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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

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Author Contributions: YM and GK conceived the idea, designed the experiments, conducted field work, analyzed the data, and wrote the manuscript.

Abstract

To clarify the linkage between flowering phenology and pollination success in alpine plant communities, we quantified the seasonality of flower visitors, the temporal transition of floral resources, and the variation in pollination success of alpine plants in northern Japan. Bumble bees, syrphid flies, and non-syrphid flies were the predominant flower visitors. Foraging activity of bumble bees increased toward the late flowering period reflecting the life-cycle of colony development. The activity of syrphid flies was sensitive to ambient temperature, while that of non-syrphid flies remained high throughout the season. Flower production of bee-pollinated plants fluctuated significantly between years with a bimodal pattern peaking in the early and late periods, while flower production of fly-pollinated plants was less variable between years. Fruit-set success of bee-pollinated plants increased considerably from the early to the late flowering period, while the trend for fly-pollinated plants was less marked. Three times more visits of dipteran insects are necessary for fly-pollinated plants to achieve fruiting success comparable to bee-pollinated plants. Bumble bees are potentially excellent pollinators but the visitation frequency is low early in the season. Lower pollination ability of dipteran insects may be compensated for by abundant flower visits. The relationships between flowering phenology and fruit-set success of alpine plant communities highly depend on the type of pollinators.

Key words: Alpine ecosystem, Bumble bee, Diptera, Flower production, Pollinator

Introduction

Hymenopteran and dipteran insects are common and important pollinators in high-altitude and high-latitude environments (Arroyo et al. 1982; Kevan and Baker 1983; Kudo 2016). Most plant species inhabiting these environments can be classified into bee-pollinated, fly-pollinated, or bee-and-fly-pollinated types (Yumoto 1986; Kudo 2016). Bumble bees have an annual social life-cycle and are important pollinators in alpine and boreal ecosystems because of their high pollen transportation ability and flower constancy (Heinrich 1979; Bingham and Orthner 1998; Willmer 2011). The foraging activity of bumble bees varies considerably within a growth season in parallel with the life-cycle of colony development and changes in the community of flowering plants (Pyke et al. 2011; Amsalem et al. 2015). Overwintered queen bees emerge from hibernation early in the summer at low frequency, while worker bees emerge in greater numbers in the middle of the season in keeping with the timing of colony development. In parallel with the seasonal dynamics of foraging activity, the pollination success of bee-pollinated plants varies significantly within and among species depending upon flowering time (Kudo 2006, 2016).

Dipteran insects are ubiquitous flower visitors across wide elevational and latitudinal ranges (Totland 1993, 1994; Elberling and Olesen 1999; Tiusanen et al. 2016), and their importance generally increases with environmental harshness at higher elevations and latitudes (Kevan 1972; Arroyo et al. 1982; McCall and Primack 1992; Elberling and Olesen 1999; Wagner et al. 2016). Although the pollination effectiveness of dipteran insects is assumed to be generally low because of their opportunistic floral visits and their low pollen uptake ability in comparison with hymenopteran insects

63 (Bischoff et al. 2013; Inouye et al. 2015; Orford et al. 2015), they can act as effective
64 pollinators when high visitation rates compensate for low pollination ability (Kearns
65 and Inouye 1994; Orford et al. 2015; Tiusanen et al. 2016). Furthermore, considerable
66 flower constancy is reported in syrphid flies (Goulson and Wright 1998; Campbell et al.
67 2010). A few studies have demonstrated the importance of fly pollination (Larson et al.
68 2001; Tiusanen et al. 2016), but comparative studies of pollination efficiency or of the
69 differences between dipteran pollinators and hymenopteran pollinators are limited
70 (Bischoff et al. 2013; Orford et al. 2015). Furthermore, the seasonal activity of dipteran
71 pollinators has rarely been compared with that of bumble bees in alpine habitats (Kudo
72 2016). Therefore, the relative importance of fly pollination and bee pollination should
73 be evaluated in the same environment.

74 The flowering phenology of alpine plant communities may be affected by various
75 selective forces (both of abiotic and biotic factors) acting on the reproductive success of
76 individual species (Rathcke and Lacey 1985; Kudo 2006). The flowering patterns of
77 alpine plants are strongly influenced by snowmelt regimes and thermal conditions, i.e.,
78 proximate cause of phenological variation (Holway and Ward 1965; Molau et al. 2005;
79 Kudo 2006). At the same time, biological interactions for pollinator acquisition may
80 regulate flowering patterns among species to maximize pollination success, i.e.,
81 ultimate cause of phenological variation (Rathcke and Lacey 1985). If there is a
82 significant difference in seasonal activity between dipteran and hymenopteran
83 pollinators, the flowering patterns of bee- and fly-pollinated species may differ and may
84 reflect seasonal trends in foraging activity specific to particular pollinator types (Kudo
85 2016).

86 The pollination success of alpine plants often reflects the seasonal activity and
87 pollination ability of pollinators (Kudo 2006; Kudo et al. 2011; Straka and Starzomski
88 2015). If the pollination ability of dipteran insects is generally low, the fruit-set success
89 of fly-pollinated plants may be lower than that of bee-pollinated plants in less plenty of
90 visits (Straka and Starzomski 2015). In contrast, the fruit-set success of bee-pollinated
91 plants may vary depending upon flowering time within the growth season, in keeping
92 with the life-cycle of the colony (Kudo et al. 2011). In other words, quantification of
93 seasonal trends of dipteran and hymenopteran pollinators, of flowering structure at
94 community scales, and of pollinator-specific fruit-set success are crucial for
95 understanding the structure and function of pollination systems in alpine ecosystems.
96 Because the flowering of alpine plants progresses along the snowmelt gradient,
97 pollinators can utilize the floral resources of specific plants for long periods by moving
98 short distances in parallel with the progress of snowmelt. Floral composition of alpine
99 plant communities drastically changes along the snowmelt gradient in which not only
100 different species but also same species indicate large variation in flowering time
101 dependent on the snowmelt pattern at micro-scale (Kudo 1991, 2006). Therefore,
102 availability of floral resources for pollinators highly varies spatiotemporally within a
103 local area. Under such a dynamics of flowering patterns, comparisons among plots
104 across the snowmelt gradient are necessary for understanding of plant–pollinator
105 interactions in the alpine ecosystem.
106 In this study, we examined the relative importance of bumble bees and dipteran
107 insects as pollinators of alpine plants, as well as the flowering pattern of alpine plants in
108 relation to pollination mode and seasonality of pollinator activity along the snowmelt
109 gradient in the Taisetsu Mountains, northern Japan. First, we compared the seasonal

