



Title	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
Author(s)	Mizunaga, Yuki; Kudo, Gaku
Citation	Oecologia, 185(3), 453-464 <a href="https://doi.org/10.1007/s00442-017-3946-9">https://doi.org/10.1007/s00442-017-3946-9</a>
Issue Date	2017-11
Doc URL	<a href="http://hdl.handle.net/2115/71818">http://hdl.handle.net/2115/71818</a>
Rights	The final publication is available at <a href="http://link.springer.com">link.springer.com</a>
Type	article (author version)
File Information	Oecologia185,453-464(2017).pdf



[Instructions for use](#)

1 **A linkage between flowering phenology and fruit-set success of alpine plant**  
2 **communities with reference to the seasonality and pollination effectiveness of bees**  
3 **and flies**

4

5 **Yuki Mizunaga<sup>1</sup> & Gaku Kudo<sup>1</sup>**

6

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

8 Japan

9

10 Corresponding author: Y. Mizunaga

11 e-mail: mizunaga@ees.hokudai.ac.jp

12 fax: +81-11-706 4954

13

14

15 Author Contributions: YM and GK conceived the idea, designed the experiments,

16 conducted field work, analyzed the data, and wrote the manuscript.

17

18 **Abstract**

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

37

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

39

## 40 **Introduction**

41 Hymenopteran and dipteran insects are common and important pollinators in  
42 high-altitude and high-latitude environments (Arroyo et al. 1982; Kevan and Baker  
43 1983; Kudo 2016). Most plant species inhabiting these environments can be classified  
44 into bee-pollinated, fly-pollinated, or bee-and-fly-pollinated types (Yumoto 1986; Kudo  
45 2016). Bumble bees have an annual social life-cycle and are important pollinators in  
46 alpine and boreal ecosystems because of their high pollen transportation ability and  
47 flower constancy (Heinrich 1979; Bingham and Orthner 1998; Willmer 2011). The  
48 foraging activity of bumble bees varies considerably within a growth season in parallel  
49 with the life-cycle of colony development and changes in the community of flowering  
50 plants (Pyke et al. 2011; Amsalem et al. 2015). Overwintered queen bees emerge from  
51 hibernation early in the summer at low frequency, while worker bees emerge in greater  
52 numbers in the middle of the season in keeping with the timing of colony development.  
53 In parallel with the seasonal dynamics of foraging activity, the pollination success of  
54 bee-pollinated plants varies significantly within and among species depending upon  
55 flowering time (Kudo 2006, 2016).

56 Dipteran insects are ubiquitous flower visitors across wide elevational and  
57 latitudinal ranges (Totland 1993, 1994; Elberling and Olesen 1999; Tiusanen et al.  
58 2016), and their importance generally increases with environmental harshness at higher  
59 elevations and latitudes (Kevan 1972; Arroyo et al. 1982; McCall and Primack 1992;  
60 Elberling and Olesen 1999; Wagner et al. 2016). Although the pollination effectiveness  
61 of dipteran insects is assumed to be generally low because of their opportunistic floral  
62 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

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

144 This study was conducted in six plots (designated O, A, B, C, D, and E; Fig. S1)  
145 that were established in 1988 (Kudo and Hirao 2006; Kudo 2016). O plot ( $50 \times 50$  m) is  
146 located in a fellfield on the plateau, where the soil surface is almost free of snow cover  
147 during the winter due to strong winds. The remaining five  $20 \times 20$  m plots, A to E, are  
148 arranged on a southeast-facing slope along a snowmelt gradient between 1790–1910 m  
149 elevation. Variation in snowmelt conditions largely reflects the heterogeneous winter  
150 snow distribution that is determined by topographic features and slope direction. The  
151 mean snowmelt time was early June at A plot, mid-June at B plot, early July at C plot,  
152 late July at D plot, and early August at E plot (Table S1). The average day of snowmelt  
153 during the last 27 years ranged from 4 June at A plot to 3 August at E plot. Because  
154 these plots include typical alpine vegetation from fellfield to the bottom of the snowbed,  
155 and so cover a wide range of snow conditions, phenological research across the plots  
156 enables us to quantify the representative phenological structure of the alpine ecosystem  
157 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

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

189

### 190 **Seasonal dynamics of floral resources**

191 We quantified the seasonal dynamics of floral resources at the study site by recording,  
192 almost every week, the flowering species in each plot and the flower numbers of  
193 individual species within ten  $2 \times 2$  m quadrats per plot that were set arbitrarily on floral  
194 patches in each plot during flowering periods (i.e., 60 quadrats in each measurement at  
195 most). Setting of quadrats was conducted to reflect averaging flowering situations in  
196 each plot as possible. We counted individual flowers for most species except  
197 umbelliferous and asteraceous species. For umbelliferous species, the number of small  
198 umbels composing a compound umbellate inflorescence was recorded. For asteraceous  
199 species, the number of heads was recorded instead of the number of florets. In total,  
200 12-week records were accumulated in each year from early June to mid- or late  
201 September. For weeks lacking data (it was six of 18 weeks in both years), we estimated  
202 flower numbers by averaging the values from one week before and one week after.

