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# Composition and Dynamics of Hexapod Communities on Yushan Bamboo (*Yushania niitakayamensis*) in the Subtropical Montane Areas of Taiwan

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Plant communities that colonize high-elevation zones generally have short growing seasons which lead to specialized adaptations in such zones. In montane areas of Taiwan, Yushan bamboo (YB, *Yushania niitakayamensis*) is dominant at elevations ranging from 2500 to 3300 m and grows in a grassland-like open habitat. In this study, hexapods were collected from YB bimonthly between 2009 and 2012 by using a sweeping net. The composition of and several bioindices for the hexapods were determined, and multivariate analyses were conducted to explore the dynamics and seasonal distribution of the hexapods. A total of 32,000 individuals belonging to 11 orders and 113 families were collected, with adult individuals being collected more frequently in warmer seasons (from June to October). Of the sampled individuals, 90% belonged to the orders Collembola (42%), Hemiptera (35%), and Hymenoptera (13%). The number of individuals belonging to Hemiptera were stable in all seasons, and the number of hymenopteran wasps was influenced by temperature and exhibited a stable dynamic pattern. The number of individuals belonging to Collembola fluctuated dramatically. The multivariate analyses revealed that the collected hexapods could be divided into two major family groups according to survey season (*i.e.*, summer and winter groups). Several families were collected only in summer, but a few were collected only in winter. Eigenvalues obtained from a principal component analysis revealed that the families Chironomidae, Delphacidae, Entomobryidae, Hypogastruridae, Sminthuridae, and Thripidae (all dominant) were the major contributors to the winter group. These families were abundant all year, although some were more abundant during winter. The three dominant orders Collembola, Hemiptera, and Hymenoptera, each of which has a distinct community structure and dynamic pattern, may have their own adaptive mechanisms in the subtropical regions of Taiwan. Hemiptera individuals, which feed on YB, were most abundant in the adult stage in summer and in the nymphal stage in winter. The abundance of parasitic hymenopteran wasps, which had stable dynamic patterns, was associated with that of their host insects and temperature. The drastic fluctuations in the abundance of Collembola may have been caused by abiotic factors, such as precipitation and microhabitat factors. The early onset of spring and the late onset of winter might also affect the dynamics of the studied hexapods.

**Key words:** Entomofauna, Biodiversity, Montane Hexapoda, Insecta.

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## BACKGROUND

High-elevation zones typically contain unique ecosystems with short growing seasons which result in specialization and fluctuations in the abundance of species. Warmer seasons in these zones are associated with higher biodiversity and abundance (Mani 1968; Nagy et al. 2003) (Mani 1968; Nagy et al. 2003). Several studies have documented periodic fluctuations in the abundance of insect populations in temperate montane areas (Berryman 1996; Kendall et al. 1998; Stenseth 1999; Bjørnstad et al. 2002). Extremely high population densities of herbivores can lead to massive defoliation, which might fundamentally affect ecological systems (Mattson and Addy 1975; Lovett et al. 2002). A long-term study revealed regular outbreaks of an abundance of alpine larch budmoths (*Zeiraphera diniana*) every 9 years (Esper et al. 2007; Büntgen et al. 2009). A study on montane pollination systems revealed that the family-level taxonomic assignment of host plants (rather than their color) significantly affected whether they were pollinated by bumblebees. Habitat conservation efforts must thus be made to reduce habitat loss due to land use (Bhusal et al. 2019). High levels of plant diversity and endemism were noted in the high-altitude, tropical mountains of Sabah, Borneo (Merckx et al. 2015). In subtropical Taiwan, ground beetles have been reported to locally diversify, possibly because of their limited dispersal ability and mountaintop isolation (Weng et al. 2016a b).