110 trends in foraging activity between bumble bees and dipteran insects (syrphid and
111 non-syrphid flies), and their sensitivity to micro-climate conditions. We expected a
112 consistently increasing pattern of foraging activity in bumble bees reflecting their
113 life-cycle, but a diverse array of foraging patterns with a less-clear seasonal trend in
114 dipteran insects. Second, we quantified within-year and between-year patterns of flower
115 production (floral resources) at the community scale with reference to pollination mode.
116 We expected that the flowering pattern of bee-pollinated plants might have a more
117 distinctive seasonal trend than the flowering pattern of fly-pollinated plants if the
118 activity of dipteran insects did not exhibit clear seasonality. Third, we analyzed the
119 relationships between fruit-set success and flowering period with reference to
120 pollination mode. We expected that fruit-set rates of bee-pollinated plants might
121 increase in response to the life-cycle of bumble bees as the season progresses, while
122 seasonal variation in fruit-set rates of fly-pollinated plants would be less clear if the
123 seasonal trend of dipteran insects is obscure. Finally, we compared the relationships
124 between visitation frequency and fruit-set rates in bee-pollinated and fly-pollinated
125 plants to evaluate pollination effectiveness. We expected that the fruit-set rates of
126 bee-pollinated plants would increase more rapidly because of the higher pollination
127 ability of bumble bees in comparison to dipteran insects. Based on these analyses, we
128 discuss the phenological structure of pollination systems in alpine ecosystems.
129

130 **Materials and methods**

131 **Study site**

132 This study was conducted at an alpine site in the central part of Daisetsuzan National
133 Park (Taisetsu Mountains), Hokkaido, northern Japan (43° 33′ N, 142° 53′ E) in 2013

and 2014. Daisetsuzan National Park is the largest national park in Japan. Mt. Asahidake is the highest peak (2291 m), and the tree line is located around 1500–1600 m elevation. The Taisetsu Mountains are characterized by cold and snowy winters, and warm and wet summers. The annual mean temperature at 1700 m elevation is –1.8°C and ranges from –16.1°C in January to 12.6°C in August (average of 2002–2013 measured at the weather station near the site). The plant growth season usually starts in early June and lasts until mid-September. Monthly mean temperature during the summer season is 8.7°C in June, 12.0°C in July, 12.6°C in August, and 7.8°C in September. Monthly mean precipitation is 133 mm in June, 234 mm in July, 346 mm in August, and 245 mm in September.

This study was conducted in six plots (designated O, A, B, C, D, and E; Fig. S1) that were established in 1988 (Kudo and Hirao 2006; Kudo 2016). O plot (50 × 50 m) is located in a fellfield on the plateau, where the soil surface is almost free of snow cover during the winter due to strong winds. The remaining five 20 × 20 m plots, A to E, are arranged on a southeast-facing slope along a snowmelt gradient between 1790–1910 m elevation. Variation in snowmelt conditions largely reflects the heterogeneous winter snow distribution that is determined by topographic features and slope direction. The mean snowmelt time was early June at A plot, mid-June at B plot, early July at C plot, late July at D plot, and early August at E plot (Table S1). The average day of snowmelt during the last 27 years ranged from 4 June at A plot to 3 August at E plot. Because these plots include typical alpine vegetation from fellfield to the bottom of the snowbed, and so cover a wide range of snow conditions, phenological research across the plots enables us to quantify the representative phenological structure of the alpine ecosystem of this region (Kudo 1991, 2016; Kudo and Hirao 2006). All our research on flower

158 visitors and flowering situations (phenology and floral density) was conducted in 2013
159 and 2014.
160
161 **Frequency and seasonality of flower-visiting insects**
162 To determine the frequency and seasonality of flower visitors, insects foraging on
163 flowers and their visited flower species were recorded using a route census method by
164 walking slowly along a fixed route almost every week. The observation route was set
165 depending on the flowering situation in order to connect various plant communities
166 each week. Each observation period was 30 minutes, and we tried to sample more than
167 six times in every week. Because observations were not made under windy, foggy, or
168 rainy weather conditions, the number of observation sets varied to some extent. In total,
169 we made 53 sets of observations throughout the summer in 2013, and 43 sets in 2014.
170 Time, weather, and wind conditions were also recorded using the data of the weather
171 station. Insects observed on flowers were classified to the ordinal level as Diptera,
172 Hymenoptera, Lepidoptera, Coleoptera, or Hemiptera. Dipteran insects were further
173 classified into syrphid flies (Syrphidae), empidid flies (Empididae), and other flies, as
174 much as possible. Bumble bees were identified at the species level, and other
175 hymenopteran insects were classified into wasps, solitary bees, and others such as
176 Tenthredinidae, as much as possible. Lepidopteran insects were classified into
177 butterflies and moths, and species identification was also conducted for butterflies as
178 much as possible. We did not record grasshoppers or spiders because they were
179 accidental visitors with very low frequency and not apparently acting as pollinators.
180 Based on the observation records of flower visitors in previous surveys (Kudo
181 2016 and unpublished data), most entomophilous species growing at the study site were

grouped into one of three pollination types: predominantly bee-pollinated plants (B-type; hymenopteran insects occupy >70% of all visitors), predominantly fly-pollinated plants (F-type; dipteran insects occupy >70% of all visitors), and plants pollinated by both bees and flies (BF-type; sum of hymenopteran and dipteran insects occupy >70% of all visitors). Because the proportion of non-dipteran and non-hymenopteran insects was very small, we recognized only these three pollination types (Table S2).

Seasonal dynamics of floral resources

We quantified the seasonal dynamics of floral resources at the study site by recording, almost every week, the flowering species in each plot and the flower numbers of individual species within ten 2 × 2 m quadrats per plot that were set arbitrarily on floral patches in each plot during flowering periods (i.e., 60 quadrats in each measurement at most). Setting of quadrats was conducted to reflect averaging flowering situations in each plot as possible. We counted individual flowers for most species except umbelliferous and asteraceous species. For umbelliferous species, the number of small umbels composing a compound umbellate inflorescence was recorded. For asteraceous species, the number of heads was recorded instead of the number of florets. In total, 12-week records were accumulated in each year from early June to mid- or late September. For weeks lacking data (it was six of 18 weeks in both years), we estimated flower numbers by averaging the values from one week before and one week after.

Fruit-set success of different pollination types under natural conditions

To quantify variation in pollination success of the different pollination types across the flowering season, fruit-set rates (fruits/flowers) were measured under natural conditions for the common species in each plot. Individual plants and branches were marked using the following three methods: by putting tags on stems for shrubby species, by setting 10 × 10 cm quadrats for mat-forming species, and by placing flags for herbaceous species. For species with a wide distribution range along the snowmelt gradient, fruit-set success was measured for multiple populations with different flowering periods. Fruit-set measurements were replicated over 25 quadrats, 30 tags, or 30 flags per population. We measured fruit-sets for 50 populations of 25 species in 2013, and for 56 populations of 27 species in 2014.

