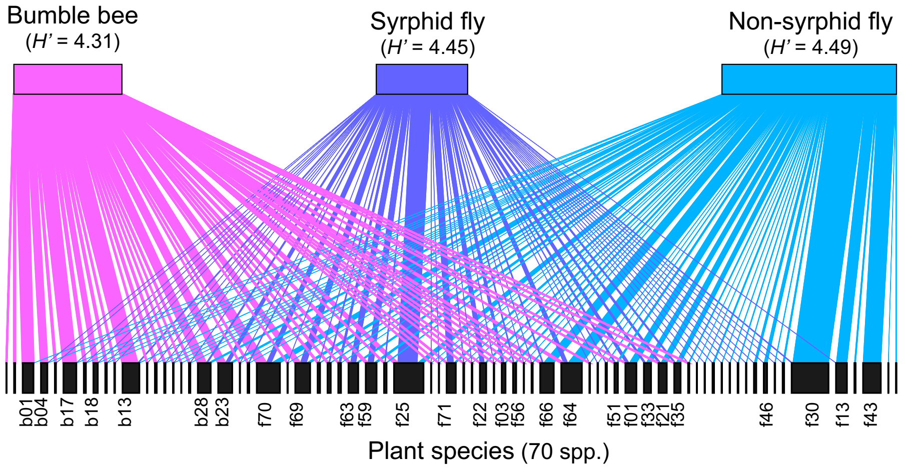
on the ambient temperature in alpine environments (McCall & Primack, 1992; Totland, 1994). For instance, a field survey of flower visitors in the alpine site of northern Japan reported that syrphid flies were most sensitive to ambient temperature, while foraging activity of non-syrphid flies was independent 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

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 S2 for the species code of major plant species.

(a) Order level network



(b) Major group level network



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 (Figure 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).

4.2 | 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; Jabis et al., 2020; Molau et al., 2005; Thórhallsdóttir, 1998), and some of them focused on the relationship between plants and flower visitors (e.g., Bosch et al., 1997; Iler et al., 2013; Makrodimos et al., 2008; Pelayo et al., 2019, 2021). However, comparative studies of flowering phenology 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

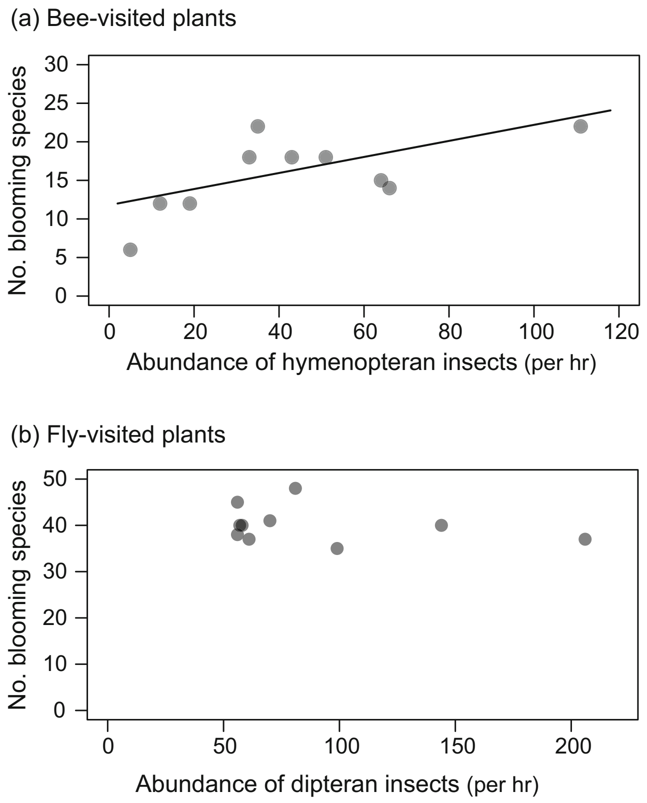


FIGURE 6 Relationships between the mean abundance of flower-visiting insects and the number of blooming species observed in each term. (a) Bee-visited plants; (b) fly-visited plants. A regression line is shown when a significant relationship was detected by GLM ($p < 0.05$). GLM, generalized linear model.

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 an elevational gradient of Taiwan also found evidence 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 at high altitudes 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, that is, temporal dynamics of floral diversity and floral resources, may be influenced by the relative composition of bee-visited and fly-visited species.

4.3 | 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 dissimilarity of foraging flowers between syrphid and non-syrphid flies was moderate (0.57). This means that floral preference varies even within dipteran insects. As syrphid flies have relatively high floral constancy and high pollination efficiency (Fontaine et al., 2005; Kearns, 1992; McGuire & Armbruster, 1991), 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, that is, 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 networks 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., Harder, 1985; Inouye, 1980; 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.

5 | CONCLUSIONS

The present study successfully draws a whole structure of flowering phenology and dynamics of major flower visitors in the subtropical alpine ecosystem. As expected, flowering of bee-visited plants tended to increase in the active season of workers of eusocial bees. In contrast, flowering patterns of fly-visited plants had less clear seasonality, reflecting the unpredictable seasonal activity of dipteran insects. These results strongly suggest that the compositions of bee and fly pollinators can act as a selective force affecting the flowering patterns of alpine plant communities.

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 lower elevations 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 (Doyle et al., 2020; Iler et al., 2013). This 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.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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