Patterns of flower-visiting insects depend on flowering phenological shifts along an altitudinal gradient in subalpine moorland ecosystems

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Abstract

Alpine and subalpine moorland ecosystems contain unique plant communities, often with many endemic and threatened species, some of which depend on insect pollination. Although alpine and subalpine moorland ecosystems are vulnerable to climatic change, few studies have investigated flower-visiting insects in such ecosystems and examined the factors regulating plant-pollinator interactions along altitudinal gradients. Here, we explored how altitudinal patterns in flower visitors change according to altitudinal shifts in flowering phenology in subalpine moorland ecosystems in northern Japan. We surveyed flower-visiting insects and flowering plants at five sites differing in altitude in early July (soon after snowmelt) and mid-August (peak growing season). In July, we found a higher visiting frequency by more variable insect orders including Dipteran, Hymenopteran, Coleopteran, and Lepidopteran species at the higher altitude sites in association with the mass flowering of *Geum pentapetalum* and *Nephrophyllidium crista-galli*. In August, such altitudinal patterns were not observed, and Dipteran species dominated across the sites due to the flowering of *Narthecium asiaticum* and *Drosera rotundifolia*. Earlier snowmelt associated with recent climate change is expected to extend the growth period of moorland plants and modify flowering phenology in moorland ecosystems, leading to altered plant-pollinator interactions. Our study provides key baselines for the detection of endangered biotic interactions and extinction risks of moorland plants under ongoing climate change.

Introduction

Alpine and subalpine moorland ecosystems contain unique plant communities, often with large numbers of endemic and threatened species (Galeuchet et al. 2005; Hájková et al. 2006; Sasaki et al. 2013). Such ecosystems also provide important ecosystem services, particularly biodiversity maintenance and cultural services including recreation and aesthetic values (Tomitaka et al. 2021). Many alpine and subalpine plants depend on insects for pollination (Ollerton et al. 2011; Lefebvre et al. 2018), with approximately 78% of plant species pollinated by animals in temperate regions (Ollerton et al. 2011), forming complex, interactive plant-pollinator networks (Bascompte et al. 2003). Because the abundance and diversity of pollinators can be higher in habitats with higher flower abundance (Hegland and Boeke 2006; Hines and Hendrix 2009; Scriven et al. 2013), biodiverse mountainous moorlands are considered essential sites for insect foraging.

Alpine and subalpine moorland ecosystems are considered vulnerable to external stressors, such as climatic changes (Chapin et al. 2000; Sasaki et al. 2014; Makishima et al. 2021). Despite the ecological and conservation significance of Japan's alpine and subalpine moorland ecosystems, few studies have investigated the flower-visiting insects in these ecosystems and examined the factors regulating plant-pollinator interactions along altitudinal gradients. Such understanding is essential to provide key baselines for detecting endangered plant-pollinator interactions as well as the extinction risks of moorland plants subject to ongoing climate change.

In mountainous regions, abiotic factors such as temperature and soil conditions vary with altitude (Beniston 2006), and flowering phenology is delayed in response to drops in temperature with increasing altitude (Cornelius et al. 2013). Indeed, the same species show different flowering periods among sites with different altitudes, and clear altitudinal patterns of flowering plant species can be observed (Blionis et al. 2001). Consequently, plant-pollinator interactions are expected to change according to altitudinal shifts in flowering phenology (Zoller et al. 2002; Mizunaga and Kudo 2017; Lefebvre et al. 2018). Previous studies have generally shown that Dipteran flower visitors predominate over Hymenopteran flower visitors at higher altitudes, which can be attributed to the preference of Dipteran species for cool and moist environments compared to other flower-visiting insect orders (Chatelain et al. 2018). Moreover, Lefebvre et al. (2018) clearly demonstrated that Diptera, Coleoptera, and Hymenoptera differed significantly in the angiosperm assemblages they visited.

Here, we explored how altitudinal patterns in flower-visiting insects change according to altitudinal shifts in flowering phenology in subalpine moorland ecosystems in northern Japan. Based on the data from five sites obtained in early July (soon after snowmelt) and mid-August (peak growing season), we describe plant-pollinator interaction networks along an altitudinal gradient and during both periods of observation.