Statistical analyses

Analyses of insect visitation frequencies and floral use patterns

Seasonal dynamics of the number of flower visitors were analyzed under generalized linear models (GLMs) postulating a negative-binomial error distribution with a log-link function. Because bumble bees, non-syrphid flies, and syrphid flies were predominant (90% of visitors in both years; see Results), the visitation frequencies of these groups were analyzed. In the GLMs, the number of insect visits recorded during a 30-min observation period was the response variable; year (2013, 2014), week number from 1 June (included as both a linear and quadratic term), and visitor group (bumble bees, syrphid flies, non-syrphid flies) were included as explanatory variables. The model included interaction terms between visitor group and temporal variables (week). Furthermore, the frequency of each visitor group was analyzed separately by GLM to clarify the factors affecting the activity of each insect group; year, air temperature, and

229 wind speed during the observation period were included as explanatory variables.
230 Weather data were recorded at the weather station (1700 m) located approximately 1.5
231 km from O plot. Air temperature and wind speed were measured every hour at 1.5 m
232 and 2 m above the ground, respectively. Wind speed was classified into three levels as
233 breeze (wind-L: <2 m s^{-1} hourly mean), moderate (wind-M: 2–5 m s^{-1}), and strong
234 (wind-H: >5 m s^{-1}) in 2014. Because the wind speed records were incomplete in 2013
235 due to mechanical trouble, we made approximate wind speed estimates based on
236 experience during the observations. In each GLM, best-fit model was selected by
237 Akaike's information criterion (AIC).
238 In order to clarify the differences in flower preference among the visitor groups,
239 floral use patterns were compared among visitor groups (bumble bee, other
240 hymenopteran insect, syrphid fly, non-syrphid fly, and butterfly) using a database of
241 floral visits of major insect groups in this area (G. Kudo, unpublished data; Table S2).
242 The database is based on field records collected over six years and includes the data
243 from this study for 2013 and 2014. For the calculation of floral use similarity across
244 insect groups, we performed non-metric multidimensional scaling (NMDS) based on
245 Chao distances using the vegan package (Oksanen et al. 2016).
246
247 *Yearly variation in floral resource dynamics*
248 The seasonal patterns of floral resources at the community scale (total number of
249 flowers of each species in each week) were divided into whole plants, bee-pollinated
250 plants (B-type), and fly-pollinated plants (F-type), and were compared between 2013
251 and 2014 by the Kolmogorov-Smirnov test. The seasonal patterns of floral resources
252 were also compared between B-type and F-type plants in each year.

253

254 *Analysis of fruit-set success*

255 First, fruit-set rates at the community scale under natural conditions were compared
256 among pollination types by GLMM, postulating a binomial error distribution with a
257 logit-link function using the lme4 package (Bates et al. 2015). In the GLMM, the
258 fruit-set success (ratio of fruit number to non-fruiting flower number) of individual
259 populations was an response variable; year (2013, 2014), peak flowering period of
260 individual populations (week number from 1 June), and pollination type of individual
261 species (B-, F-, BF-type) were included as explanatory variables; and plant species was
262 set as a random variable. Interactions between week and pollination type were included
263 in the GLMM. Peak flowering period in each population was defined as the week
264 number when flower number of the target species attained at the maximum in the plot.
265 When flowering occurred very late in the season (after 31 August), fruit maturation was
266 often restricted due to the short period for development, irrespective of pollination
267 success. Because we focused on the pollination function in this study, only populations
268 that bloomed during weeks 1–13 (from 1 June to 30 August) were included in the
269 analysis.

270 In order to clarify the pollination effectiveness of bumble bees and dipteran insects,
271 furthermore, we compared the relationships between visitation frequency at peak
272 flowering and fruit-set rates by fitting a logistic function. In this analysis, we separately
273 examined the relationships between bumble bee visitation frequency and fruit-set
274 success of B-type plants, and the relationship between visitation frequency of dipteran
275 insects (sum of syrphid and non-syrphid flies) and fruit-set success of F-type plants. To
276 fit the data, we used estimated visitation frequencies of bumble bees and dipteran

277 insects at weekly intervals and estimated fruit-set rates at the community scale at
278 weekly intervals in each year by the GLM or GLMM mentioned above. All analyses
279 were conducted in R version 3.2.4 (R Core Team 2016).
280
281 **Results**
282 **Seasonality of flower visitors**
283 In total, 4269 and 3908 insects were recorded throughout the survey periods in 2013 and
284 2014, respectively (Table 1). In 2013, hymenopteran insects comprised 36% of the total
285 and dipteran insects comprised 61%, while in 2014 hymenopteran insects comprised
286 24% and dipteran insects comprised 72%. The proportion of other insects was less than
287 5% in both years. Hymenopteran and dipteran insects are thus the predominant flower
288 visitors in this area. Approximately 84–86% of hymenopteran insects were bumble bees
289 (*Bombus* spp.). Visual identification of dipteran insects in the field was very difficult,
290 even to the family level, except for Syrphidae and Empididae spp. Syrphid flies
291 comprised 28% of all dipteran insects in 2013, but were 71% in 2014, indicating large
292 variation in syrphid fly numbers between years. Empidid flies comprised less than 3%
293 of dipteran insects, and most of the other flies were recognized as Anthomyiidae,
294 Muscidae, and Calliphoridae spp. We therefore grouped the dipteran insects into
295 syrphid and non-syrphid categories in the following analyses.
296 The visitation frequency of bumble bees was very low from June to early July
297 (week 1–6), increased from mid-July (week 7–8) to early August (week 10) in both
298 years, and decreased beginning in late August (week 12–13; Fig. 1). Overwintered
299 queen bees emerged in early June but at low frequency. The rapid increase in visitation
300 frequencies from mid-July to early August was due to the emergence of worker bees.

301 Although the number of workers decreased in late August, the reproductive castes
302 (males and new queens) appeared from late August to mid-September. Therefore, floral
303 visitation by bumble bees was observed at a consistent level until mid-September.
304 Seasonal trends in foraging activity were different between syrphid and
305 non-syrphid flies (Fig. 1). The visitation frequency of syrphid flies increased from
306 mid-July (week 7-8) to mid-August (week 12) in both years, but the frequency at peak
307 was much larger in 2014 than in 2013. The frequency of non-syrphid flies tended to
308 increase gradually as the season progressed, but they sometimes showed outbreaks at
309 unpredictable times from mid-August (week 12) to early September (week 14).
310 The GLM results indicated that the visitation frequency of flower visitors was
311 larger in 2014 than in 2013 and it generally increased toward later season but differently
312 among visitor group (Table 2). Bumble bees and syrphid flies clearly increased as the
313 season progressed with a peak in middle or late season, while the seasonal trend of
314 non-syrphid flies was obscure (i.e., a negative week × visitor group interaction; Table 2,
315 Fig. 1). A significant week^2 × visitor group interaction in syrphid flies indicates that the
316 peak season of foraging activity was different from bumble bees, i.e., it comes earlier
317 than that of bumble bees (Table 2, Fig. 1).
318 The GLM conducted for each visitor group indicated that the foraging activity of
319 syrphid flies was most sensitive to temperature (Table 3). Their visitation frequency was
320 negatively correlated with strong wind, while the effects of temperature and wind were
321 not significant or excluded by the model selection in bumble bees and non-syrphid flies.
322 The foraging activity of non-syrphid flies was independent on weather condition but
323 indicated a significant variation between years.