Taiwan mainly comprises tropical and subtropical areas. Taiwan has 250 mountain peaks exceeding 3000 m, and these peaks are distributed in four major mountain ranges formed by the collision of the Eurasian and Philippine tectonic plates (Teng 1990; Huang et al. 1997). Elevated zones exceeding 3500 m have subarctic climates (Su 1984). The distribution of the hexapod fauna in the montane areas of Taiwan has rarely been studied. Chen and Lin (1989) conducted a preliminary study of insects associated with Yushan bamboo (YB; *Yushania niitakayamensis* (Hayata) Keng f.) at Mt. Hohuan at an elevation of approximately 3100 m. They identified the members of 59 families, with Chironomidae, Cicadellidae, Aphididae, and Formicidae being the most abundant. Another study revealed that more than 91% of the aquatic insect individuals sampled in ponds on Mt. Hohuan belonged to the Chironomidae family (Lin et al. 2006). An alpine survey conducted at an elevation exceeding 3600 m revealed that the numbers of the highly abundant psyllid (*Cacopsylla strauvaesiae* Yang) and aphid (*Ericolophium itoe* (Takahashi)) species were highest in summer. However, the numbers of the dominant hexapods associated with juniper and rhododendron species sampled in leaf litter fluctuated annually (Yeh et al. 2012). A unique effect of mountain-sky isolation on subalpine carabid beetles has also been demonstrated (Weng et al. 2016a b). In addition, temperature was identified as the major factor affecting the compositions of eriophyoid mites collected from YB distributed in the subalpine areas of Taiwan (Wang et al. 2014).

Extreme weather conditions in montane areas are generally vital for the adaptation of biota, particularly in winter (Halsch et al. 2021). The forests of the montane areas of Taiwan at an elevation of approximately 3000 m are dominated by *Tsuga chinensis* (Franch) Pritz. var. *formosana* (Hayata) Li & Keng and *Pinus taiwanensis* (Hayata). Nonforested grassland-like areas are mainly populated by YB and Formosan grass (*Miscanthus transmorrisonensis* (Hayata)) (Su 1984; Chou et al. 2005). The plant community is limited to a few abundant species with high adaptive capabilities (Su 1984), which considerably affect the composition of the associated insect fauna. For example, aphids (*E. itoe* (Takahashi)) constitute the dominant insect species in the alpine rhododendron communities above the timberline area in the glacial cirque of Mt. Shei, and psyllids (*C. strauvaesiae* Yang) constitute the dominant species in the juniper vegetation in the same area (Yeh et al. 2012).

In the montane areas of Taiwan, YB is abundant at elevations ranging from 2500 to 3300 m. YB grows in grassland-like open habitats surrounded by woody forests and plays a crucial role in the ecological system (Su 1984; Chou et al. 2005; Cheng et al. 2012). Hexapods are frequently used as ecological indicators of the effects of various biotic and abiotic factors. However, hexapod communities in montane areas have rarely been reported on. Accordingly, to fill this gap, the present study was conducted in a YB phytocoenosis located at an elevation of 3100 m above sea level in the Shei Mountain Range of the subtropical regions of Taiwan. Hexapods on the plants were sampled bimonthly over a 4-year period by using a sweeping net. The morphospecies were identified to the family level, and their community structures and seasonal dynamics were analyzed. The effects of abiotic factors (*e.g.*, temperature and precipitation) were assessed. The results revealed that the three most abundant orders—Collembola, Hemiptera, and Hymenoptera—may have their own adaptive mechanisms with distinct community structures and dynamic patterns. These results may contribute to the understanding of the ecological roles of the montane hexapod fauna on subtropical islands.

## MATERIALS AND METHODS

### Locality and survey methods

The selected sampling areas (N24.390780, E121.255810) were along the eastern line of the Shei Mountain Range at an elevation of 3100 m; the sampling areas were colonized by a phytocoenosis that was dominated by YB along with sporadic *Miscanthus* and rhododendron species. Hexapods were collected using sweep nets along an approximately 200-m-long transect line that passed through grassland-like YB with a height of 50–150 cm; sampling was conducted using 67 sweeps in triplicate. The study was conducted bimonthly from 2009 to 2012 (in February, April, June, August, October, and December). The survey dates, temperature data, and precipitation data are listed in table S1. Collection permits were granted by the authorities of the Shei-Pa National Park (Nos. 1001000534 and 1011000570).

### Specimen preservation and identification

Caught specimens were sealed in plastic bags and stored at -20°C in a lab until identification could be conducted. The specimens were grouped into morphospecies identified to the family level. The individuals and body lengths of the morphospecies were quantified and recorded (Roy and Foote 1997; Yeh et al. 2012). Voucher specimens were preserved in 95% ethanol in glass containers and stored at room temperature in the Laboratory of Molecular Systematics at National Chung Hsing University, Taichung, Taiwan.

