*Original Article*

**Different factors dominate in each guild in Aculeata communities along an elevational gradient in a boreal forest**

Running head: Elevational patterns of Aculeata feeding guilds

Kazushige Uemori\*1, Toshiharu Mita2, and Takuo Hishi3, 4

1 Department of Agro-environmental Sciences, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka-city, Fukuoka 8190395, Japan (https://orcid.org/0000-0001-6467-9372)

2 Department of Bioresource Sciences, Faculty of Agriculture, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka-city, Fukuoka 8190395, Japan (https://orcid.org/0000-0001-8322-6045)

3 Department of Agro-environmental Sciences, Faculty of Agriculture, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka-city, Fukuoka 8190395, Japan (https://orcid.org/0000-0001-9714-8279)

4 Kyushu University Forest, 394 Tsubakuro, Sasaguri-machi, Fukuoka 8112415, Japan

\*Correspondence to: Kazushige Uemori

E-mail: [uemori.kazushige.951@s.kyushu-u.ac.jp](mailto:uemori.kazushige.951@s.kyushu-u.ac.jp)

Tel: +81-92-948-3109

Fax: +81-92-948-3127

**Abstract**

1. The response of communities to climate change is expected to vary among feeding guilds. To evaluate the response of guilds to environmental factors without considering the taxonomic specificities, it is useful to examine Aculeata bees and wasps, which consist of closely related taxa including different guilds, pollinators, predators, and parasitoids.
2. In this study, we evaluated changes in species diversity (SD) and functional traits of each feeding guild along an elevational gradient in a boreal forest in northern Japan.
3. We used yellow pan traps to collect Aculeata bees and wasps at 200–1600 m above sea level. We investigated six functional traits (trophic level, flight duration, body size, elevational range, nesting position, and soil dependency) and the horizontal distribution of the species.
4. The SD of all Aculeata predators and parasitoids decreased with an increase in elevation; however, the SD of pollinators did not show any specific trend. Although the functional trait composition of all Aculeata species did not show any trend, that of each feeding guild responded to elevation in different ways. Pollinators increased in body size and showed a decrease in flight duration with increasing elevation, suggesting that tolerance and seasonal escape from physical stress at high elevations are important for shaping pollinator communities. Predators showed increased elevational range and above-ground nesting species with increasing elevation, suggesting that the ability to live in a wider range of environments and avoid unsuitable soil environments at high elevations might be important. Parasitoids changed their hosts and variable traits with increasing elevation, suggesting that brood parasitoids have difficulty in surviving at high elevation.
5. The traits for each guild responded in different ways, even if they were dominated by the same environmental factors. Our findings imply that differences in the responses of functional traits would produce different community assembly patterns in different guilds during further climate change.

Keyword: Boreal forest, Climate change, Elevational gradient, Feeding guild, Functional trait, Hymenoptera

**Introduction**

Evaluating the impacts of climate change is one of the challenges in community ecology. Climate change strongly affects boreal forests (Bartomeus et al., 2011; IPCC, 2007; Walsh, 2014). Many studies have used elevational gradient as a model for climate change at a particular location (Hodkinson, 2005; Beck et al., 2010). However, the results were unclear, with different patterns of community assemblies for different regions, climatic conditions, landscapes, vegetation, feeding guilds, and taxonomic groups. Recent, trait-based approaches developed in plant community studies have enabled comparisons between communities in different regions (Götzenberger et al., 2012; HilleRisLambers et al., 2012). For terrestrial invertebrates, a protocol for morphological and behavioural trait-based approaches has also been developed (Moretti et al., 2016). However, detailed analysis is difficult unless the community is composed of species with similar traits, for example, closely related taxa.

Studies on the effects of climate change on communities would benefit from a focus on feeding guilds. This is because each feeding guild is expected to respond differently to different environmental gradients (Pilliod & Rohde, 2016). In a multi-trophic study, species richness patterns along an elevational gradient were different in each guild (Fontana et al., 2020). However, as these findings were based on comparing different taxonomic groups, it is problematic that they did not consider taxa-specific traits for the comparison of guilds. Since a trait-based analysis was not performed, it was not possible to explain why the patterns differed between guilds.