The NMDS ordination diagrams showed that the similarity in plant species visited by insects was low between bumble bees and other hymenopteran insects within the same order (Fig. S2). The similarity in floral resource use by syrphid and non-syrphid flies was relatively high, but it was different between butterflies and other taxa.

Temporal variation in floral resources

In total, the flowering of 51 entomophilous species was observed over six plots (Table S3). These species included 11 bee-pollinated plants (B-type), 19 fly-pollinated plants (F-type), and 18 bee-and-fly-pollinated plants (BF-type) according to our observations of flower visitors. No insect visits were observed in three species.

Snowmelt progressed from 4 June (A plot) to 19 August (E plot) in 2013, and from 26 May (A plot) to 2 August (E plot) in 2014 (Table S1). The progress of snowmelt in 2013 was later than usual in the late snowmelt locations. However, the snowmelt in 2014 was approximately one week earlier than usual at A plot and B plot, although it proceeded as usual in other plots. The flowering period at the community scale was longer in 2013, with flowering lasting from early June to late September, while flowering in 2014 was largely finished by early September (Fig. 2).

The seasonal pattern of flower production in all plants varied between years (Kolmogorov-Smirnov $D = 0.50$, $P = 0.022$; Fig. 2). Floral resources in 2013 tended to increase in the later part of the season, while floral resources in 2014 reached a peak in late July. Flower production in B-type plants significantly varied between years ($D = 0.83$, $P < 0.0001$; Fig. 2), exhibiting a bimodal pattern in 2013 (clear peaks early and late in the season). In contrast, flower production in B-type plants was very small in 2014 throughout the season. The reason was that flower production of both

early-bloomers in the fellfield habitat (*Arctous alpinus* var. *japonicus*) and late-bloomers in the snowbed habitat (*Phyllodoce caerulea* var. *yezoensis* and *Phyllodoce aleutica*) was very small in 2014. Flower production of F-type plants was relatively low in both years ($D = 0.33$, $P = 0.27$; Fig. 2). Seasonal trends in flower production were significantly different between B-type and F-type plants in 2013 ($D = 0.83$, $P < 0.0001$), but the difference was not significant in 2014 ($D = 0.28$, $P = 0.49$). These results suggest that yearly variation in floral resources at the community scale is caused by fluctuations in flower production of B-type plants, mostly ericaceous shrubs.

Temporal variation in fruit-set success

Fruit-set success under natural conditions was measured in six species of B-type plants in 2013 (10 populations) and eight species in 2014 (12 populations); in eight species of F-type plants (14 populations in 2013 and 17 populations in 2014); and in 11 species of BF-type plants (26 populations in 2013 and 27 populations in 2014). The GLMM results for all plants indicate that fruit-set success at the community level was higher in 2014 and clearly increased with the delay in flowering period (Table 4). Fruit-set patterns were significantly different between B-type and F-type plants: the slopes of the fruit-set rates over the course of the seasons were steepest in B-type plants, and low in F-type plants, especially in 2014 (Fig. 3). There was no significant difference in fruiting patterns between B-type and BF-type plants.

The relationships between estimated pollinator frequency at flowering peak and estimated fruit-set success at the community scale were fitted to logistic functions (Fig. 4). Both the bumble bee–B-type plant relationship and the dipteran insect–F-type plant relationship were clear, indicating that fruit-set success in alpine plants strongly

372 depends on pollinator activity in both bee-pollinated and fly-pollinated species.
373 However, the sensitivity of fruit-set success to pollinator frequency was more apparent
374 in B-type plants, where fruit-set rates abruptly increased with the visitation frequency of
375 bumble bees and attain their maximum at values around 20 visits per 30 min. In contrast,
376 fruit-set rates of F-type plants gradually increase with the visitation frequency of
377 dipteran insects. These differences suggest a higher pollination ability in bumble bees
378 than that in dipteran insects.
379

380 **Discussion**

381 A series of surveys of alpine plant communities revealed that: (1) seasonal trends in the
382 foraging activity of flower visitors varied among bumble bees, syrphid flies, and
383 non-syrphid flies; (2) B-type and F-type plants showed different flowering patterns; (3)
384 fruit-set success increased as the season progressed in every type of plants but this trend
385 was most apparent in B-type plants; and (4) pollination ability of bumble bees was
386 higher than that of dipteran insects.
387

388 **Seasonal activity of flower visitors**

389 Visitation frequency of bumble bees consistently increased from the early to the middle
390 part of the growth season, as reported in previous studies (Kwak and Bergman 1996;
391 Kameyama and Kudo 2009; Pyke et al. 2011; Kudo 2014). This seasonal trend reflects
392 the life-cycle of the bumble bees: overwintering queens are available early in the season,
393 while workers increase with colony development as the season progresses (Pyke et al.
394 2011; Amsalem et al. 2015). Although the abundance of syrphid flies also attained its
395 maximum level in the middle of the season, their foraging activity was sensitive to

396 ambient temperature and wind conditions, and they showed large variation between
397 years. In contrast, the seasonal trend of non-syrphid flies was less marked in comparison
398 with other groups, and their frequency was independent of ambient temperature.
399 Previous studies have reported that the visitation frequency of dipteran insects
400 commonly depends on ambient temperature in the mountains of northern Europe and
401 North America (McCall and Primack 1992; Totland 1994). This discrepancy between
402 our result and previous reports might be in part because our observations of flower
403 visitors were conducted only under relatively suitable weather conditions. Nevertheless,
404 we detected differences in temperature dependence among pollinator groups. The
405 foraging activity of syrphid flies was most sensitive to weather conditions.
406 In this study, we grouped dipteran insects simply into syrphid and non-syrphid
407 species because their identification in the field was extremely difficult. However, there
408 are at least 21 species of syrphid flies alone in the Taisetsu Mountains (Konno 2006).
409 Although inter-specific variation in the life-cycles of syrphid species has been little
410 studied (but see also Rotheray and Gilbert 2011), seasonal trends in foraging activity
411 and pollination effectiveness may vary among dipteran species (Herrera 1987).
412 Visitation frequencies of syrphid and non-syrphid flies showed large variation within
413 and between years in our study, in comparison with bumble bees. Furthermore, we
414 detected a few outbreaks of syrphid flies (2014) and non-syrphid flies (2013) between
415 July and early September. It is known that insects with solitary and short life-cycles
416 tend to exhibit more variation in floral-resource-dependent population dynamics than
417 social insects such as bumble bees (Totland 1994; Crone 2013). Iler et al. (2013)
418 reported that the phenology of syrphid flies responded to yearly variation in snowmelt

time and cumulative temperature in North America. Syrphid flies may encompass a more diverse array of life-cycles than bumble bees (Rotheray and Gilbert 2011).