### Statistical analysis

The basic composition and biomass of the studied hexapods, determined on the basis of their body lengths, were analyzed using Microsoft Excel (Microsoft Corp. 2007). The biomass of each hexapod body was determined from body length as follows: Weight (mg) = $a$ × Length (in mm)$^b$ (Gruner 2003). To determine the dominance of the surveyed hexapod families, a dominance index ($D_i$) was applied (Engelmann 1978; Schirkonyer et al. 2013): $D_i = n_i \times 100/N$ (in percentages, 100%), where $n_i$ is the total number of individuals of family $i$, and $N$ is the total number of all individuals collected in the year. $D_i$ was assessed on the following scale: 100%–32.00% = eudominant; 31.99%–10.00% = dominant; 9.99%–3.20% = subdominant; 3.19%–1.00% = recedent; 0.99%–0.32% = subrecedent; and 0.31%–0% = rare.

PRIMER software (Clarke and Gorley 2001) was used to assess Evenness, Shannon, and Simpson diversity indices in order to determine the abundance of the individuals in the hexapod family over the surveyed locality and thus understand the bimonthly changes in abundance during 2009–2012. To determine the spatial ordination of the surveyed individuals belonging to each hexapod family, multivariate principal component analysis (PCA) and nonmetric multidimensional scaling (NMDS) analysis were performed using the PAST software package (Hammer et al. 2001). Hierarchical clustering based on the unweighted pair-group average (UPGMA) method was conducted using PAST software to elucidate the similarity of the hexapod compositions at the family level. Bray-Curtis similarity matrices were derived to calculate the distances between every pair of analyzed items, after which NMDS and UPGMA analyses were performed.

Redundancy analysis (RDA) was conducted to test the associations between the hexapod compositions at the family level and the abiotic data (*i.e.*, temperature and precipitation data) by using PC-ORD software (McCune and Mefford 2016). On the basis of the eigenvalues derived from the PCA, the first 19 families observed in the first two principal components (*i.e.*, PC1 and PC2) were subjected to RDA. The bimonthly surveys were classified into seasons (spring: April; summer: June and August; fall: October; and winter: December and February; Central Weather Bureau (CWB 2023)). The monthly average temperature (MAT) and monthly cumulative precipitation (MCP) in the classified seasons were determined (Table S1). To analyze the associations between the climatic factors and the collected hexapods, the Pearson correlation coefficients between the collected individuals belonging to each hexapod family and the MAT or MCP were obtained using SPSS software (IBM Corp. 2017).

## RESULTS

### Hexapod compositions on YB

The surveys recorded a total of 32,000 individuals belonging to 11 orders and 113 families during 2009–2012. table S2 lists the 11 orders as well as the numbers of individuals in each of the 113 hexapod families. Relevant data on each morphospecies in the hexapod collection are presented in table S3. The results indicated that 90% of the individuals belonged to three orders: Collembola (42%), Hemiptera (35%), and Hymenoptera (13%, Table 1). Only a small proportion of the specimens belonged to the other orders, including Dermaptera, Neuroptera, and Trichoptera. For the common Coleoptera and Lepidoptera orders, only 351 and 100 individuals, respectively, were obtained in the sweeping collection of the YB plant. Annual differences in abundance were observed; the highest abundance of hexapods was detected in 2011. For the Collembola order, members of the Sminthuridae and Entomobryidae families were the most abundant, followed by those of the Hypogastruridae family; members of the Onychiuridae family were scarce and were identified only in 2009 (Fig. 1A, Table S3). For the Hemiptera order, members of the Cicadellidae and Delphacidae families were the most abundant, followed by those of the Aphididae family. Individuals in the remaining eight families, including those in Eriosomatinae and Miridae families, were few, particularly those in the Lygaeidae and Cercopidae families (Fig. 1B, Table S3). Among the 30 families in the Hymenopteran order, Eulophidae and Pteromalidae had the highest abundance every year, followed by approximately 10 other families, including Platygastridae and Mymaridae. The members of the