Methods

Study area and moorland site characteristics

The study area is located in the Hakkoda Mountains (peak coordinates: 40°41N, 140°52E; 1,584 m above sea level [a.s.l.]) in Aomori Prefecture, northern Japan (Fig. 1). According to the Japan Meteorological Agency, the annual maximum snow depth, mean temperature, and mean precipitation between 2009 and 2018 ranged from 3 to 6 m, 5 to 6°C, and 1,600 to 2,200 mm, respectively, at the Sukayu Meteorological Station (40°38.9N, 140°50.9E).

Moorlands are a form of wetland that are most often found in cool climates (Ramsar Convention Bureau, 2002). Many moorlands exist in the study area, most of which have developed in depressions in a layer of volcanic ash that settled following a huge eruption during the Pleistocene, and others are created in snow patches on gentle slopes (Muraoka and Takakura, 1988). In Japan, the development of subalpine moorlands is largely influenced by spatial patterns of snow accumulation, resulting in an interspersed distribution across the landscape.

We selected the following five moorland sites across an altitudinal gradient: (1) Tamoyachi (1,254 m a.s.l.), (2) Kamikenashi (1,217 m a.s.l.), (3) Shimokenashi (1,047 m a.s.l.), (4) Takada (1,005 m a.s.l.), and (5) Tashiro (574 m a.s.l.) sites (Table 1). The moorland plant communities at these sites are dominated by *Moliniopsis japonica*, *Eriophorum vaginatum*, and *Narthecium asiaticum* (Sasaki et al. 2013). In all cases, taxonomic nomenclature follows the 'Plant Japanese name-Scientific name index YList YList' (BG Plants index: <http://ylist.info/index.html>). General descriptions of the study area and sites are provided by Sasaki et al. (2013).

Table 1

Flower abundance (i.e., the number of inflorescence) and richness (species richness of flowering species) in early July and mid-August at five moorland sites in the Hakkoda mountain range, Aomori Prefecture, northern Japan. Data were pooled along survey transects at each site.

Site	Altitude (m above sea level)	Flower abundance		Flowering plant richness	
		July	August	July	August
Tamoyachi	1,254	605	568	3	3
Kamikenashi	1,217	561	942	3	4
Shimokenashi	1,047	389	123	5	4
Takada	1,005	81	452	5	11
Tashiro	574	92	103	4	5

The studied sites are located within the special protected zone of the Towada-Hachimantai National Park, and, therefore, human disturbance such as building development, harvesting, and mining is restricted by law. Across the study sites, we observed little evidence of deer herbivory based on browsed plants and dung. Mowing and livestock grazing were not conducted at or around these sites during our sampling. Trampling into moorlands is strictly prohibited, but boardwalks are built for hiking at some sites. At these sites, our sampling transects were located far from the boardwalks to minimize potential disturbance effects. Despite these protections, habitat loss and fragmentation of these moorlands are progressing rapidly, with moorland coverage decreasing by an average of 50.01% over approximately 50 years (Makishima et al. 2021). Indeed, even when direct human impacts are minimal, earlier snowmelt in spring associated with recent climate change is facilitating the expansion of shrubby species alongside moorland habitat loss and fragmentation in Japan's mountainous regions (Kudo et al. 2017). However, the drivers of such change remain underexplored and need to be further studied based on long-term observational data.

Flowering Plants

We investigated flowering plant species in early June and mid-August in 2019 along four 2 × 20 m transects (separated by at least 20 m) at each site, with a total of 20 transects across all sites. Flowering abundance (i.e., the number of inflorescences) along each transect was recorded for all flowering plant species, except for wind-pollinated plant species.

To examine altitudinal shifts in flowering phenology, additional surveys were carried out at the Tamoyachi and Takada sites. For this, seven 2 × 2 m plots were randomly placed within each site, and flowering abundance was recorded weekly in each plot for all flowering species from the beginning of June to the end of September 2019.