The visitation frequency of dipteran insects was higher than that of bumble bees throughout both seasons although bumble bees may be more important pollinators at least in terms of pollen deposition per visit (Kerns and Inouye 1994). Dipteran insects visit flowers not only for floral resources (pollen and nectar) but also for non-nutritive reasons, such as warmth, shelter, and mating opportunities (Woodcock et al. 2014). In subarctic-alpine regions, the proportion and abundance of dipteran flower visitors increases with elevation and latitude (Elberling and Olesen 1999), indicating the high generality of dipteran insects as pollinators in cold climates (Tiusanen et al. 2016).

Flowering patterns of bee-pollinated and fly-pollinated plants

The flowering patterns of alpine plant communities varied significantly between B-type and F-type plants. B-type flowers showed a bimodal pattern with peaks in early and late summer in 2013, a year during which the total flowering period extended from early June to mid-September. The early flowering period corresponds to the active period of overwintered queens, while the late flowering period corresponds to the active period of workers. Similar flowering trend was reported also in a montane meadow in the Rocky Mountains (Aldridge et al. 2011). However, flower production of B-type plants was considerably reduced in 2014, with little seasonal variation and a short flowering period from early June to mid-August. The shorter flowering period in 2014 was due to earlier snowmelt than in 2013. The reduced monotonic flowering pattern in 2014 reflected the intermittent mass flowering of some dominant shrubby species that only occurs during certain years (e.g., small flower production of *A. alpinus* var. *japonicus* and *A. nana* in

443 fellfield sites and *Phyllodoce* spp. in snowbed sites). The B-type species at our site
444 consisted largely of ericaceous dwarf shrubs (Table S3). Ericaceous shrubs are a major
445 component of alpine, subarctic, and temperate heathlands in the Northern Hemisphere,
446 and they are important floral resources for bumble bees (Reader 1975, 1977; Rathcke
447 1988; Kudo and Suzuki 2002; Moquet et al. 2017). There are several reports of large
448 fluctuations in flower and fruit production between years in ericaceous shrubs (Selås
449 2000; Kasagi and Kudo 2003; Krebs et al. 2009). Therefore, the floral resources of
450 B-type plants vary significantly between years in alpine ecosystems of the northern
451 hemisphere.
452 On the other hand, yearly variation in the flower production of F-type plants was
453 much smaller in comparison with B-type plants. The F-type plants included various
454 families but many of them are herbaceous species (Table S3) as reported in other
455 mountain regions (Yumoto 1986; Iler et al. 2013). Interestingly, flower production of
456 F-type plants mainly occurred after early July, and floral density in June was very small.
457 This may reflect seasonal trends in the dipteran pollinators, especially syrphid flies.
458 Previous studies demonstrated that fly-pollinated plant species tend to bloom
459 simultaneously with large overlaps among species, probably due to enhanced pollinator
460 attraction (Yumoto 1986; Totland 1993), resulting in shorter and more concentrated
461 flowering patterns within plant communities. Because the frequency of flower visitors
462 was recorded on flowers, seasonal trend of pollinator activity might be not independent
463 of flowering phenology. In spite of this limitation, our data collected from all plant
464 species throughout the season across multiple years imply that the flowering patterns of
465 B-type and F-type plants may be related to the seasonal activity or life-cycles of bumble
466 bees and dipteran pollinators, respectively (e.g., Makrodimos et al. 2008).

467

468 **Fruit-set patterns in relation to pollination type**

469 Most entomophilous alpine plants rely on pollinators for seed production. In our
470 preliminary pollination experiment conducted for several species, fruit-set rates of
471 bagged plants were lower than fruit-set rates under natural pollination in every
472 pollination type (Fig. S3). This result indicates that seed production in alpine plants
473 strongly depends on pollination services from pollinators, irrespective of pollination
474 type. Therefore, variation in fruit-sets under natural conditions mainly reflects the
475 intensity of pollen limitation caused by spatiotemporal variation in pollinator
476 availability (Kudo and Suzuki 2002; Kameyama and Kudo 2009). Higher fruit-set
477 success in 2014 might be related to higher visitation frequencies of flower visitors,
478 especially syrphid flies (Tables 2, Fig. 1).

479 Clear increases in fruit-set success of B-type plants with seasonal progress
480 correspond to the seasonality of bumble bee activity and reflects the life-cycle of colony
481 development (Pyke et al. 2011). Fruit-set success of F-type plants also increased as the
482 seasons progressed, but its trend was less marked than the trend in B-type plants.
483 BF-type plants exhibited an intermediate pattern between B-type and F-type plants.
484 These differences in seasonal variation in fruit-set success may be related to the
485 seasonality of foraging activity of each pollinator type. Lower fruit-set success due to
486 pollen limitation has been reported in several early-blooming bee-pollinated species
487 both within (Kudo 1993; Kameyama and Kudo 2009) and among species (Kudo and
488 Suzuki 2002) in this area. Therefore, seed production of bee-pollinated alpine plants is
489 the most sensitive to flowering phenology, reflecting the life-cycle of the bumble bees.

490 Our study successfully revealed differences in pollination effectiveness between
491 bumble bees and dipteran insects, i.e., in their contributions to fruit-set per visit.
492 Fruit-set rates of B-type plants rapidly increased and saturated with increasing bumble
493 bee visitation frequencies (Fig. 4). In contrast, fruit-set rates of F-type plants gradually
494 and continuously increased with increases in the visitation frequencies of dipteran
495 insects (Fig. 4). These patterns indicate the higher pollination effectiveness of bumble
496 bees in comparison to dipteran insects. Nevertheless, F-type plants and B-type plants
497 showed generally similar fruit-set rates under natural pollination. It seems that the lower
498 pollination ability of dipteran insects may be compensated for by greater visitation
499 frequency (Kearns and Inouye 1994). In our estimation, saturated pollination success
500 (80% fruit-set rate) in B-type plants was attained through about 20 bumble bee visits per
501 30 min, while more than 60 dipteran visits per 30 min were needed to achieve similar
502 fruit-set rates in F-type plants (Fig. 4), indicating that about three times more dipteran
503 visits are necessary for fruiting success in F-type plants than in B-type plants.
504 In our study, about one-third of plant species were visited by both dipteran and
505 hymenopteran insects. The classification of pollination types in this study was simply
506 based on visitation frequency, not on the true pollination efficiency of individual insects.
507 Therefore, we cannot discriminate the contributions to seed production of dipteran and
508 hymenopteran pollinators in BF-type flowers. For example, *Rhododendron aureum*,
509 which was classified as a BF-type based on visitor composition, can set fruits only when
510 visited by bumble bees (Kudo et al. 2011). The pollination success of many BF-type
511 plants may thus be enhanced by a few visits from bumble bees rather than several visits
512 from dipteran insects (Herrera 1987).
513

