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SPECIAL FEATURE

Phenology in a community context: Toward a better understanding of the causes and consequences of phenology in seasonal environments

Contrasting altitudinal patterns of diversity between bumblebees and bumblebee-visited flowers: Poverty of bumblebee diversity in a high mountain of Japan

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Abstract

Range shifts of mountain organisms toward higher elevations in response to global warming may result in spatial mismatches between plants and their pollinators. Here, we aimed to examine whether bumblebee diversity decreases in a high-altitude zone, and whether it parallels a decrease in the altitudinal diversity of bumblebee-visited plants. We surveyed the alpha diversities of flower-visiting bumblebees and bumblebee-visited plants along an altitudinal gradient on a Japanese high mountain. Then, we examined whether the alpha diversities of bumblebees and bumblebee-visited plants could be explained by altitude, or by other factors such as season, surveyed area and flower abundance. We found that a model including only altitude best explained bumblebee diversity, and that flower abundance and plant diversity had considerable value in explaining bumblebee diversity. In contrast, none of the studied factors explained plant diversity. Bumblebee diversity was minimal in the high-altitude zone (1,900–2,600 m a.s.l.), where the only dominant bumblebee species, *Bombus beaticola*, visited many species of flowering plants. In contrast, five to seven bumblebee species were distributed in the low- (700–1,300 m a.s.l.) and middle- (1,300–1,900 m a.s.l.) altitude zones. These results show that plant–pollinator mutualism in high-altitude zone of a Japanese mountain is asymmetric: many bee-pollinated plants rely almost exclusively on one bumblebee species (*B. beaticola*) for pollination. Monitoring future changes in the distribution and abundance of *B. beaticola* is indispensable for the conservation of alpine plant in Japan.

KEYWORDS

alpine plant fauna, altitudinal change, *Bombus beaticola*, insect–plant interaction, mountain biodiversity

1 | INTRODUCTION

Organisms that live at high altitude are expected to be particularly sensitive to climate warming. They are expected to shift their geographical ranges to remain in compatible climate zones. For example, the distributions of some species have shifted toward higher elevations under the consistent of global warming (Narins & Meenderink, 2014; Pizzolotto, Gobbi, & Brandmayr, 2014; Urli et al., 2014). Such range shifts may result in spatial mismatches between plants and their pollinators because of their different responses to climatic variables (Pyke, Thomson, Inouye, & Miller, 2016).

Bumblebees (*Bombus* spp.) are essential wild pollinators of native plant communities throughout temperate

ecosystems (Corbet, Williams, & Osborne, 1991; Fontaine, Dajoz, Meriguet, & Loreau, 2006; Hegland & Totland, 2008; Kremen, Williams, & Thorp, 2002; Memmott, Waser, & Price, 2004). They have also been domesticated, and consequently, they are of growing economic importance for crop pollination (Delaplane, Mayer, & Mayer, 2000). In recent decades, bumblebees have declined in both diversity and abundance in both Europe and North America (Goulson, Lye, & Darvill, 2008). For instance, in the United Kingdom, 6 of the 16 nonparasitic bumblebee species have shown notable declines, 4 species might be in decline, and only 6 species are stable or increasing (Williams & Osborne, 2009). Declines in bumblebee populations can have serious consequences for plant communities. In particular, a decline in the abundance of pollinators is likely to affect populations of obligatory outcrossing, animal-pollinated plants (Biesmeijer et al., 2006), and may also reduce plant species diversity. Indeed, in the United Kingdom, the frequency of 76% of forage plant species used by bumblebees declined between 1978 and 1998 (Carvell et al., 2006). However, it is not clear whether the loss of bumblebees has caused a decline in the number of bumblebee-visited plant species, or the loss of bumblebee-visited plant species has resulted in a loss of bumblebee species (Scheper et al., 2014).