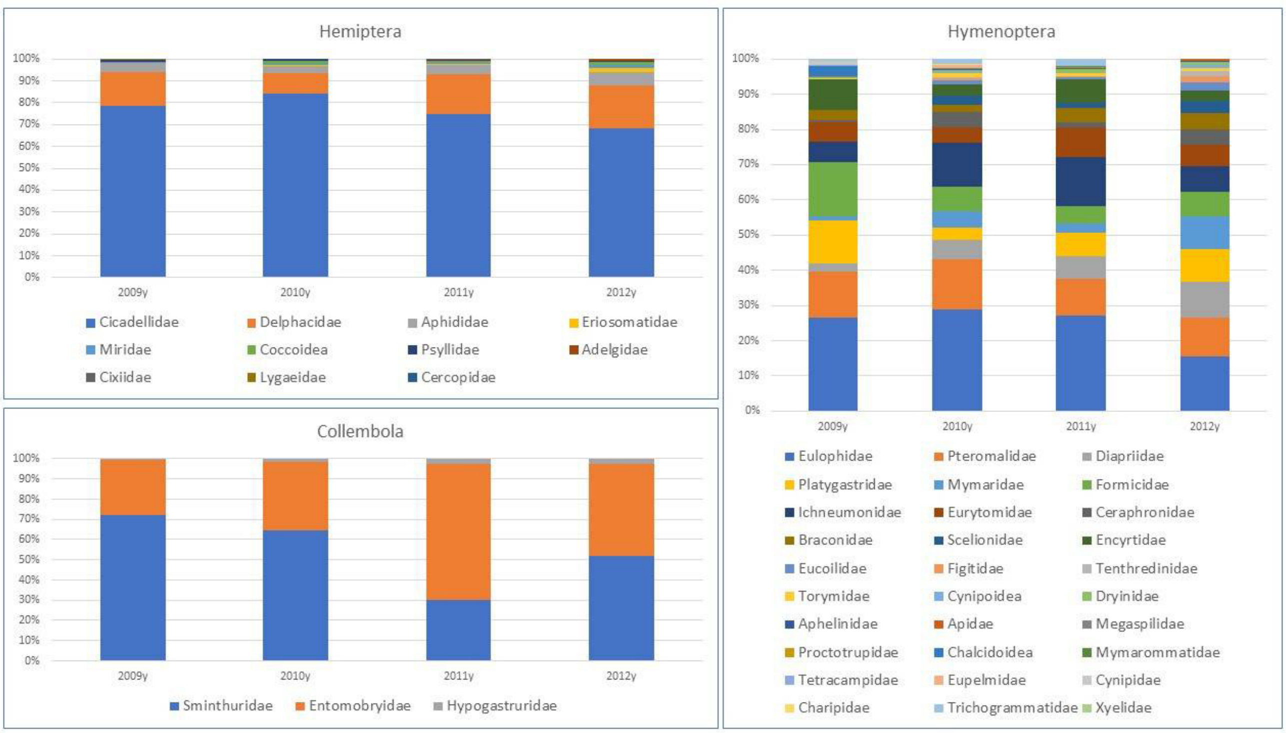


**Fig. 1.** Percentage distribution of individuals belonging to hexapod families of the dominant orders of Hemiptera, Collembola, and Hymenoptera surveyed on Yushan bamboo during 2009–2012. Family names are listed beneath the axis. Families were presented in colors.

**Table 1.** Individual number and the proportional percentage for collected hexapod orders in Yushanian bamboo (*Yushanian niitakayamensis*) during 2009 to 2012

| Order name | 2009 | 2010 | 2011 | 2012 | Total | % |
|---|---|---|---|---|---|---|
| Collembola | 632 | 1871 | 8693 | 2270 | 13466 | 42 |
| Hemiptera | 2644 | 4070 | 3037 | 1441 | 11192 | 35 |
| Hympenoptera | 335 | 1819 | 1214 | 892 | 4260 | 13 |
| Diptera | 364 | 742 | 571 | 232 | 1909 | 6 |
| Thysanoptera | 67 | 114 | 117 | 83 | 381 | 1 |
| Coleoptera | 136 | 104 | 67 | 44 | 351 | 1 |
| Psocoptera | 85 | 138 | 60 | 38 | 321 | 1 |
| Lepidoptera | 20 | 25 | 28 | 27 | 100 | 0.31 |
| Dermaptera | 3 | 12 | 2 | 3 | 20 | 0.06 |
| Neuroptera | 1 | 2 | 2 | 1 | 6 | 0.02 |
| Trichoptera | 1 | 5 | 0 | 0 | 6 | 0.02 |
| | 4288 | 8902 | 13791 | 5031 | 32012 | 100 |

remaining families, including the Apidae and Xyelidae families, were rarely detected (Fig. 1C, Table S3).