Conclusion

Bumble bees and dipteran insects are the most common pollinators in alpine ecosystems, but their foraging activity varies significantly during the flowering period. Although bumble bees are effective pollinators in alpine ecosystems, their foraging activity is consistently low early in the flowering period. Dipteran insects are ubiquitous pollinators that exhibit diverse population dynamics, and their lower pollination ability may be compensated for by abundant flower visits. To clarify the relative importance and functional roles of dipteran and hymenopteran pollinators, however, further studies are necessary based on more precise evaluations of pollination efficiency, pollen flows, outcrossing rate, and genetic diversity of pollen load. Furthermore, yearly variations in phenological matching between flowering time and the life-cycles of pollinators at the community scale will be crucial for evaluating the robustness of plant–pollinator interactions in alpine ecosystems (e.g., Aldridge et al. 2011).

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Table 1. The number and species composition of flower visitors observed in 2013 and 2014. For bumble bees, caste numbers (queen/worker/male) are shown in parentheses.

Order	Family/Species	2013	2014
Hymenoptera	Apidae spp.		
	Bombus hypocrita sapporoensis	765 (22/701/42)	295 (19/248/28)
	Bombus beaticola moshkarareppus	499 (58/411/30)	451 (5/442/4)
	Bombus yezoensis	7 (0/7/0)	41 (0/41/0)
	Bombus hypnorum koropokkrus	4 (2/2/0)	3 (0/3/0)
	Bombus terrestris	17 (0/17/0)	0
	Tenthredinidae spp.	211	96
	Solitary bees (Halictidae or Andrenidae spp.)	43	6
	Wasps	0	27
	Subtotal	1546 (36.2%)	919 (23.5%)
Diptera	Flies (small)**	436	164
	Flies (medium)**	1327	527
	Flies (large)**	59	43
	Empididae spp.	50	81
	Syrphidae spp.	732	2016
	Subtotal	2604 (61.0%)	2831 (72.4%)
Lepidoptera	Nymphalidae (mainly *Aglais urticae connexa*)	63	116
	Papilionidae spp.	1	1
	Pieridae spp.	0	3
	Hesperiidae spp.	4	0
	Lycaenidae spp.	0	1
	Moths	18	8
	Subtotal	86 (2.0%)	129 (3.3%)
Hemiptera	Miridae spp.	24	0
	Anthocoridae spp.	0	22
	Other bugs	9	0
	Subtotal	33 (0.8%)	22 (0.6%)
Coleoptera	Staphylinidae spp.	0	4
	Elateridae spp.	0	1
	Other beetles	0	2
	Subtotal	0 (0%)	7 (0.2%)
Total		4269	3908

**mainly Anthomyiidae, Muscidae, or Calliphoridae spp.

Table 2. Results of GLM analysis for visitation frequency of bumble bees, non-syrphid flies, and syrphid flies. Year (2013, 2014), season (week) and pollinator type are included in the explanatory variables.

Variables	Coefficient	Std. Error	*z* value	*P* level
Intercept (Bumble bee, Year 2013)	–10.97	0.77	–14.19	**<0.001**
Year (2014)	0.53	0.11	4.67	**<0.001**
Week	1.19	0.16	7.38	**<0.001**
$Week^2$	–0.048	0.008	–5.98	**<0.001**
Non-syrphid fly	6.13	0.93	6.59	**<0.001**
Syrphid fly	–0.62	1.03	–0.61	0.54
Week × Non-syrphid fly	–1.20	0.20	–5.94	**<0.001**
Week × Syrphid fly	0.31	0.22	1.42	0.16
$Week^2$ × Non-syrphid fly	0.054	0.010	5.31	**<0.001**
$Week^2$ × Syrphid fly	–0.023	0.011	–2.04	**0.041**

Table 3. Results of GLM analysis for visitation frequency of bumble bees (a), non-syrphid flies (b), and syrphid flies (c). Year (2013, 2014), air temperature, and wind speed* are included in the explanatory variables of full models. Best-fit models after parameter selection based on AIC are indicated.

Variables	Coefficient	Std. Error	*z* value	*P* level
(a) Bumble bee frequency				
Intercept	1.95	0.62	3.13	**0.002**
Temperature	0.077	0.043	1.80	0.072
(b) Syrphid fly frequency				
Intercept (Year 2013, Wind-L)	–1.28	0.83	–1.56	0.12
Year (2014)	1.64	0.34	4.85	**<0.001**
Temperature	0.26	0.05	4.87	**<0.001**
Wind-M	–0.05	0.37	–0.15	0.88
Wind-H	–1.63	0.52	–2.16	**0.002**
(c) Non-syrphid fly frequency				
Intercept (Year 2013)	8.51	0.15	24.00	**<0.001**
Year (2014)	–0.57	0.22	–2.16	**0.009**

* Wind conditions were grouped into three classes: breeze (wind-L), moderate (wind-M), and strong (wind-H).

Table 4. Results of GLMM analysis for fruit-set success of plants of all pollination-types at the population level under natural pollination. Season (week), year (2013, 2014), and pollination type (B-, F-, BF-type) are explanatory variables, and plant species is a random variable.

Variables	Coefficient	Std. Error	*z* value	*P* level
Intercept (Year 2013, B-type)	–2.23	0.57	–3.92	**<0.001**
Week	0.26	0.02	18.98	**<0.001**
BF-type	–0.25	0.74	–0.34	0.73
F-type	2.79	0.81	3.44	**0.006**
Year 2014	0.66	0.03	25.43	**<0.001**
Week × BF-type	0.04	0.03	1.70	0.088
Week × F-type	–0.19	0.03	–7.64	**<0.001**