Bumblebee fauna is known to be poor at high altitudes in temperate regions (Goulson et al., 2008). Only seven bumblebee species are distributed in the Rocky Mountains of North America (2,500–3,000 m a.s.l.; Pyke, 1982), and only 10 species in the high mountain areas of Spain (2,000–2,200 m a.s. l.; Ploquin, Herrera, & Obeso, 2013), much fewer then are distributed at lower altitudes. Miller-Struttmann and Galen (2014) showed that only two bumblebee species dominated at even higher elevation (3,500–4,300 m a.s.l.) in the Rocky Mountains, and that they visited a wider variety of plant species at higher elevations than lower elevations. Likewise, Yumoto (1986) and Mizunaga and Kudo (2017) found that

only two bee pollinator species (*Bombus beaticola* and *Bombus hypocrita*) predominated in high-altitude zones (2,500 m a.s.l.) of Mt. Kisokoma, Central Japan, and Taisetsu Mountains (1,700–1900 m a.s.l.), northern Japan, respectively. In contrast, eight bumblebee species and many other kinds of bees are present in low-altitude areas of Central Japan, eight species of bumblebees and many other kinds of bees have been reported (Tomono & Sota, 1997). Further, Yumoto (1986) identified two pollination syndromes in alpine plants: bee-pollinated and fly-pollinated. As bumblebees and hoverflies are almost the only flower visitors in the Japanese high-altitude zone, it is reasonable to assume that bumblebees are efficient pollinators of large flowers in the high mountains of Japan.

It is unknown whether the paucity of bee fauna at high altitudes is correlated with the low diversity of bumblebee-visited plant species in such locations. In this study, we addressed this question by comparing altitudinal patterns of species diversity between bumblebees and bumblebee-visited plants. We hypothesized that bumblebee-visited plant diversity does not change with a decrease in bumblebee diversity in the Japanese high mountains. This hypothesis is based on the fact that a generalist pollinator bumblebee species can potentially visit and pollinate many kinds of plant species, and that many plant species have evolved traits to survive in the face of frequent pollinator limitation, such as selfing and asexual reproduction.

2 | MATERIALS AND METHODS

2.1 | Study area

Surveys of flower-visiting bumblebees were conducted along a roadway from the foot (700 m a.s.l.) to nearly the top of Mt. Norikura (2,600 m a.s.l), Nagano Prefecture, Central Japan (Figure 1). The roadway runs through cool-
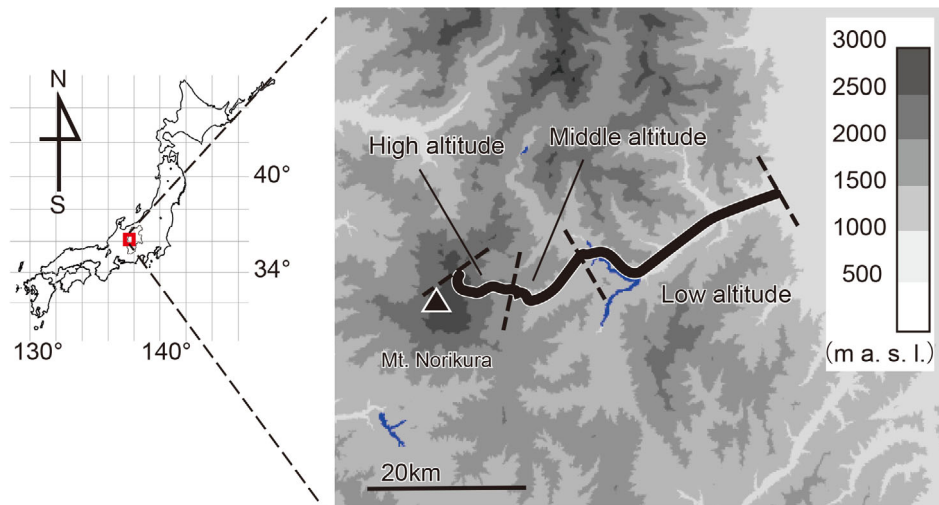
FIGURE 1 Location of study area on Mt. Norikura, Nagano Prefecture, Central Japan. Survey was conducted along roadway (bold line). Low- (700–1,300 m a.s.l.), middle- (1,300–1900 m a.s.l.) and high- (1,900–2,600 m a.s.l.) altitude zones are indicated [Color figure can be viewed at wileyonlinelibrary.com]

temperate deciduous broad-leaved forest (700–1,500 m a.s. l.) and subalpine coniferous forest (1,500–2,600 m a.s.l.), and is bordered by meadows and shrubs. The flowering season differs among the different altitudinal zones: from late May to early October in the low-altitude zone (700–1,300 m a.s.l.), from mid-June to late September in the middle-altitude zone (1,300–1900 m a.s.l.), and from early July to mid-September in the high-altitude zone (1,900–2,600 m a. s.l.). The foraging periods of bumblebees overlap with the flowering seasons.