The numbers of individuals belonging to the eudominant and dominant families differed in different years. In general, the dominant families were the hemipteran Cicadellidae and the collembolan Entomobryidae and Sminthuridae, and the subdominant families were the hemipteran Delphacidae and dipteran Chironomidae (Table 2).

## Seasonal dynamics of montane hexapods

Each year, the number of collected hexapods increased starting from April. However, the dynamic patterns indicated that the hexapod numbers were not necessarily lower in winter; this was particularly true for the hexapods in the Collembola order (Fig. 2). The number of individuals belonging to the Hemiptera order was highly stable, with the number of sampled individuals ranging between 100 and 1000. The number of parasitic hymenopteran wasps collected had a stable association with temperature and was higher in June, August, and October. A notable dynamic pattern was discovered for Collembola; the number of individuals belonging to this eudominant order was occasionally low in summer and fall. The dynamic patterns of the three dominant families, Cicadellidae, Entomobryidae, and Sminthuridae, fluctuated (Fig. S1). Only the number of individuals belonging to Cicadellidae was stable; this was not the case for the collembolans belonging to Entomobryidae and Sminthuridae, which had tiny body sizes.

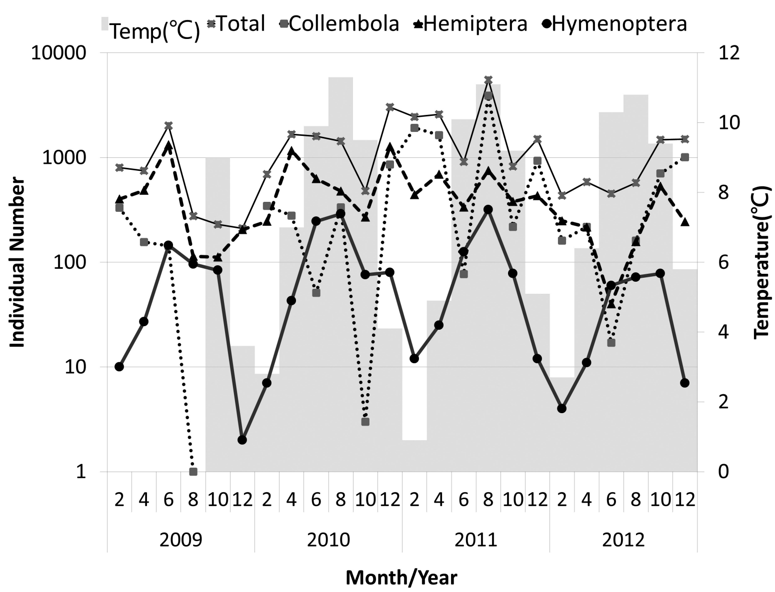


**Fig. 2.** Bimonthly dynamics of numbers of individuals in the dominant hexapod orders Collembola (square), Hemiptera (triangle), and Hymenoptera (circle) surveyed during 2009–2012. Temperature is indicated by gray bars.

**Table 2.** The dominant families on in Yushanian bamboo (*Yushanian niitakayamensis*) during 2009 to 2012

| Dominant scale* | 2009 | | 2010 | | 2011 | | 2012 | |
|---|---|---|---|---|---|---|---|---|
| | family | % | family | % | Family | % | family | % |
| Eudominant (32~100%) | Cicadellidae | 46 | Cicadellidae | 38 | Entomobryidae | 43 | | |
| Dominant (10~31.9%) | Sminthuridae | 11 | Sminthuridae | 14 | Sminthuridae | 19 | Sminthuridae | 23 |
| | | | Chironomidae | 12 | Cicadellidae | 16 | Entomobryidae | 20 |
| | | | | | | | Cicadellidae | 19 |
| Subdominant (3.2~9.9%) | Delphacidae | 9 | Entomobryidae | 7 | Delphacidae | 4 | Chironomidae | 8 |
| | Entomobryidae | 4 | Delphacidae | 4 | Chironomidae | 3 | Delphacidae | 6 |
| | Chironomidae | 4 | | | | | | |

*Dominant scale was labeled according to Engelmann (1978) and Schirkonyer (2013).