Different traits are expected to vary depending on the dominant factors of the community structure. Abiotic factors, such as temperature, affect body size, nesting position (Hoiss et al., 2012), and elevational range (McCain, 2009; Rapoport, 1982). Phenological factors, such as seasonality, affect flight duration time (Randall et al., 1981; Macgregor et al., 2019; Uemori et al., 2021). Resource supply factors, such as productivity, affect the trophic level (Uemori et al., 2021) and soil dependency for food resources. Pollinators are predicted to respond to abiotic and phenological factors (Hoiss et al., 2012; Pilliod & Rohde, 2016). The abundance and SR of predators and parasitoids is affected by the abundance of prays and hosts (Fornoff et al., 2021; Mayr et al., 2020). They are therefore expected to respond to resource supply factors in addition to abiotic and phenological factors.

Aculeata bees and wasps have several feeding guilds. Therefore, they are useful in studying differences in guilds. They are closely associated with various plants and arthropods, which contribute to the regulation of ecosystems and the maintenance of biodiversity (Brock et al., 2021). Moreover, they include three guilds with different foraging behaviours—pollinators, predators, and parasitoids—in a closely related taxonomic group (three superfamilies: Apoidea, Chrysidoidea, and Vespoidea; Aguiar et al., 2013). Their similarity facilitates the use of common traits and allows the observation of guild-specific responses without taxonomic features.

This study aimed to clarify whether the pattern of species diversity (SD) and trait response differs between feeding guilds in an Aculeata community along an elevational gradient in a boreal forest in eastern Hokkaido, northern Japan. Each guild could potentially have a different combination of relationships between environmental factors and the functional traits that drive communities. We predicted that pollinators are most affected by abiotic and phenological factors with changes in body size, elevational range, nesting position, and flight duration time; predators and parasitoids are most affected by resource supply factor with change in trophic level and soil dependency .

**Materials and Methods**

**Study site**

The study was carried out in old secondary and natural forests in the Ashoro Research Forest, Kyushu University (43°18′N, 143°31′E), and Mt. Kumaneshiri-dake, the Ashoro-cho National Forest (43°31′N, 143°15′E) in the East Taisetsu Mountains (Fig. 1, see Uemorietal., 2022 for full detail). We set 14 sites at different elevations from 223 m above sea level (a. s.l.) to 1581 m a. s.l. in these areas (Table 1, see Uemori et al., 2022 for full details). The lower elevation areas (223, 312, and 392 m a. s.l.) in the Ashoro Research Forest support deciduous broad-leaved trees, such as *Quercus crispula* and *Tilia maximowicziana*, with *Sasa nipponica* as the understory vegetation. The middle elevation areas (507, 594, 695, 800, 993, 1097, and 1209 m a. s.l.) of this study on Mt. Kumaneshiri-dake support a mixed forest dominated by *Alnus alnobetula*, *Betula platyphylla*, *Abies sachalinensis*, *Picea jezoensis*, and *Picea glehnii*, with *Sasa senanensis* as the understory vegetation. Higher elevation areas (1284 and 1396 m a. s.l.) are dominated by dwarfed *Betula ermanii* and *Acer ukurunduense*, with moss and fern communities as the understory vegetation. The top elevation areas (1509 and 1581 m a. s.l.) are dominated by *Pinus pumila,* with *Calamagrostis* sp. as the understory vegetation. The annual mean temperature was 6.22 °C at 90 m a. s.l. in Ashoro from 2001 to 2017 (AMeDAS data from the Japan Meteorological Agency). The mean annual precipitation in Ashoro from 2001 to 2017 was 828 mm (AMeDAS data from the Japan Meteorological Agency).

**Data collection**

Yellow pan traps (15 cm in diameter) were used to collect bees and wasps. Each pan was filled with approximately 150 mL of water, with a few drops of dishwashing detergent as the surfactant.