2.2 | Surveys of flower-visiting bumblebees

Surveys of flower-visiting bumblebees were carried out only on sunny, nonwindy days between 0900 and 1400 local time from July to September 2012. We set quadrats (dimensions, 18 m × 2 m on average) along the roadway where many flowers were present. The placement of the quadrats was generally haphazardly but they were spread along the whole range of attempts. The mean distances between quadrats within each altitudinal zone (405 m ± 824 m SD) were smaller than the nearest distances between different altitudinal zones (2,278 ± 1,750 m SD). Each quadrat was surveyed only once. During each survey, a single collector searched the quadrats and examined all the flowering plants. The same collector surveyed 29 quadrats in July (low-altitude zone, 10 quadrats; middle, 12; high, 7), 36 quadrats in August (low, 6; middle, 16; high, 14) and 35 quadrats in September (low, 9; middle, 14; high, 12). During each survey, the collector walked at a steady pace around each quadrat for 20 min, caught every flower-visiting bumblebee, recorded the bumblebee species, counted the number of flowers of the blooming bumblebee-visited plant species in the quadrats, and measured the dimension of each quadrat (meter × meter). The bumblebees were released after identification unless they were not altitude to be identified in the field. In that case, the specimens were brought to the laboratory and identified under a microscope. The survey was conducted on several days per week and spread almost equally across each month.

2.3 | Statistical analyses

To examine the altitudinal distribution of each bumblebee species, we calculated the mean, median, maximum and minimum elevation at which each individual species was observed. We used one-way analysis of variance (ANOVA) in R version 3.5.0. (R Core Team, 2018) to examine interspecific and monthly differences in the altitudinal distribution of the bumblebee species. Tukey's HSD post hoc test in R version 3.5.0. (R Core Team, 2018) was used to analyse pairwise comparisons.

Patterns in alpha diversity were explored using Shannon's diversity index (H′). The alpha diversity values of bumblebees and blooming bumblebee-visited flowers were,

respectively, calculated using the "vegan" community ecology package in R version 3.5.0. (Oksanen et al., 2013; R Core Team, 2018). These calculations were based on the number of individuals of each bumblebee species caught on flowers, and on the number of blooming flowers of each bumblebee-visited plant species in the quadrats. To avoid a skewed distribution of bumblebee- and flower occurrences, the data from several quadrats from the same month and of similar altitude (200-m altitudinal intervals) were pooled. For example, the data from four quadrats in the altitudinal range of 700–900 m a.s.l. in July were pooled, and the diversity of the pooled quadrats was calculated.

The alpha diversities of bumblebees and plants (flowers) were analysed using linear mixed-effect models (lme4 package in R version 3.5.0; Bolker et al., 2009), using Gaussian distribution and 200-m altitudinal interval as a random effect. We used an information theoretical approach to assess the extent to which explanatory variables (predictors) were related to bee and flower diversity. We constructed a set of linear mixed-effects models containing all possible combinations of the different predictors. The full model for bumblebee diversity included altitude, the square of altitudes, months (July, August, September), surveyed area, total number of flowers and alpha diversity of blooming bumblebee-visited flowers as predictors. It was reasonable to include the total number of flowers and flower diversity as candidate predictors because floral display is known to have a positive effect on flower visitation (Sanchez-Lafuente et al., 2005) and flower diversity may have a positive effect on bumblebee diversity. The full model for flower diversity included altitude, square of altitude, months, surveyed area and alpha bumblebee diversity, as predictors.