203

### 204 **Fruit-set success of different pollination types under natural conditions**

205 To quantify variation in pollination success of the different pollination types across the  
206 flowering season, fruit-set rates (fruits/flowers) were measured under natural conditions  
207 for the common species in each plot. Individual plants and branches were marked using  
208 the following three methods: by putting tags on stems for shrubby species, by setting 10  
209 × 10 cm quadrats for mat-forming species, and by placing flags for herbaceous species.  
210 For species with a wide distribution range along the snowmelt gradient, fruit-set success  
211 was measured for multiple populations with different flowering periods. Fruit-set  
212 measurements were replicated over 25 quadrats, 30 tags, or 30 flags per population. We  
213 measured fruit-sets for 50 populations of 25 species in 2013, and for 56 populations of  
214 27 species in 2014.

215

## 216 **Statistical analyses**

### 217 *Analyses of insect visitation frequencies and floral use patterns*

218 Seasonal dynamics of the number of flower visitors were analyzed under generalized  
219 linear models (GLMs) postulating a negative-binomial error distribution with a log-link  
220 function. Because bumble bees, non-syrphid flies, and syrphid flies were predominant  
221 (90% of visitors in both years; see Results), the visitation frequencies of these groups  
222 were analyzed. In the GLMs, the number of insect visits recorded during a 30-min  
223 observation period was the response variable; year (2013, 2014), week number from 1  
224 June (included as both a linear and quadratic term), and visitor group (bumble bees,  
225 syrphid flies, non-syrphid flies) were included as explanatory variables. The model  
226 included interaction terms between visitor group and temporal variables (week).  
227 Furthermore, the frequency of each visitor group was analyzed separately by GLM to  
228 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:  $<2 \text{ m s}^{-1}$  hourly mean), moderate (wind-M:  $2\text{--}5 \text{ m s}^{-1}$ ), and strong  
234 (wind-H:  $>5 \text{ m s}^{-1}$ ) 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  $\times$  visitor group interaction; Table 2,  
315 Fig. 1). A significant week<sup>2</sup>  $\times$  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.

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

328

### 329 **Temporal variation in floral resources**

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

334 Snowmelt progressed from 4 June (A plot) to 19 August (E plot) in 2013, and from  
335 26 May (A plot) to 2 August (E plot) in 2014 (Table S1). The progress of snowmelt in  
336 2013 was later than usual in the late snowmelt locations. However, the snowmelt in  
337 2014 was approximately one week earlier than usual at A plot and B plot, although it  
338 proceeded as usual in other plots. The flowering period at the community scale was  
339 longer in 2013, with flowering lasting from early June to late September, while  
340 flowering in 2014 was largely finished by early September (Fig. 2).

341 The seasonal pattern of flower production in all plants varied between years  
342 (Kolmogorov-Smirnov  $D = 0.50$ ,  $P = 0.022$ ; Fig. 2). Floral resources in 2013 tended to  
343 increase in the later part of the season, while floral resources in 2014 reached a peak in  
344 late July. Flower production in B-type plants significantly varied between years ( $D =$   
345  $0.83$ ,  $P < 0.0001$ ; Fig. 2), exhibiting a bimodal pattern in 2013 (clear peaks early and  
346 late in the season). In contrast, flower production in B-type plants was very small in  
347 2014 throughout the season. The reason was that flower production of both



348 early-bloomers in the fellfield habitat (*Arctous alpinus* var. *japonicus*) and  
349 late-bloomers in the snowbed habitat (*Phyllodoce caerulea* var. *yezoensis* and  
350 *Phyllodoce aleutica*) was very small in 2014. Flower production of F-type plants was  
351 relatively low in both years ( $D = 0.33$ ,  $P = 0.27$ ; Fig. 2). Seasonal trends in flower  
352 production were significantly different between B-type and F-type plants in 2013 ( $D =$   
353  $0.83$ ,  $P < 0.0001$ ), but the difference was not significant in 2014 ( $D = 0.28$ ,  $P = 0.49$ ).  
354 These results suggest that yearly variation in floral resources at the community scale is  
355 caused by fluctuations in flower production of B-type plants, mostly ericaceous shrubs.

356

### 357 **Temporal variation in fruit-set success**

358 Fruit-set success under natural conditions was measured in six species of B-type plants  
359 in 2013 (10 populations) and eight species in 2014 (12 populations); in eight species of  
360 F-type plants (14 populations in 2013 and 17 populations in 2014); and in 11 species of  
361 BF-type plants (26 populations in 2013 and 27 populations in 2014). The GLMM  
362 results for all plants indicate that fruit-set success at the community level was higher in  
363 2014 and clearly increased with the delay in flowering period (Table 4). Fruit-set  
364 patterns were significantly different between B-type and F-type plants: the slopes of the  
365 fruit-set rates over the course of the seasons were steepest in B-type plants, and low in  
366 F-type plants, especially in 2014 (Fig. 3). There was no significant difference in fruiting  
367 patterns between B-type and BF-type plants.