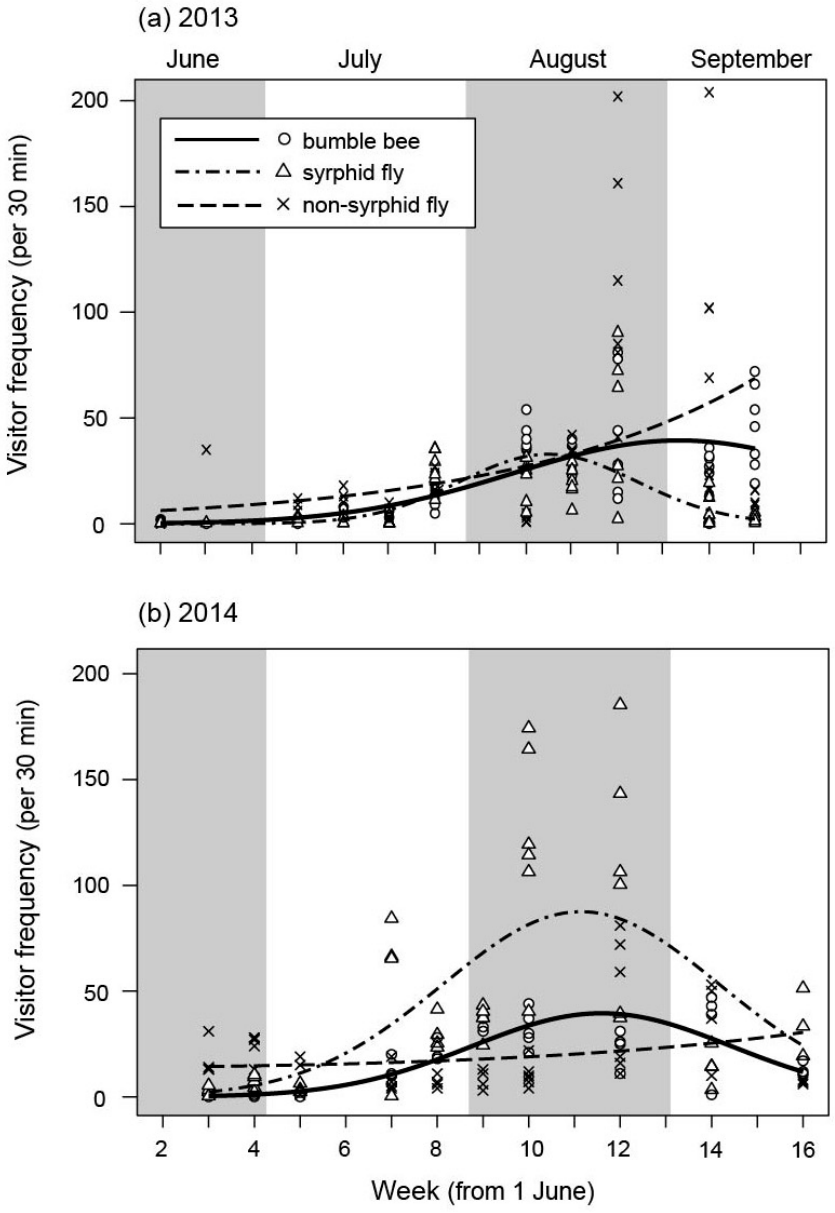

Fig. 1 Seasonal patterns in the visitation frequencies of bumble bees (solid line), syrphid flies (chained line), and non-syrphid flies (broken line) in 2013 (a) and 2014 (b). Lines indicate the fit to the log-link functions, including the quadratic week variable. Refer to Table 2 for GLM results.

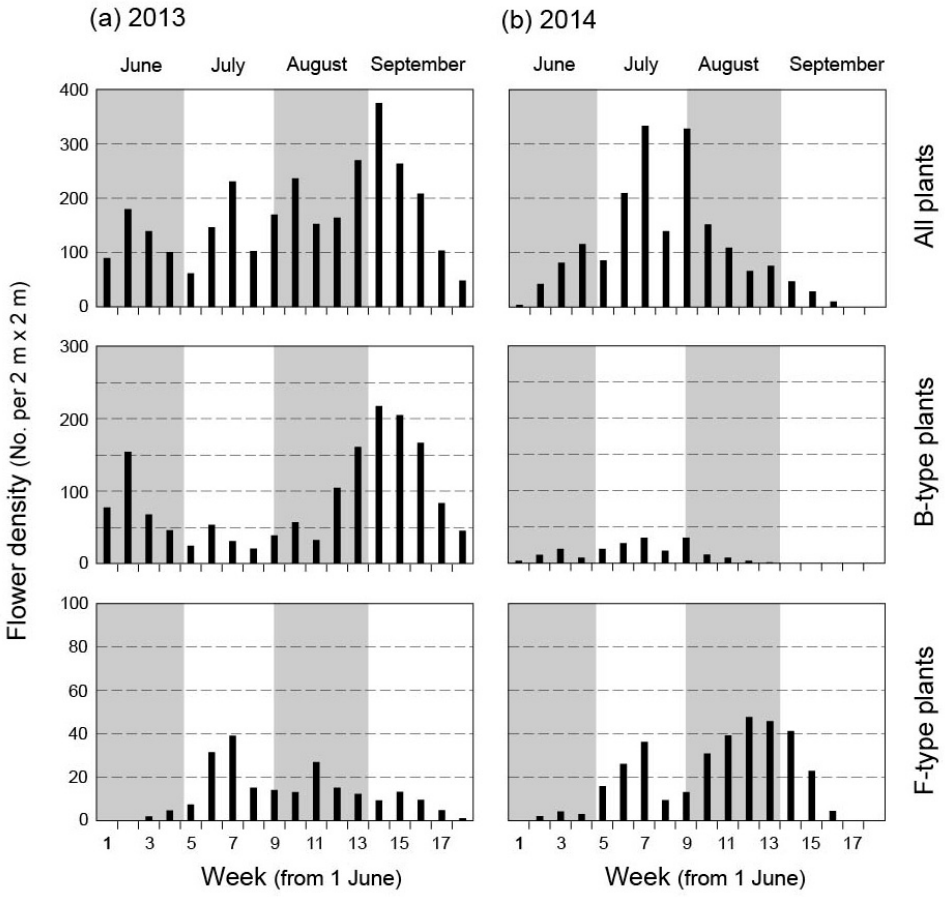

Fig. 2 Seasonal patterns in floral resources expressed as floral density per quadrat (2 m × 2 m) for all plants, B-type plants, and F-type plants in 2013 (a) and 2014 (b). Flowering patterns of all plants and B-type plants significantly varied between years, while flowering patterns of F-type plants were similar between years (see text for details).