At each elevation site, we set up five plots under different tree individuals’ canopies (at least 5 m apart). Four yellow pans were placed on the ground for each plot; therefore, 20 yellow pans were set up per elevation site. The samples in the yellow pans were collected in ethanol bottles at 48 h after installation. Because the prevalent species varied depending on the season, sampling was conducted three times in different seasons: 11–14 June (early summer), 1–7 August (mid-summer), and 16–27 August (late summer) in 2019.

We sorted and identified the Aculeata from the collected samples at the species level. Formicidae were excluded as our sampling methodology was not suitable for this group. The identification of the bee and wasp species was conducted as per the guidelines of Tadauchi and Murao (2014) and Terayama and Suda (2016), respectively. Family groups followed Aguiar et al. (2013). All the species were divided into three guilds: pollinators, predators, and parasitoids. Voucher specimens were deposited at the Entomological Laboratory, Kyusyu University, Fukuoka, Japan (ELKU collection).

**Functional traits and distribution index**

We selected six functional traits expected to respond to changes in elevation: trophic level, flight duration, body size, elevational range, nesting position, and dependence on soil for food resources (Table 2, Table S1). The trophic level was divided into three levels (herbivorous, primary predators, and hyperpredators). The trophic level is expected to decrease with increasing elevation because lower temperatures reduce productivity (Uemori et al., 2021). The flight duration was counted as the number of collection seasons. Because low temperatures and high seasonality at high elevations promote seasonal segregation, flight duration is expected to decrease with increasing elevation (Uemori et al., 2021). Body size was the average of the literature data from Tadauchi and Murao (2014) (for bees) and Terayama and Suda (2016) (for wasps). Body size is expected to increase with increasing elevation (Hodlinson, 2005; Hoiss et al., 2012 for bees; see Uemori et al., 2021 for all Aculeata). The elevational range was defined as the difference between the lowest and highest elevations at which the species was collected. Species living at high elevations are expected to have a wider stress tolerance and, hence, a wider elevational range (Rapoport, 1982). Therefore, the elevational range of species is expected to increase with increasing elevation (Hoiss et al., 2012; McCain, 2009). Two types of nesting positions during overwintering were identified: below-ground nesting (including parasitoids of soil insects; rank 1) and above-ground nesting (e.g. stems and wood; rank 2). The increase in below-ground nesting with increasing elevation occurs because belowground nests provide the insects better protection against extreme climatic conditions (Hoiss et al., 2012). The dependence on soil for food resources was classified into two types: using soil animals (detritivorous cycle; as in beetle larvae, flies, and non-nesting spiders; rank 1) and using flowers and terrestrial animals (herbivorous cycle; as in grasshoppers, caterpillars, and nesting spiders; rank 2) as a food resource for their young. To the best of our knowledge, there have been no previous studies on soil dependency in the Aculeata community. Extreme climatic conditions at high elevations and the reduction of aboveground structures as they approach the forest limit may increase soil dependency.

We also considered the species distribution bias, which reflects species dispersion and adaptation to temperature. The distribution index selected by Uemori et al. (2021) was used, which index increased as the distribution of the species became more southerly (Table S1). In addition, distribution information for species was obtained from the data collected by Tadauchi and Murao (2014) and Terayama and Suda (2016). Finally, a distribution index of morphological species without a distribution record was applied to Region 2 (Hokkaido).

**Statistical analyses**

All samples were pooled for each elevation before analysis. The community was analysed in two different ways: 1) all Aculeata and 2) three guilds (pollinator, predator, and parasitoid). For each elevational site, abundance, species richness (SR), and Simpson’s index of SD were calculated. The functional diversity (FD) was also calculated for each trait based on the Rao index of diversity (Rao, 1982). Finally, the community-weighted mean (CWM) was calculated for each trait. In the calculations for pollinators, diversities and CWMs were not calculated because the trophic level and soil dependence were identical for all species. These values were calculated using the R package ‘vegan’ (Oksanen et al., 2018) and ‘FD’ (Laliberte & Legendre, 2010; Laliberte et al., 2014). The relationships between elevation and community indices, such as abundance, SR, SD, FD, and CWMs, were analysed using a linear regression model. All statistical analyses were performed using R version 3.5.0 for Windows (R Core Team, 2018). The diversity and CWM results for each elevation are shown in Table S2.