For bumblebee and flower diversity, we ranked 64 and 32 possible models, respectively, according to their Akaike information criterion corrected for a small sample size (AIC$_c$), and restricted our candidate model set to models with ΔAIC$_c$ < 2 (Burnham, Anderson, & Huyvaert, 2011). For the models in the candidate set, we calculated the Akaike model weight (ω_m), which reflects the probability that a model is the best approximating model given the set of candidate models considered (Burnham et al., 2011). The relative importance (ω_p) of a predictor was based on the sum of the Akaike weights across all models in the candidate model set that included the predictor (Burnham et al., 2011). These analyses were conducted using the packages lme4 (Bolker et al., 2009) and MuMIn version 1.40.4 in R version 3.5.0. (Barton, 2018).

3 | RESULTS

3.1 | Altitudinal distribution of bumblebees

We recorded 765 bumblebee individuals belonging to 8 species and 1 unidentified species, and 56 bumblebee-visited
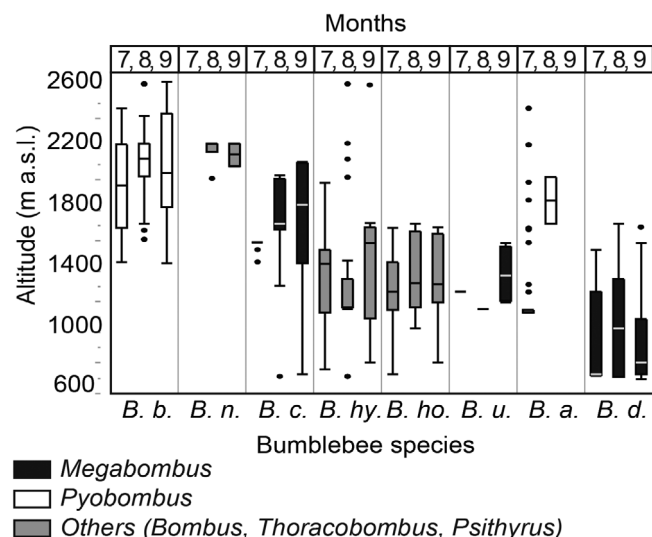
FIGURE 2 Box plots of altitudinal distributions of bumblebee species. Each box shows interquartile range of data, slit shows the median, and whiskers show ±1.5 *SD*. Outliers are plotted individually. Box shading indicates subgenus of each species. Numbers above box plots indicate the months (7, July; 8, August; 9, September) *B. b., Bombus beaticola beaticola; B. n., Bombus norvegicus japonicas; B. c., Bombus consobrinus wittenburgi; B. hy., Bombus hypocrita hypocrita; B. ho., Bombus honshuensis; B. u., Bombus ussurensis; B. a., Bombus ardens ardens; B. d., Bombus diversus diversus*

plant species (Tables S1 and S2 in Supporting Information). The altitudinal distribution of the bumblebees differed among species (ANOVA, $df = 7$, $F = 177.89$, $p < 0.001$; Figure 2). *B. beaticola* was distributed at the highest altitude, and *Bombus diversus* at the lowest (Tukey's HSD post hoc test, $p < 0.001$; Figure 2). Among the bumblebee species, only *B. beaticola* (ANOVA, $df = 2$, $F = 6.778$, $p = 0.0013$) and *Bombus ardens* (ANOVA, $df = 1$, $F = 5.067$, $p = 0.0278$) changed their altitudinal distribution during the survey months. Although several (5–7) bumblebee species were distributed in the low (700–1,300 m a.s.l.) and middle (1,300–1,900 m a.s.l.) altitudinal zones, *B. beaticola* dominated in the high-altitude zone (1,900–2,600 m a.s.l.) (Figure 3).

3.2 | Altitudinal changes in diversity of bumblebees and plants

Model averaging across the set of candidate models ($\Delta AIC_c < 2$, Burnham et al., 2011) revealed that the most important factor associated with bumblebee diversity was square of altitude ($\omega_p = 0.60$, Table 1). The model with just square of altitude best explained bumblebee diversity ($AIC_c = 74.2$, $\omega_m = 0.24$, log likelihood = −32.3), and had a probability of 0.24 of being the best model among the three models in the candidate set. The other three factors (number of flowers, altitude and flower diversity) also had considerable value explaining bumblebee diversity (numbers of flowers: $\omega_p = 0.34$; altitude: $\omega_p = 0.33$; diversity of flowers: $\omega_p = 0.25$). Bumblebee diversity was lower in the

high-altitude zone than in the low- and middle-altitude zones (Figure 4a, Table S3).