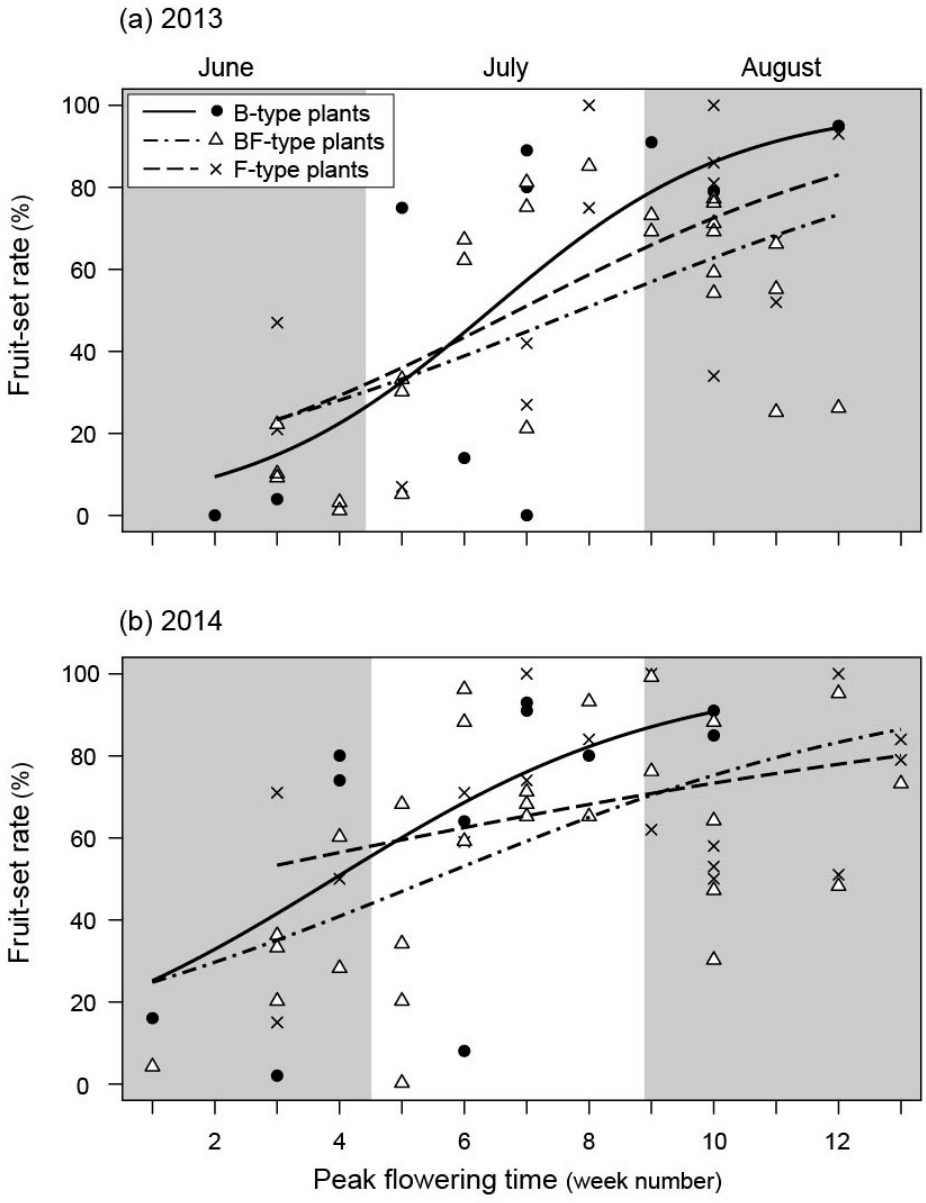

Fig. 3 Relationships between fruit-set success under natural conditions and the major flowering periods of populations of individual pollination types (B-type, solid line; BF-type, chained line; F-type, broken line) in 2013 (a) and 2014 (b). Lines are fitted to the logistic function applied to each pollination type and each year. Refer to Table 4 for GLMM results.

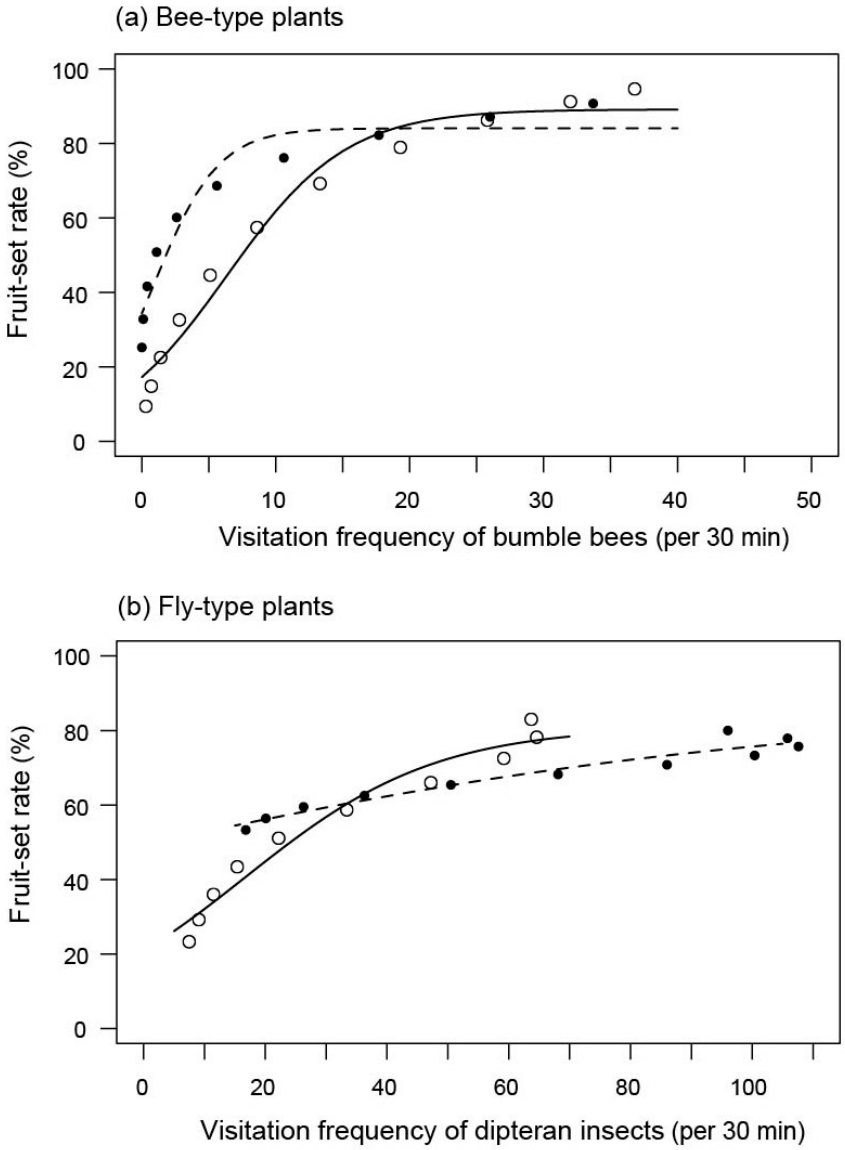

Fig. 4 Relationships between pollinator frequency at flowering peak and fruit-set success at the community scale for the combination of bumble bees and B-type plants (a), and dipteran insects and F-type plants (b). Open circles and the solid line indicate 2013, and closed circles and the broken line indicate 2014. Lines are fitted to the logistic function applied to each year using estimated values of pollinator frequencies (Fig. 1) and community-scale fruit-set rates (Fig. 3).