**Results**

In total, we collected 246 Aculeata individuals (68 in spring, 95 in summer, and 83 in autumn) and 64 species (including 23 pollinators, 30 predators, and 10 parasitoids) (Uemori et al., 2022). The most abundant species was *Lasioglossum problematicum* (38 individuals),which was collected at 392–1581 m a. s.l. and had the largest elevation range in this study.

For all Aculeata communities, the SR decreased with increasing elevation (Fig. 2a; *r*= -0.73, *p* = 0.003). The SD based on Simpson’s index also showed a significant linear decrease with increasing elevation (Fig. 3a; *r*= -0.75, *p* = 0.008). The FD of flight duration decreased with increasing elevation (*r* = -0.73, *p* = 0.007). The CWM of the distribution index decreased with increasing elevation (*r*= -0.67, *p* = 0.009). The abundance (Fig 4a), other FDs, and other CWMs did not show a significant pattern (*p* > 0.05).

For the pollinator community, SR, SD, and abundance did not show significant patterns with elevation (*p* > 0.05; Figs 2b, 3b, 4b). The FD of flight duration decreased with increasing elevation (*r* = -0.73, *p* = 0.007). The FD of the body size increased with increasing elevation (*r* = 0.71, *p* = 0.01). The diversity of the distribution index increased with increasing elevation (*r* = 0.70, *P* = 0.01). The flight duration CWM decreased with increasing elevation (*r* = -0.65, *p* = 0.02). The CWM of body size increased with increasing elevation (*r* = -0.62, *p* = 0.03). The other FDs and CWMs did not show a significant pattern along the elevation.

For the predator community, the abundance did not show a significant pattern with elevation (Fig. 4c, *p* > 0.05). However, the SR decreased with increasing elevation (Fig. 2c, *r* = -0.80, *p* = 0.003), and the SD also decreased with increasing elevation (Fig. 3c; *r* = -0.91, *p* < 0.001). The FDs of trophic level (*r* = -0.75, *p* = 0.008), flight duration (*r* = -0.64, *p* = 0.03), nesting position (*r* = -0.72, *p* = 0.01), and soil dependence (*r* = -0.73, *p* = 0.01) decreased with increasing elevation. The CWM of elevational range increased with increasing elevation (*r* = 0.66, *p* = 0.03), whereas, the CWM of the nesting position showed that above-ground nesting species increased with increasing elevation (*r* = 0.73, *p* = 0.009). The diversity of the distribution index decreased with increasing elevation (*r* = -0.67, *p* = 0.02). At high elevations, the above-ground nesting species (*Trypoxylon* spp.) were dominant, and few below-ground nesting species were present. The other FDs and CWMs did not show a significant pattern along the elevation.

For the parasitoid community, abundance and SR did not show significant patterns with elevation (Figs 2d, 4d, *p* > 0.05). The SD decreased with increasing elevation (Fig. 3d; *r* = -0.61, *p* = 0.03). The FDs of trophic level (*r* = -0.69, *p* = 0.01) and flight duration (*r* = -0.70, *p* = 0.01) decreased with increasing elevation. The CWMs at the trophic level (*r* = -0.74, *p* = 0.006) and body size (*r* = -0.66, *p* = 0.02) decreased with increasing elevation. However, the CWMs in the elevational range (*r* = 0.65, *p* = 0.03) increased with increasing elevation, whereas the CWM of the distribution index decreased with increasing elevation (*r* = -0.64, *p* = 0.03). The lower elevations (below 507 m a. s.l.) were inhabited by brood parasitoid species (e.g. *Nysson trimaculatus* and *Sphecodes* spp., which attack bees and wasps), whereas the middle and higher elevations (above 507 m a. s.l.) were inhabited by koinobiont parasitoid species (*Anteon* spp., which attack leafhoppers).