In contrast to bumblebee diversity, plant diversity was not expected by any of the predictors. Model averaging across the set of candidate models ($\Delta AIC_c < 2$, Burnham et al., 2011) revealed that the model with only a random factor was most appropriate to explain plant diversity ($AIC_c = 80.8$, $\omega_m = 0.41$). Square of altitude, bumblebee diversity, surveyed area and altitude were relatively unimportant predictors to explain plant diversity (square of altitude: $\omega_p = 0.19$; bumblebee diversity at quadrats: $\omega_p = 0.19$; surveyed area: $\omega_p = 0.16$; altitude: $\omega_p = 0.15$). In contrast to the case for bumblebee diversity, altitude was only of minor importance in explaining plant diversity (Figure 4b, Table S4).

4 | DISCUSSION

Bumblebees and flowers showed contrasting patterns of diversity along an altitudinal gradient. Bumblebee diversity was lower in the high-altitude zone than in the middle- and low-altitude zones, while flower diversity did not change markedly across altitudes (Figure 4). A single bumblebee species, *B. beaticola*, was by far the most dominant in the high-altitude zone, and almost all plants with large flowers in that zone were visited by this species (Figure 3). *B. beaticola* has also been reported to be abundant in other high mountains of Central Japan (Kato, Matsumoto, & Kato, 1993; Yumoto, 1986), suggesting that it is an important pollinating agent of bee-pollinated large flowers in the central high mountains of Japan.

Contrasting altitudinal patterns of diversity between bumblebees and bumblebee-visited plants may also occur in the alpine zone of the Rocky Mountains of North America (3,500–4,300 m a.s.l.) where two bumblebee species dominate, and many bee-visited plant species are distributed (Miller-Struttmann & Galen, 2014). Unfortunately, however, Miller-Struttmann and Galen (2014) did not measure the diversity of bee-visited plants.