368       The relationships between estimated pollinator frequency at flowering peak and  
369 estimated fruit-set success at the community scale were fitted to logistic functions (Fig.  
370 4). Both the bumble bee–B-type plant relationship and the dipteran insect–F-type plant  
371 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

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

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

429

#### 430 **Flowering patterns of bee-pollinated and fly-pollinated plants**

431 The flowering patterns of alpine plant communities varied significantly between B-type  
432 and F-type plants. B-type flowers showed a bimodal pattern with peaks in early and late  
433 summer in 2013, a year during which the total flowering period extended from early  
434 June to mid-September. The early flowering period corresponds to the active period of  
435 overwintered queens, while the late flowering period corresponds to the active period of  
436 workers. Similar flowering trend was reported also in a montane meadow in the Rocky  
437 Mountains (Aldridge et al. 2011). However, flower production of B-type plants was  
438 considerably reduced in 2014, with little seasonal variation and a short flowering period  
439 from early June to mid-August. The shorter flowering period in 2014 was due to earlier  
440 snowmelt than in 2013. The reduced monotonic flowering pattern in 2014 reflected the  
441 intermittent mass flowering of some dominant shrubby species that only occurs during  
442 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

514 **Conclusion**

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

527

528 **Acknowledgements**

529 We are grateful to Y. Amagai, Y. Aoshima, K. Chen, M. Tomita, H. Muroya, and Y.  
530 Kamano for their assistance in the field surveys and laboratory works. This study is  
531 partly supported by JSPS KAKENHI Grant Number 23405006, 15H02641, and  
532 17K07551.

533

534 **References**

535 Aldridge G, Inouye DW, Forrest JRK, Barr WA, Miller-Rushing AJ (2011) Emergence  
536 of a mid-season period of low floral resources in a montane meadow ecosystem



537 associated with climate change. *J Ecol* 99:905-913  
538 doi:10.1111/j.1365-2745.2011.01826.x

539 Amsalem E, Grozinger CM, Padilla M, Hefetz A (2015) Bumble bee sociobiology: the  
540 physiological and genomic bases of bumble bee social behaviour. *Adv Insect*  
541 *Physiol* 48:37-93 doi:10.1016/bs.aiip.2015.01.001

542 Arroyo MTK, Primack R, Armesto J (1982) Community studies in pollination ecology  
543 in the high temperate Andes of central Chile. I. Pollination mechanisms and  
544 altitudinal variation. *Am J Bot* 69:82-97 doi:10.2307/2442833

545 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models  
546 using lme4. *J Stat Soft* 67:1-48 doi:10.18637/jss.v067.i01

547 Bingham RA, Orthner AR (1998) Efficient pollination of alpine plants. *Nature*  
548 391:238-239 doi:10.1038/34564

549 Bischoff M, Campbell DR, Lord JM, Robertson AW (2013) The relative importance of  
550 solitary bees and syrphid flies as pollinators of two outcrossing plant species in the  
551 New Zealand alpine. *Austral Ecol* 38:169-176  
552 doi:10.1111/j.1442-9993.2012.02389.x

553 Campbell DR, Bischoff M, Load JM, Robertson W (2010) Flower color influences  
554 insect visitation in alpine New Zealand. *Ecology* 91:2638-2649  
555 doi:10.1890/09-0941.1

556 Crone EE (2013) Response of social and solitary bees to pulsed floral resources. *Am*  
557 *Nat* 182:465-473 doi:10.1086/671999

558 Elberling H, Olesen JM (1999) The structure of a high latitude plant-flower visitor  
559 system: the dominance of flies. *Ecography* 22:314-323  
560 doi:10.1111/j.1600-0587.1999.tb00507.x

561 Goulson D, Wright NP (1998) Flower constancy in the hoverflies *Episyrphus balteatus*  
562 (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). Behav Ecol 9:213-219  
563 doi:10.1093/beheco/9.3.213

564 Heinrich B (1979) “Majoring” and “minoring” by foraging bumblebees, *Bombus*  
565 *vagans*: an experimental analysis. Ecology 60:245-255 doi:10.2307/1937652

566 Herrera CM (1987) Components of pollinator “quality”: comparative analysis of a  
567 diverse insect assemblage. Oikos 50:79-90 doi:10.2307/3565403

568 Holway JG, Ward RT (1965) Phenology of alpine plants in northern Colorado. Ecology  
569 46:73-83 doi:10.2307/1935259

570 Iler AM, Inouye DW, Høye TT, Miller-Rushing AJ, Burkle LA, Johnston EB (2013)  
571 Maintenance of temporal synchrony between syrphid flies and floral resources  
572 despite differential phenological responses to climate. Glob Chang Biol  
573 19:2348-2359 doi:10.1111/gcb.12246

574 Inouye DW, Larson BMH, SSybank A, Kevan PG (2015) Flies and flowers III.  
575 Ecology of foraging and pollination. J Pollination Ecol 16:115-133