Flower-visiting Insects

In early June and mid-August in 2019, the frequency of flower-visiting insects (i.e., the number of visits to a flower with contact with its stamens or stigma) along each transect was counted by individuals using the protocol of Pollard and Yates (1994). The observation survey was performed for 40 min per transect (20 min each in the morning and afternoon) under sunny and warm conditions. For post-hoc identification based on morphology and taxonomy at the genus or species level, we recorded pollinator visitation by taking pictures using a single-lens reflex camera (Nikon D5300) with a telephoto lens (AF-P DX NIKKOR 70-300 mm f/4.5-6.3G ED VR). As previously noted, the study sites are located within the special protected zone and, therefore, direct sampling of flower-visiting insects was not possible. We did not distinguish between individual pollinators, but counted the number of times each flower-visiting insect visited each flowering species.

Data analysis

We first generated plant and flower-visitor networks using the “bipartite” package and pooled data from the two 20-min surveys for each transect at the site level. For each sampling period (early July and mid-August), we regressed species richness and the frequency of flower-visiting insects along each transect against flower richness and abundance as well as altitude (as a surrogate for air temperature) using generalized linear mixed models (GLMMs). To account for the differences in visiting frequency sampled along each transect (Heck et al. 1975), the species richness of flower visitors was rarefied to the lowest visiting frequency for each survey. Before running the GLMMs, we checked for multicollinearity in the explanatory variables, with no variables having a variance inflation factor (VIF) score > 10. For both species richness and visiting frequency, we ran the GLMMs with a Poisson error structure and a square-root link function. We included the transect identity nested within site identity as a random effect in the models.

Finally, we visualized the time-series data (i.e., weekly data from the beginning of June to the end of September) of flower abundance of three dominant species in July and August at the Tamoyachi and Takada sites, namely *Geum pentapetalum*, *Nephrophyllidium crista-galli*, and *N. asiaticum*. All data analyses were performed using R software (version 4.0.3; R Development Core Team, 2020) using the “bipartite”, “vegan”, “ggplot2”, and “lme4” packages.

Results

We recorded 23 Dipteran species or species groups (i.e., spp.) from order to genus level, six Hymenopteran species or species groups from superfamily to genus level, four Coleopteran species or species groups from subfamily to genus level, and five lepidopteran species from order to genus level (Table 2). In July, we recorded higher visiting frequencies and more variable insect orders including Dipteran, Hymenopteran, Coleopteran, and Lepidopteran species, at the higher altitude sites (Kamikenashi

and Tamoyachi; Fig. 2a). In August, such altitudinal patterns were not observed, and Dipteran species were dominant across all the sites (Fig. 2b).

Table 2

Pollinator species identified in this study. Insects were identified based on morphology and taxonomy from order to genus level. Each species or species group is coded as "Order_ID": H, Hymenoptera; D, Diptera; C, Coleoptera; L, Lepidoptera; and O, other order.

Species Code	Taxonomic level	Species
D_01	Genus	<i>Allograpta</i> sp.
D_02	Genus	<i>Betasyrphus</i> spp.
D_03	Family	Calliphoridae spp.
D_04	Genus	<i>Didea</i> spp.
D_05	Order	Diptera sp.1
D_06	Order	Diptera sp.2
D_07	Order	Diptera sp.3
D_08	Order	Diptera sp.4
D_09	Order	Diptera spp.
D_10	Family	Empididae sp.1
D_11	Family	Empididae sp.2
D_12	Genus	<i>Episyrphus</i> sp.
D_13	Genus	<i>Eristalinus</i> spp.
D_14	Genus	<i>Eristalis</i> sp.
D_15	Genus	<i>Eupeodes</i> spp.
D_16	Genus	<i>Helophilus</i> sp.
D_17	Tribe	Melanostomatini spp.
D_18	Family	Mycetophilidae sp.1
D_19	Genus	<i>Parhelophilus</i> sp.
D_20	Genus	<i>Scathophaga</i> sp.
D_21	Genus	<i>Sphaerophoria</i> spp.
D_22	Genus	<i>Stomorphina</i> sp.
D_23	Tribe	Syrphini spp.
H_01	Superfamily	Apoidea spp.
H_02	Genus	<i>Bombus</i> sp.1