The diversity of the hexapod families in the investigated locality was low. Both the Simpson index and the evenness index were approximately 0.6–0.7 and were occasionally lower than 0.5 (Fig. 3). The Shannon index was lower than 3 and exhibited a fluctuating pattern. Temperature appeared to be a major factor affecting the diversity of the hexapod fauna associated with YB.

The biomass calculated on the basis of the specimens' body lengths was consistent with the numbers of individuals (Fig. 4). However, inconsistencies in the biomass calculations were discovered during some sampling events; this might have been because numerous hexapods with small body sizes or few hexapods with large body sizes were collected. For example, the biomass calculations were lower in the surveys conducted in February and April 2011, which might have been caused by the high abundance of specimens of the smaller Collembola order (> 1500 individuals; Fig. S1, Table S3).

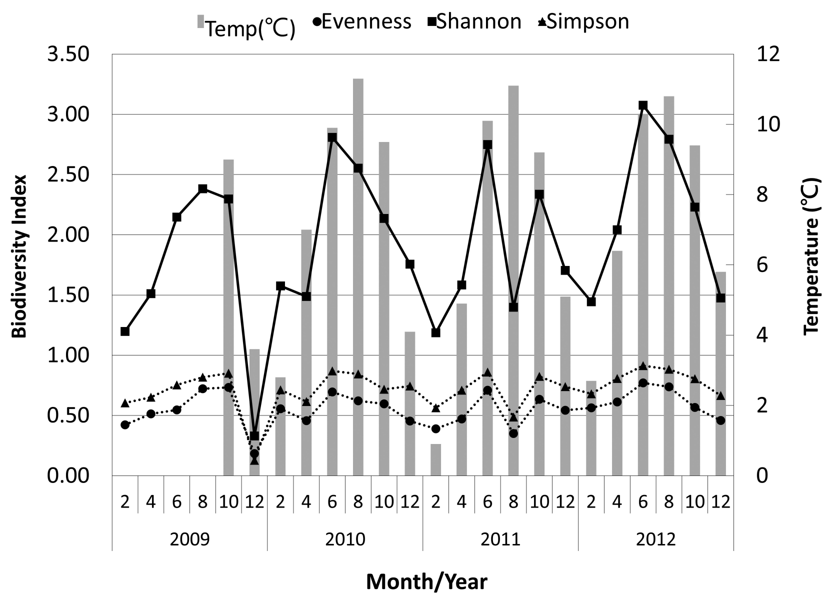


**Fig. 3.** Variations of hexapod biodiversity indices in bimonthly surveys. Variations of Evenness (circle), Shannon (square), and Simpson (triangle) indices during 2009–2012. Temperature is indicated by gray bars.

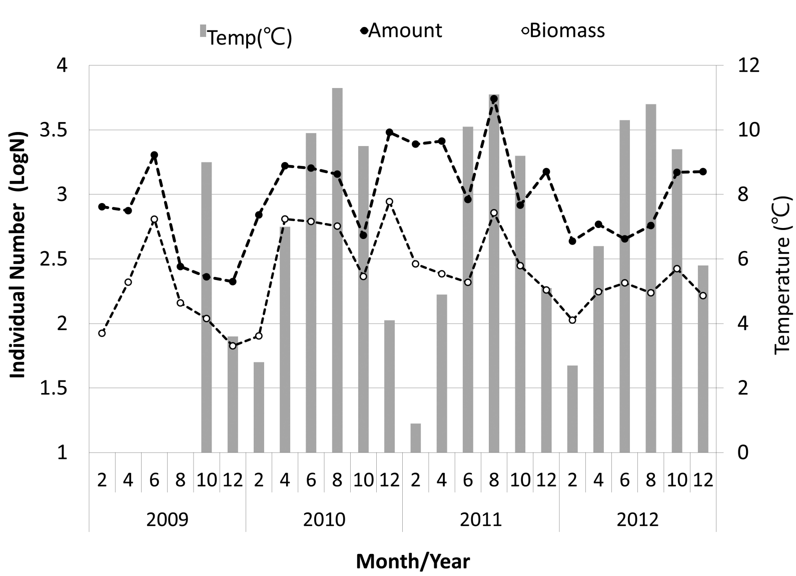


**Fig. 4.** Numbers of individuals and the biomass transformed on the basis of body length data collected in bimonthly survey during 2009–2012. The numbers of individuals (solid circles) and biomass (empty circles, mg) were transformed into logN values. Temperature is indicated by gray bars.