576 Kameyama Y, Kudo G (2009) Flowering phenology influences seed production and  
577 outcrossing rate in populations of an alpine snowbed shrub, *Phyllodoce aleutica*:  
578 effects of pollinators and self-incompatibility. Ann Bot 103:1385-1394  
579 doi:10.1093/aob/mcp037

580 Kasagi T, Kudo G (2003) Variations in bumble bee preference and pollen limitation  
581 among neighboring populations: comparisons between *Phyllodoce caerulea* and  
582 *Phyllodoce aleutica* (Ericaceae) along snowmelt gradients. Am J Bot 90:1321-1327  
583 doi:10.3732/ajb.90.9.1321

584 Kearns CA, Inouye DW (1994) Fly pollination of *Linum lewisii* (Linaceae). Am J Bot  
585 81:1091-1095 doi:10.2307/2445470

586 Kevan PG (1972) Insect pollination of high arctic flowers. Ecology 60:831-847  
587 doi:10.2307/2258569

588 Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev  
589 Entomol 28:407-453 doi:10.1146/annurev.en.28.010183.002203

590 Konno Y (2006) Species composition of anthophilous Diptera and Hymenoptera in the  
591 Daisetsu Mountains. Japanese J Appl Entomol Zool 50:25-32  
592 doi:10.1303/jjaez.2006.25

593 Krebs CJ, Boonstra R, Cowcill K, Kenney AJ (2009) Climatic determinants of berry  
594 crops in the boreal forest of the southwestern Yukon. Botany 87:401-408  
595 doi:10.1139/B09-013

596 Kudo G (1991) Effects of snow-free period on the phenology of alpine plants inhabiting  
597 snow patches. Arct Alp Res 23:436-443 doi:10.2307/1551685

598 Kudo G (1993) Relationship between flowering time and fruit set of the entomophilous  
599 alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. Am J  
600 Bot 80:1300-1304 doi:10.2307/2445714

601 Kudo G, Suzuki S (2002) Relationships between flowering phenology and fruit-set of  
602 dwarf shrubs in alpine fellfields in northern Japan: a comparison with a subarctic  
603 heathland in northern Sweden. Arct Ant Alp Res 34:185-190 doi:10.2307/1552470

604 Kudo G (2006) Flowering phenologies of animal-pollinated plants: reproductive  
605 strategies and agents of selection. In: Harder LD, Barrett SCH (eds) Ecology and  
606 evolution of flowers. Oxford University Press, New York, USA, pp 139-158

607 Kudo G, Hirao AS (2006) Habitat-specific responses in the flowering phenology and  
608 seed set of alpine plants to climate variation: implications for global-change impacts.  
609 *Popul Ecol* 48:49-58 doi:10.1007/s10144-005-0242-z

610 Kudo G, Hirao AS, Kawai Y (2011) Pollination efficiency of bumblebee queens and  
611 workers in the alpine shrub *Rhododendron aureum*. *Int J Plant Sci* 172:70-77  
612 doi:10.1086/657282

613 Kudo G (2014) Vulnerability of phenological synchrony between plants and pollinators  
614 in an alpine ecosystem. *Ecol Res* 29:571-581 doi:10.1007/s11284-013-1108-z

615 Kudo G (2016) Landscape structure of flowering phenology in alpine ecosystems:  
616 significance of plant-pollinator interactions and evolutionary aspects. In: Kudo G  
617 (ed) *Structure and function of mountain ecosystems in Japan*. Springer, pp 41-62  
618 doi: 10.1007/978-4-431-55954-2

619 Kwak MM, Bergman P (1996) Early flowers of *Bartsia alpina* (Scrophulariaceae) and  
620 the visitation by bumblebees. *Acta Bot Neerl* 45:355-366  
621 doi:10.1111/j.1438-8677.1996.tb00522.x

622 Larson BMH, Kevan PG, Inouye DW (2001) Flies and flowers: taxonomic diversity of  
623 anthophiles and pollinators. *Can Entomol* 133:439-465 doi:10.4039/Ent133439-4

624 Makrodimos N, Blionis GJ, Krigas N, Vokou D (2008) Flower morphology, phenology  
625 and visitor patterns in an alpine community on Mt Olympos, Greece. *Flora*  
626 203:449-468 doi:10.1016/j.flora.2007.07.003

627 McCall C, Primack RB (1992) Influence of flower characteristics, weather, time of day,  
628 and season on insect visitation rates in three plant communities. *Am J Bot*  
629 79:434-442 doi:10.2307/2445156

630 Molau U, Nordenhäll U, Eriksen B (2005) Onset of flowering and climate variability in  
631 an alpine landscape: a 10-year study from Swedish Lapland. *Am J Bot* 92:422-431  
632 doi:10.3732/ajb.92.3.422

633 Moquet L, Vanderplanck M, Moerman R, Quinet M, Roger N, Michez D, Jacquemart  
634 AL (2017) Bumblebees depend on ericaceous species to survive in temperate  
635 heathlands. *Insect Conserv Divers* 10:78-93 doi:10.1111/icad.12201