Species Code	Taxonomic level	Species
H_03	Genus	<i>Bombus</i> sp.2
H_04	Genus	<i>Bombus</i> spp.
H_05	Order	Hymenoptera sp.
H_06	Order	Hymenoptera spp.
C_01	Genus	<i>Cephaloon</i> sp.
C_02	Genus	<i>Dasytes</i> spp.
C_03	Subfamily	Donaciinae spp.
C_04	Genus	<i>Oedemeronia</i> sp.
L_01	Genus	<i>Colias</i> sp.
L_02	Genus	<i>Fabriciana</i> sp.
L_03	Order	Lepidoptera spp.
L_04	Family	Lycaenidae spp.
L_05	Genus	<i>Thoressa</i> sp.
O_01	Family	Acrididae sp.1
O_02	Family	Acrididae sp.2
O_03	Family	Acrididae sp.3
O_04	Family	Acrididae sp.4
O_05	Order	Araneae spp.
O_06	Genus	<i>Cicadella</i> sp
O_07	Order	Hemiptera spp.
O_08	Genus	<i>Pantala</i> sp.
O_09	Family	Salticidae sp.
O_10	Family	Tettigoniidae spp.

In July, *G. pentapetalum*, *N. crista-galli*, *Schizocodon soldanelloides*, *N. asiaticum*, and *Pogonia japonica* were the dominant flowering plants, with rarer species including *Aletris foliata*, *Ixeridium dentatum subsp. ozense*, and *Menziesia multiflora* (Fig. 3a). The abundance of *G. pentapetalum* was highest at the higher-altitude sites (Tamoyachi and Kamikenashi), while *N. crista-galli* was most abundant at the middle-altitude sites (Shimokenashi and Takada). *N. asiaticum* was only observed in flower at the Tashiro site.

In August, *N. asiaticum* and *Drosera rotundifolia* were the dominant flowering plants along with *Parnassia palustris*, *Sanguisorba tenuifolia* var. *alba*, *Platanthera tipuloides* subsp. *nipponica*, *Spiranthes sinensis* var. *amoena*, *Inula ciliaris*, and *Hosta sieboldii* var. *rectifolia* (Fig. 3b). Flowering individuals of *N. asiaticum* were commonly found across all sites in August.

The structure of plant and flower-visitor networks at each site in July and August are shown in Fig. 4 (also see Tables 2 and 3). We observed more diverse plant-pollinator interactions in July than in August. For example, in July, across all sites except for Tashiro, *G. pentapetalum*, *N. crista-galli*, and *S. soldanelloides* were linked with diverse orders including Hymenoptera, Diptera, Coleoptera, and Lepidoptera (Fig. 4a). The Tashiro site lacked these flowering species, and flower visitors were dominated by Dipteran species. In August, *N. asiaticum* was the dominant flowering plant species across all the sites, and this species was linked primarily with Dipteran species (Fig. 4b).

Table 3

All 21 flowering plant species identified in this study. Each species is coded as "F_ID". Six flowering plant species without F_ID were not visited by pollinators during our observations.

ID	Species
F_01	<i>Nephrophyllidium crista-galli</i>
F_02	<i>Schizocodon soldanelloides</i>
F_03	<i>Geum pentapetalum</i>
F_04	<i>Narthecium asiaticum</i>
F_05	<i>Drosera rotundifolia</i>
F_06	<i>Platanthera tipuloides subsp. nipponica</i>
F_07	<i>Menziesia multiflora</i>
F_08	<i>Aletris foliata</i>
F_09	<i>Parnassia palustris</i>
F_10	<i>Hosta sieboldii var. rectifolia</i>
F_11	<i>Sanguisorba tenuifolia var. alba</i>
F_12	<i>Spiranthes sinensis var. amoena</i>
F_13	<i>Inula ciliaris</i>
F_14	<i>Ixeridium dentatum subsp. ozense</i>
F_15	<i>Pogonia japonica</i>
	<i>Gaultheria adenostris</i>
	<i>Trientalis europaea</i>
	<i>Vaccinium oxycoccos</i>
	<i>Peucedanum multivittatum</i>
	<i>Hypericum kamtschaticum var. hondoense</i>
	<i>Solidago virgaurea subsp. gigantea</i>

In July, there were significant positive relationships between the visiting frequency of pollinators and flower abundance, and between visiting frequency and altitude (Table 4). In August, there were significant positive relationships between insect visiting frequency and flower abundance, and between visiting frequency and flowering species richness (Table 4). In both July and August, there were no significant relationships between pollinator species richness and the explanatory variables (Table 4).