**Discussion**

We found that each guild showed different traits along an elevational gradient. Pollinators showed changes in body size and flight duration, suggesting that they were most affected by abiotic and phenological factors. Predators changed their elevational range and nesting position, suggesting that they were most affected by abiotic factors. The parasitoids changed their trophic level, body size, elevational range, and nesting position, suggesting that they were most influenced by abiotic and resource supply factors. We also found that different traits responded to each guild even if they were influenced by abiotic factor commonly.

Our finding that SD decreased with increasing elevation for all Aculeata is consistent with that of previous studies (Rahbek 2005; Hoiss et al., 2012). Our site has a cold, dry climate like many previous study sites in Europe, where SD has been shown to decrease with increasing elevation (Hoiss et al., 2012). Compared to warmer regions in Kyushu, Japan (Uemori et al., 2021), the SD in our study area was low. The climate at our site had the effect of reducing the diversity of Aculeata with increasing elevation. However, functional traits cannot sufficiently explain the mechanism controlling the assembly of all Aculeata communities, which are affected by environmental filtering and geographical conditions. Only the results of CWM for the distribution index showed that the adaptation of species to climate responds to climate changes driven by the elevational gradient.

Contrary to the results of previous studies (Araújo et al., 2006; Hoiss et al., 2012; Sydenham et al., 2015), the SD of the pollinator community did not change with elevation. However, the effects of temperature stress on several functional traits have been observed. The shorter flight duration period of high elevation species is an adaptation to the shorter flowering period owing to the strong seasonality of the alpine zone. The alpine spring community is unique, and pollinators are sensitive to flowering (Kudo, 2014; Kudo, 2016). Some species appear only during the spring season at high elevations (*Andrena lapponica* and *Andrena subopaca*). This suggests that the SD did not drop even at high elevations because of the presence of species specialising in the blooming season. The increase in body size with increasing elevation is thought to be an adaptation to temperature stress (Hoiss et al., 2012, Horne et al., 2017). Larger species can regulate their body temperature more effectively and fly at lower temperatures, thus improving their foraging ability (Hoiss et al., 2012). Their large bodies are an adaptation enabling them to take advantage of alpine plants that bloom during cooler periods. In addition, flower abundance affects the SD of pollinators (Araújo et al., 2006; Sydenham et al., 2015; Uemori et al., 2021; but see Hoiss et al., 2012). Although flower coverage was not measured in this study, flowering trees and grasses such as *Acer* spp. were present at all sites. Therefore, the number of flowers was not considered a limitation for SD.

Our findings for predator SD are in agreement with many studies on elevation (Corcos etal., 2018), and the same is true for our finding that predator richness increases with sites with warmer minimum winter temperatures (Pilliod & Rohde 2016). The increase in the elevation range with increasing elevation indicates that highland predator species have broader environmental tolerance. According to Janzen (1967), these species have wider environmental tolerances and larger elevational ranges, owing to greater seasonality (McCain 2009). Therefore, it is likely that species with high environmental tolerance would live in highland areas. The reason for the presence of few below-ground nesting species at high elevations is unclear. One possible explanation is that high elevations have humid ground covered with mosses and ferns. In this situation, nesting in the soil may expose the insects to fungus and infection. Humidity increases the probability of parasite and pathogen spread (Hranitz et al., 2009; Fornoff et al., 2021). In addition, colder winter temperatures may indicate greater snow insulation for individuals buried just below the soil surface in pollinator communities (Pilliod & Rohde, 2016). The exact amount of snowfall at our sites was not measured, but the Tokachi region, where our site is located, is known to have low snowfall and deep soil freezing (Hirota et al., 2006). In areas with little snow cover, nesting above the ground, using dead wood instead of soil, maybe more favourable for survival.