636 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR,  
637 Hara RBO, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016)  
638 *Vegan: community ecology package*. R package version 2.4-1,  
639 <https://CRAN.R-project.org/package=vegan>

640 Orford KA, Vaughan IP, Memmott J (2015) The forgotten flies: the importance of  
641 non-syrphid Diptera as pollinators. *Proc R Soc B* 282:20142934  
642 doi:10.1098/rspb.2014.2934

643 Pyke GH, Inouye DW, Thomson JD (2011) Activity and abundance of bumble bees  
644 near Crested Butte, Colorado: diel, seasonal, and elevation effects. *Ecol Entomol*  
645 36:511-521 doi:10.1111/j.1365-2311.2011.01295.x

646 Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Ann Rev Ecol*  
647 *Syst* 16:179-214 doi:10.1146/annurev.es.16.110185.001143

648 Rathcke B (1988) Interactions for pollination among coflowering shrubs. *Ecology*  
649 69:446-457 doi:10.2307/1940443

650 R Core Team (2016) *R: a language and environment for statistical computing*. R  
651 foundation for statistical computing, Vienna. <https://www.R-project.org>

652 Reader RJ (1975) Competitive relationships of some bog ericads for major insect  
653 pollinators. *Can J Bot* 53:1300-1305 doi:10.1139/b75-156

654 Reader RJ (1977) Bog ericad flowers: self-compatibility and relative attractiveness to  
655 bees. *Can J Bot* 55:2279-2287 doi:10.1139/b77-259

656 Rotheray G, Gilbert F (2011) *The natural history of hoverflies*. Forrest Text, London

657 Selås V (2000) Seed production of a masting dwarf shrub, *Vaccinium myrtillus*, in  
658 relation to previous reproduction and weather. *Can J Bot* 78:423-429  
659 doi:10.1139/b00-017

660 Straka JR, Starzomski BM (2015) Fruitful factors: what limits seed production of  
661 flowering plants in the alpine? *Oecologia* 178:249-260  
662 doi:10.1007/s00442-014-3169-2

663 Tiusanen M, Hebert PDN, Schmidt NM, Roslin T (2016) One fly to rule them all—  
664 muscid flies are the key pollinators in the Arctic. *Proc R Soc B* 283:20161271  
665 doi:10.1098/rspb.2016.1271

666 Totland Ø (1993) Pollination in alpine Norway: flowering phenology, insect visitors,  
667 and visitation rates in two plant communities. *Can J Bot* 71:1072-1079  
668 doi:10.1139/b93-124

669 Totland Ø (1994) Influence of climate, time of day and season, and flower density on  
670 insect flower visitation in alpine Norway. *Arct Alp Res* 26:66-71  
671 doi:10.2307/1551879

672 Wagner J, Lechleitner M, Hosp D (2016) Pollen limitation is not the rule in nival plants:  
673 a study from the European Central Alps. *Am J Bot* 103:375-387  
674 doi:10.3732/ajb.1500214

675 Willmer P (2011) *Pollination and floral ecology*. Princeton University Press, Princeton

676 Woodcock TS, Larson BMH, Kevan PG, Inouye DW, Lunau K (2014) Flies and  
677 flowers II: floral attractants and rewards. *J Pollinat Ecol* 12:63-94

678 Yumoto T (1986) The ecological pollination syndromes of insect-pollinated plants in an  
679 alpine meadow. *Ecol Res* 1:83-95 doi:10.1007/BF02361207  
680

**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.		
	<i>Bombus hypocrita sapporoensis</i>	765 (22/701/42)	295 (19/248/28)
	<i>Bombus beaticola moshkarareppus</i>	499 (58/411/30)	451 (5/442/4)
	<i>Bombus yezoensis</i>	7 (0/7/0)	41 (0/41/0)
	<i>Bombus hypnorum koropokkrus</i>	4 (2/2/0)	3 (0/3/0)
	<i>Bombus terrestris</i>	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%)
Lepidoptera	Nymphalidae (mainly <i>Aglais urticae connexa</i> )	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%)
Hemiptera	Miridae spp.	24	0
	Anthocoridae spp.	0	22
	Other bugs	9	0
		Subtotal	33 (0.8%)
Coleoptera	Staphylinidae spp.	0	4
	Elateridae spp.	0	1
	Other beetles	0	2
		Subtotal	0 (0%)
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	<b>&lt;0.001</b>
Year (2014)	0.53	0.11	4.67	<b>&lt;0.001</b>
Week	1.19	0.16	7.38	<b>&lt;0.001</b>
Week <sup>2</sup>	-0.048	0.008	-5.98	<b>&lt;0.001</b>
Non-syrphid fly	6.13	0.93	6.59	<b>&lt;0.001</b>
Syrphid fly	-0.62	1.03	-0.61	0.54
Week × Non-syrphid fly	-1.20	0.20	-5.94	<b>&lt;0.001</b>
Week × Syrphid fly	0.31	0.22	1.42	0.16
Week <sup>2</sup> × Non-syrphid fly	0.054	0.010	5.31	<b>&lt;0.001</b>
Week <sup>2</sup> × Syrphid fly	-0.023	0.011	-2.04	<b>0.041</b>