Table 4

Results of generalized linear mixed models (GLMMs) regressing species richness and frequency of flower-visiting insects along each survey transect against flower richness and abundance, and altitude. Transect identity nested within site was included as a random effect in the models. Significant regression coefficients are in bold. ($P < 0.05$).

Response variables	Variables	Coefficient	SE	Z-value	P value
Visiting frequency in July	(Intercept)	1.235	0.923	1.338	0.181
	Flower abundance	0.009	0.002	4.222	0.000
	Flower richness	-0.042	0.199	-0.210	0.834
	Altitude	0.002	0.001	2.410	0.016
Pollinator richness in July	(Intercept)	0.879	0.573	1.533	0.125
	Flower richness	0.089	0.104	0.853	0.393
	Flower abundance	0.000	0.001	0.173	0.863
	Altitude	0.000	0.001	0.639	0.523
Visiting frequency in August	(Intercept)	1.761	1.226	1.436	0.151
	Flower abundance	0.008	0.003	2.690	0.007
	Flower richness	0.380	0.142	2.677	0.007
	Altitude	-0.000	0.001	-0.333	0.739
Pollinator richness in August	(Intercept)	0.994	0.477	2.085	0.037
	Flower abundance	0.000	0.001	0.117	0.907
	Flower richness	0.004	0.049	0.084	0.933
	Altitude	0.000	0.000	0.117	0.907

Time-series data of flower abundance for the three dominant species (*G. pentapetalum*, *N. crista-galli*, and *N. asiaticum*) at the Takada (1,005 m a.s.l.) and Tashiro (1,254 m a.s.l.) sites are shown in Fig. 5. Notably, the flowering phenology of *G. pentapetalum* clearly differed between these sites along with *N. crista-galli* and *N. asiaticum*, although there was some overlap.

Discussion

Our observations identified altitudinal patterns in insect flower visitors according to altitudinal variations in flowering phenology in the subalpine moorland ecosystems of northern Japan. In early July, we observed higher visiting frequencies by more variable insect orders including Dipteran, Hymenopteran, Coleopteran, and Lepidopteran species at higher altitudes than at the lower altitude sites. This is attributed to the mass flowering of *G. pentapetalum* and *N. crista-galli* at these higher-altitude sites. In

mid-August, such altitudinal patterns were not observed, and Dipteran species dominated across all the sites in association with the flowering of *N. asiaticum* and *D. rotundifolia*.

In both July and August, we observed a positive relationship between the visiting frequencies of pollinators and flower abundance (Table 4), possibly because pollinators search and select locations with high flower abundance to increase the efficiency of resource acquisition (Hegland and Boeke 2006). This also explains the positive relationship between flower-visiting frequency and altitude in July (Table 4), when flower abundance increased with altitude (Fig. 3a). In August, we observed the highest species richness (Table 1; Fig. 3b) and frequency of flower visitors (Fig. 2b; Table 4) at Takada. Compared to the other sites, Takada is surrounded by wider stretches of moorland and is located nearer to neighboring moorlands (Fig. 1). Therefore, it is likely that favorable foraging conditions (i.e., greater accessibility to nectar resources) enhanced the frequency of pollinator visits at this site. In contrast, in July, both the abundance and richness of flowering plants were low at Takada (Fig. 3a; Table 1) with correspondingly low pollinator visitor frequencies.

The plant-pollinator networks (Fig. 4) suggest that *G. pentapetalum*, *N. crista-galli*, and *S. soldanelloides* flower mainly in early summer, soon after snowmelt, and attract diverse insect orders. In comparison, *N. asiaticum* mainly flowered during the peak growing season and primarily attracted Diptera. In particular, given that Hymenopteran species have a greater preference for flowering plants than Dipteran species (Branquart and Hemptinne 2000; Mizunaga and Kudo 2017), our results suggest a greater preference for *G. pentapetalum*, *N. crista-galli*, and *S. soldanelloides* by Hymenopteran species over other species in these moorland ecosystems. In contrast, many Dipteran species are generalists (Classen et al. 2020; Zhao et al. 2021), with phenological shifts across time (i.e., between early July and mid-August) and space (i.e., with altitude) having less of an effect on their flower-visiting frequency.