Bumblebee diversity is poor in high mountains (Miller-Struttmann & Galen, 2014) and polar regions (Potapov, Kolosova, & Gofarov, 2014) despite bumblebee adaptations to extreme climatic conditions such as facultative endothermy, the annual life cycle of the colony and overwintering of single females (Potapov et al., 2014). Not only the cold climate, but also the short flowering season and limited land area may delimit bumblebee abundance and diversity in high mountains. Because bumblebees have a social life style, they need more resources (flower pollen and nectar) to maintain their colony than do other solitary organisms (Heinrich, 1976). Accordingly, among organisms adapted to cold climates, bumblebees are more likely to suffer declines of abundance and diversity in polar and high-altitude areas.
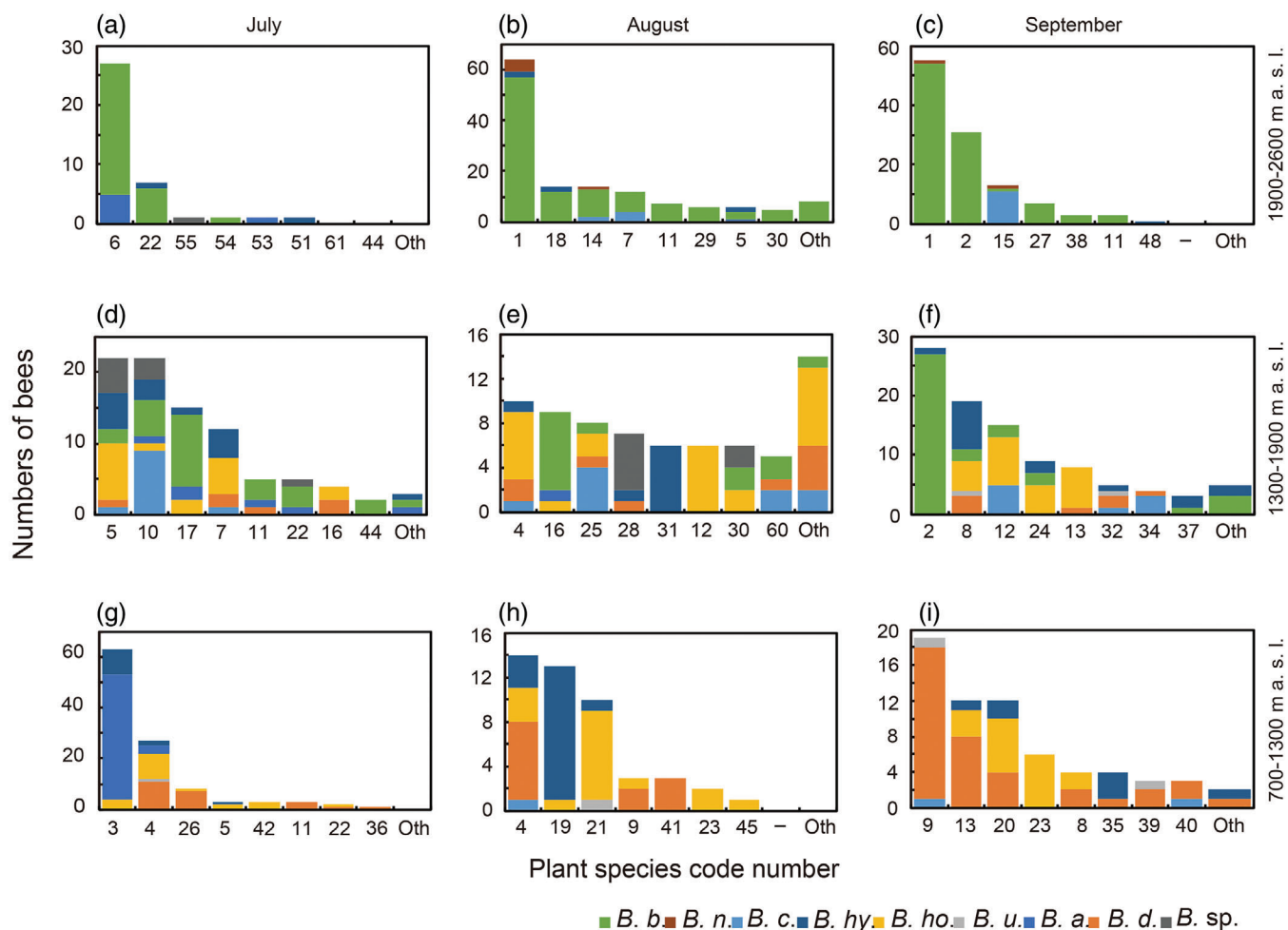
FIGURE 3 Altitudinal and seasonal changes in number of flowers visited by bumblebees; (a)–(c): July–September at high-altitude zone (1,900–2,600 m a.s. l.), (d)–(f): July–September at middle-altitude zone (1,300–1900 m a.s.l.), (g)–(i): July–September at low-altitude zone (700–1,300 m a.s.l.). Colour shows the number of visits by each bumblebee species to plant species (indicated by number on the x-axis, see Table S2 for plant species corresponding to each number). See Figure 2 for the bumblebee species abbreviations. "B. sp." indicates *Bombus* individuals that were not identified at the species level. "Oth" indicates all other plants species combined [Color figure can be viewed at wileyonlinelibrary.com]

In the high-altitude zone of the study area, the diversity of flowering species was high, despite the poor diversity of bumblebee fauna. If plants in the high-altitude zone are subject to

TABLE 1 Model selection results for candidate models explaining bumblebee diversity

	Model			
Predictor	**1**	**2**	**3**	**ω_p**
Square of altitude	−0.67	−0.67		0.60
No. of flowers				0.34
Altitude		−3.67		0.33
Flower diversity				0.25
Surveyed area				0.08
Month				0.06
ΔAIC_c	0.00	1.30	1.79	
ω_m	0.24	0.12	0.10	

Note. Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (ΔAIC_c) value. Predictors were standardized by centering and dividing by *SD*s. Akaike model weights (ω_m) indicate the probability that a model is the best approximating model given the set of models considered. For each predictor, the parameter estimate for each candidate model is given, along with its relative importance (ω_p).

pollinator limitation, the may be at risk of diversity loss or extinction. Plant–pollinator interactions are usually asymmetrical and nested, and a core set of generalist species often play a key role (Bascompte, Jordano, & Olesen, 2006). As short-tongued bumblebees function as generalist floral foragers (Miller-Struttmann et al., 2015), the dominant short tongued bumblebee species in the high-altitude zone of the study area, *B. beaticola*, may well pollinate many plant species there. Further, some plant species in high-altitude zones can reproduce by selfing (Tomono & Sota, 1997) or by vegetative propagation so that they are less affected by pollinator limitation.