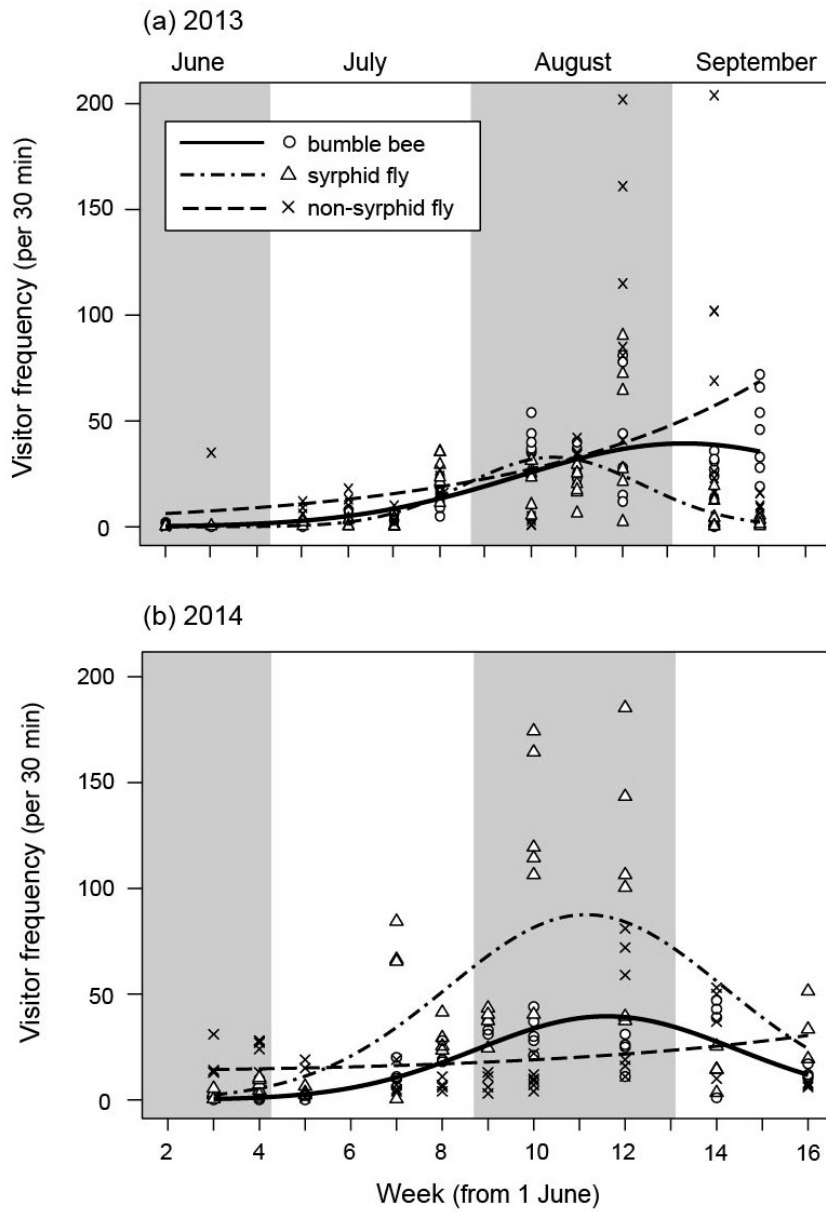
**Table 3.** Results of GLM analysis for visitation frequency of bumble bees (a), non-syrphid flies (b), and syrphid flies (c). Year (2013, 2014), air temperature, and wind speed\* are included in the explanatory variables of full models. Best-fit models after parameter selection based on AIC are indicated.

Variables	Coefficient	Std. Error	z value	P level
(a) Bumble bee frequency				
Intercept	1.95	0.62	3.13	<b>0.002</b>
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	<b>&lt;0.001</b>
Temperature	0.26	0.05	4.87	<b>&lt;0.001</b>
Wind-M	-0.05	0.37	-0.15	0.88
Wind-H	-1.63	0.52	-2.16	<b>0.002</b>
(c) Non-syrphid fly frequency				
Intercept (Year 2013)	8.51	0.15	24.00	<b>&lt;0.001</b>
Year (2014)	-0.57	0.22	-2.16	<b>0.009</b>