Many previous studies have suggested that Diptera predominates over other insect orders, such as Hymenoptera, Coleoptera, and Lepidoptera, at high altitudes and, therefore, its species play primary roles in plant-pollinator interactions (Zoller et al. 2002; Mizunaga and Kudo 2017; Lefebvre et al. 2018). Consequently, turnover between insect orders along altitudinal gradients can often be observed (Lefebvre et al. 2018). In our study, we did not observe a clear turnover between insect orders along the altitudinal gradient (Figs. 2 and 4). This might be attributed to altitudinal shifts in flowering phenology, whereby the observed patterns of flower-visiting insects reflect the degree of altitudinal differentiation in flowering time (Fig. 5). Notably, in August, the flowering period of the main flowering species, *N. asiaticum*, overlapped between the Tamoyachi and Takada sites (Fig. 5), with flowering individuals commonly found across all sites (Fig. 3). This likely explains the predominance of Diptera across these sites in August. Additionally, as our altitudinal gradient was less stratified than in the case of studies in higher mountainous areas, such as the European Alps (e.g., Lefebvre et al. 2018; ranging from 1,000 to 2,700 a.s.l.), environmental limitations on the spatial distributions of insect flower visitors could be weaker. The relatively cool summer temperatures across the Hakkoda sites (ranging 17.34–20.41°C between July and September) would have also favored Dipteran species. Based on all of these observations, we suggest that altitudinal patterns in flower-visiting insects reflect phenological variations in flowering.

Despite the ecological and conservation significance of Japan's alpine and subalpine moorland ecosystems, little is known about flower-visiting insects in these ecosystems and the factors regulating plant-pollinator interactions along altitudinal gradients. Most concerningly, habitat loss and fragmentation of these moorlands are progressing rapidly in association with climatic warming and associated environmental changes (Makishima et al. 2021). In particular, earlier snowmelt associated with recent warming is likely linked to longer moorland plant growing periods and altered flowering phenology, leading to changes in plant-pollinator interactions. Importantly, our study provides key baseline data for the detection of endangered biotic interactions and extinction risks in moorland plant communities subject to ongoing climate change.

Declarations

Conflicts of interest

None.

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Authors' contributions

NM and TS conceived and designed the study; All authors collected the data; NM analyzed the data; NM and TS wrote the first draft of the manuscript; All the authors contributed to manuscript revisions and approved the final version.

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Availability of data and material

The data supporting the result in the paper will be archived in Dryad at the time of acceptance and the data DOI will be included.

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Figures

Figure 1

Map showing the locations of the five moorland sites in the Hakkoda Mountains, Aomori Prefecture, northern Japan. Circles represent the studied moorlands and the square represents Sukayu Meteorological Station. All moorlands ($n = 365$) within the Hakkoda mountain range are delineated by black lines

Fig. 2.

Figure 2

Frequency of flower visitors by insect orders in early July and mid-August at each site: TAM, Tamoyachi; SHI, Shimokenashi; KAM, Kamikenashi; TAK, Takada; and TAS, Tashiro

Figure 3

Abundance of common flowering plants in early July and mid-August at each site: TAM, Tamoyachi; SHI, Shimokenashi; KAM, Kamikenashi; TAK, Takada; and TAS, Tashiro

Figure 4

Plant-pollinator networks in early July and mid-August at each site. The width of the upper bars represents the visiting frequency of each species or species group (see Table 2), and the width of the lower bars represents the abundance of each flowering plant species (see Table 3)

Figure 5

Time-series plot of flower abundance for three dominant species (*G. pentapetalum*, *N. crista-galli*, and *N. asiaticum*) at Takada (1,005 m above sea level [a.s.l.]) and Tashiro (1,254 m a.s.l.). Flower abundance is plotted against the days of year