Although syrphid flies and other dipterans are also major pollinators in the Japanese high mountains, they rarely visit bumblebee-visited plants (Yumoto, 1986). Syrphid-visited plants and bumblebee-visited plant species clearly differ with respect to their flower size, flowering behavior, spatial distribution of their populations and community-level flowering phenology (Yumoto, 1986). In fact, during our survey, we generally did not observe syrphid flies visiting the bumblebee-visited plants (S. Egawa, personal communication, August 7, 2012).
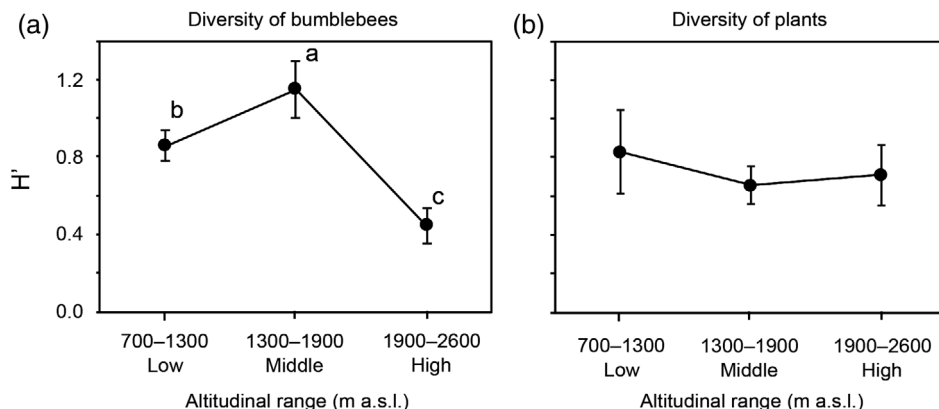
FIGURE 4 Mean ($\pm SE$) of Shannon's diversity index (H′) for (a) bumblebees ($F = 14.8$, $p < 0.05$; ANOVA) and (b) plants across the altitudinal zones ($F = 0.27$, $p = 0.765$; ANOVA). Data from July, August and September are pooled. Different lowercase letters indicate significant differences ($p < 0.05$; Tukey's HSD post hoc test). Altitudinal change in (a) bumblebee diversity was related to altitude while that in (b) plant diversity was not (see also Tables 2 and S3)

Our results show that one bumblebee species, *B. beaticola*, was the only major flower visitor and may be the only major pollinator of nearly all bee-pollinated plant species in the high-altitude zone of Mt. Norikura. This indicates that the plant–pollinator relationship at this site is vulnerable to further environmental changes. Although generalist species are often less sensitive to environmental change than specialist species (Biesmeijer et al., 2006), it is risky to rely on only a single generalist species for pollination. For example, Memmott et al. (2004) showed by numerical modelling that the local extinction of one super-generalist honeybee species could lead to the loss of considerable numbers of plant species. Therefore, the local extinction of *B. beaticola* in high-altitude zones of Japan could cause the loss of some plant species.

Owing to global warming associated with climate change, serious phenological deviations between flowers and flower visitors can potentially occur: hot midsummers triggered by global warming would cause a decrease in midsummer flower abundance as occurs in low-altitude regions in Japan. This poverty of flower resources in midsummer may negatively affect *B. beaticola* which is adapted to cool and flower-abundant summers in the high-altitude zone, and may cause declines in the *B. beaticola* population. Consequently, flowers in the high-altitude zone would be exposed to a severe pollinator shortage unless the other bumblebee species move upwards. To design successful strategies for alpine plant conservation in Japan, therefore, it is essential to monitor changes in *B. beaticola* abundance with altitude.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.