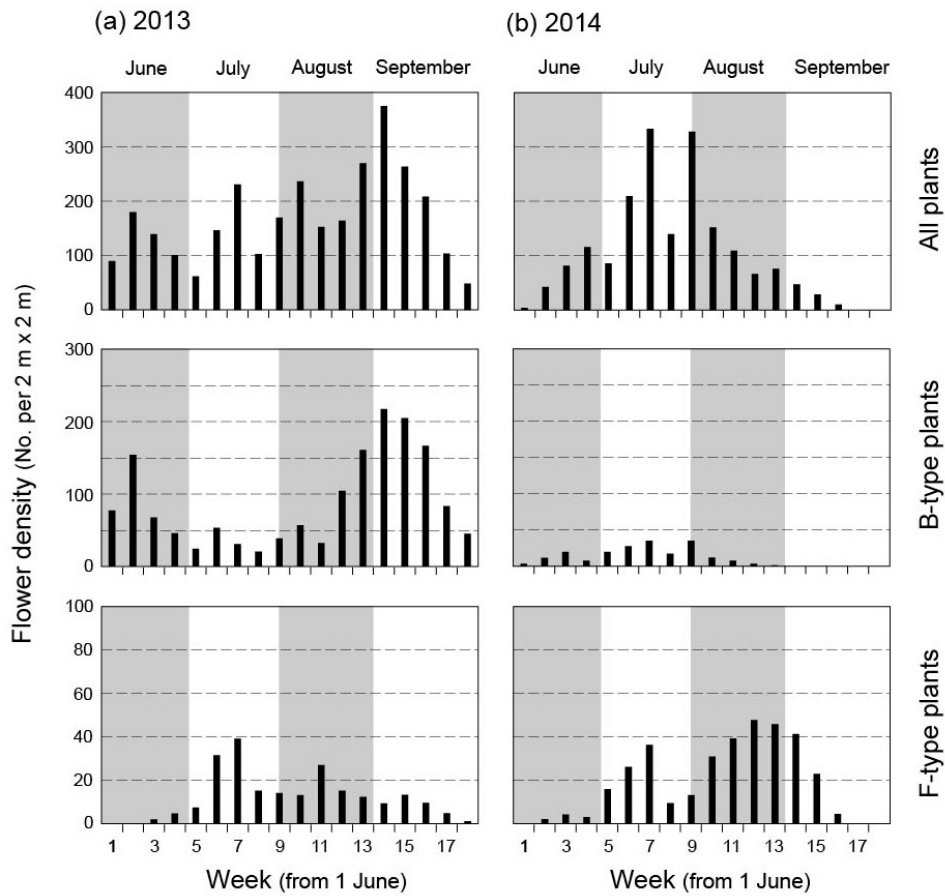
\* Wind conditions were grouped into three classes: breeze (wind-L), moderate (wind-M), and strong (wind-H).

**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.

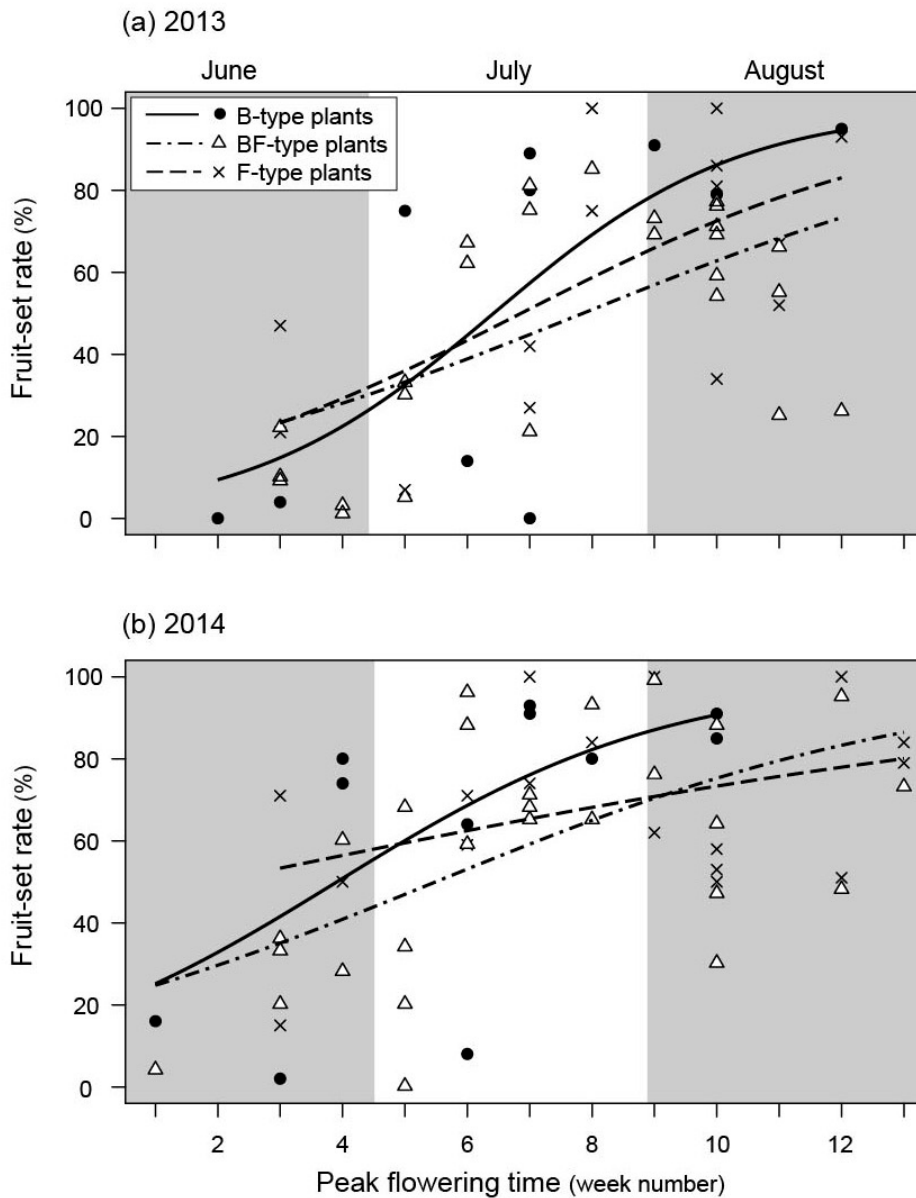
Variables	Coefficient	Std. Error	z value	P level
Intercept (Year 2013, B-type)	-2.23	0.57	-3.92	< <b>0.001</b>
Week	0.26	0.02	18.98	< <b>0.001</b>
BF-type	-0.25	0.74	-0.34	0.73
F-type	2.79	0.81	3.44	<b>0.006</b>
Year 2014	0.66	0.03	25.43	< <b>0.001</b>
Week × BF-type	0.04	0.03	1.70	0.088
Week × F-type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