The SR of the parasitoids decreased with increasing elevation, as seen in our results and those of Morris et al. (2015), or did not change along the elevation (Hoiss et al., 2012; Maunsell et al., 2015). Some traits in parasitoids were strongly affected by differences in their hosts. Morris et al. (2015) showed that parasitoids and their host species at higher elevations were nested with species at lower elevations. However, the species composition was greatly turnover along elevation in our study. The decrease in the trophic level and body size and the increase in above-ground nesting species are explained by changes in the hosts with increasing elevation. The absence of brood parasitoids at higher elevations may be due to a decline in host bees and wasps. The SR of brood parasitoids using bees decreases with increasing elevation due to a decrease in the SR of their host bees (Mayr et al., 2019). By contrast, the koinobiont parasitoid species may have emerged at higher elevations because there was a suitable habitat for their host leafhopper. *Anteon* spp. usually parasitise leafhoppers (Cicadellidae), which feed on grass and tree leaves (Guglielmino et al., 2013). At high elevations, trees are dwarfed and have lower canopies. Thus, arboreal species may be trapped more easily. Nevertheless, *Anteon scapulare*, was abundant not only in dwarfed forests at high elevations but also at low elevations of 500 to 1200 m a. s.l., where the canopy was about 20 m high. This elevational range indicates that *Anteon* spp. at higher elevations are highly stress-tolerant. The distribution index results suggest that the species can adapt to the climate at each elevation. Many questions remain regarding the diversity patterns of parasitoid insects (Santos & Quicke, 2011). It is suggested that community assembly mechanisms in parasitoids are complex, depending on the climate, environment, and host-parasitoid interaction in each case.

This study revealed that traits differ in response to factors dominated by community structure for each guild, even in closely related taxonomic groups. This finding suggests that as many traits as possible should be considered when comparing and clarifying the dominant factors for multiple guilds, even if they are expected to respond to the same dominant factor. The amount of resources, such as pollen, leafhopper, and spider, may give a clearer understanding of the mechanisms dominating each guild. The fact that guilds showing the same SD patterns respond differently to functional traits implies that differences in the responses of functional traits may lead to different community assembly patterns for each guild in the future as climate change progresses.

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**Conflict of Interest**

Authors declare no conflict of interests.

**Authors’ contributions**

KU compiled and analysed the data and wrote the manuscript; KU and TH sampled Aculeata, and conceived of the study; KU and TM identified Aculeata; KU, TM, and TH interpreted the results.

**Data Availability Statement**

Data used in this study is available on Kyushu University Library (Uemori et al. 2022, in press, will be available in the public domain).

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Legends

Table 1. Site description includes elevation, dominant tree species, and understory vegetation.

Table 2. Trait description includes value definition, expected change with increasing elevation, and reference for each trait.

Table S1. All functional traits, distribution index, and feeding guild of each species.

Table S2. Table S2. Linear regression's correlation coefficient between elevation and abundance, species richness (SR), species diversity (SD), functional diversities (FDs), and community-weighted means (CWMs) of each functional traits in all Aculeata and each guild. Trophic level, nesting position, and soil dependence in pollinator were not shown because the trait values were the same for all pollinator species.

Figure 1. Locations of the study sites of the Ashoro Research Forest (ARF) and the Ashoro-cho National Forest (ANF).

Figure 2. The relationship between elevation and species richness of all Aculeata and each feeding guild. The solid line and grey area indicate the result of linear regression and 95% CI, respectively. a) All Aculeata (r = -0.73, *p* = 0.003); b) pollinators (p > 0.05); c) predators (r = -0.80, *p* = 0.003); and d) parasitoids (p > 0.05).

Figure 3. The relationship between elevation and species diversity of all Aculeata and each feeding guild, calculated using the Simpson’s diversity index. The solid line and grey area indicate the linear regression result and 95% CI, respectively. a) All Aculeata (r = -0.75, *p* = 0.008); b) pollinators (p > 0.05); c) predators (r = -0.91, *p* < 0.001); and d) parasitoids (r = -0.61, *p* = 0.03).

Figure 4. The relationship between elevation and abundance of all Aculeata and each feeding guild, calculated using the Simpson’s diversity index. The solid line and grey area indicate the linear regression result and 95% CI, respectively. a) All Aculeata; b) pollinators; c) predators; and d) parasitoids (*p* > 0.05).