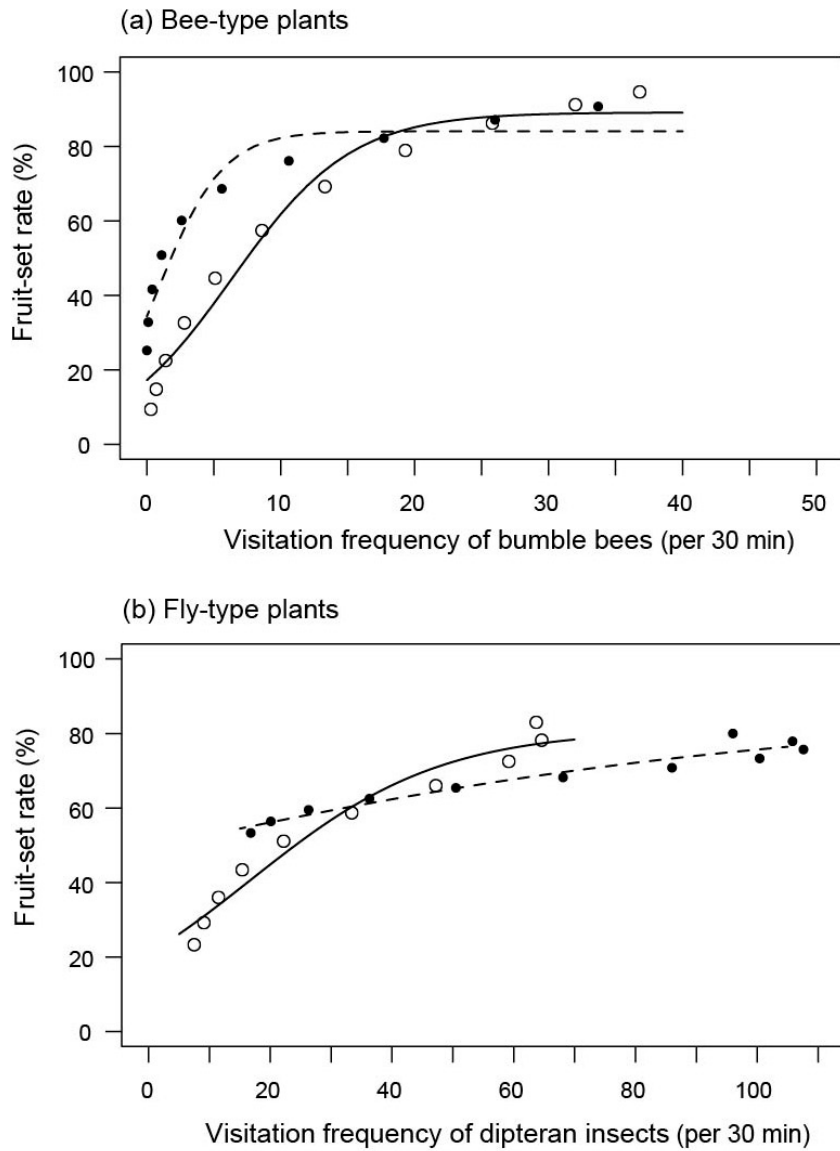
**Fig. 1** Seasonal patterns in the visitation frequencies of bumble bees (solid line), syrphid flies (chained line), and non-syrphid flies (broken line) in 2013 (a) and 2014 (b). Lines indicate the fit to the log-link functions, including the quadratic week variable. Refer to Table 2 for GLM results.



**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).