## Dynamics of dominant leafhoppers

The eudominant hemipteran Cicadellidae had the highest biomass, which was likely due to its considerably larger average body size than that of the collembolans. Both adults and nymphs were recorded in each survey (Fig. 5). Most nymphs appeared in late fall, winter, and early spring, and relatively few nymphs appeared in summer (*i.e.*, June and August). Adults were discovered to be most abundant in late spring and summer (*i.e.*, April, June, and August) but much less abundant in winter (*i.e.*, December and February). However, the surveys conducted in February 2010 and October 2012 also yielded a high number of adult cicadellids. The early onset of spring and the late onset of winter can affect the life cycle of members of this family. In the survey on February 3 in 2010, the temperature in the sampling areas increased from 0°C to 4°C–6°C, and this temperature persisted for 2 weeks before the survey was conducted. In October 2012, the temperature was higher than 10°C before the sampling event on October 28 (Table S1). Considering the adult and nymph community structure of cicadellids, only one generation per year was likely collected from the YB in the studied montane communities.

## Ordination distribution of hexapod fauna on YB

Of the individuals identified to the family level in the bimonthly surveys during 2009–2012, the values of those in PC1 and PC2 were derived. On the basis of the results, two major family groups were established according to survey time (Fig. 6). One group was detected in June, August, and October (denoted as the summer group), and the other group was detected in December, February, and April (denoted as the winter group). The summer group (Fig. 6, left area in PC1) differed considerably from the winter group (Fig. 6, right area in PC1). According to the spatial distribution and eigenvalues of the families, the winter group comprised the dominant families of Entomobryidae, Sminthuridae, Chironomidae, Delphacidae, Thripidae, and Hypogastruridae. All of these families had extremely low PC2 values (Table S4).

NMDS analysis was conducted with a stress value of 0.09. The analysis results revealed distinct summer and winter groups (Fig. S2), although a few surveys (*i.e.*, April, October, and December 2009) revealed discrete distributions. On the basis of the UPGMA analysis, a dendrogram was constructed, which revealed similar results for the summer and winter groups (Fig. S3); specifically, two basal lineages for April–October and December in 2009 were noted.

RDA revealed that the hexapod compositions at the family level were associated with MAT and MCP, with the variables on the first and second axes explaining 77.3% and 22.2% of the variance, respectively (Fig. 7). The Spearman's correlation index ($\rho$) between the first axis of RDA and MAT was 0.73 ($P < 0.05$). The second axis of RDA also showed a high correlation with MCP (0.50, $P < 0.05$). The family distribution was more clearly grouped in winter than it was in spring (Fig. 7A). The correlation between the dominant families of collembolan Sminthuridae, Hypogastruridae,

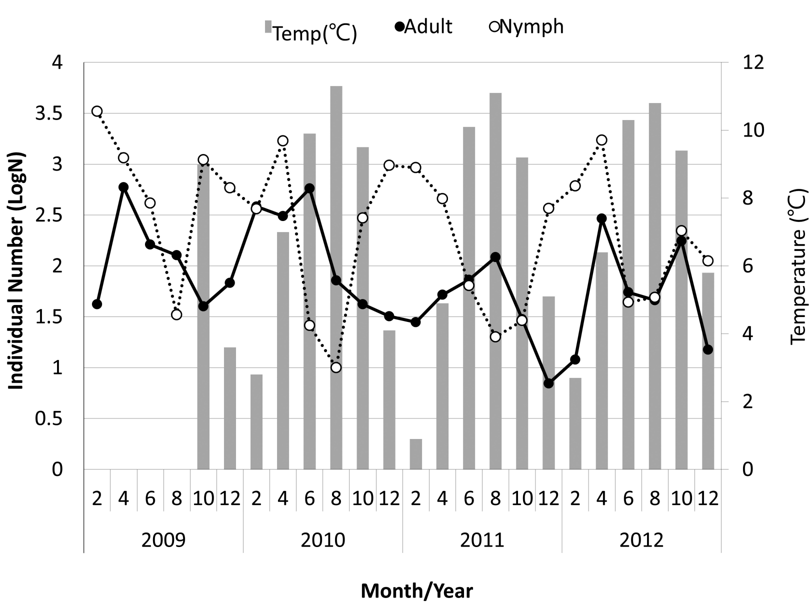


**Fig. 5.** Transformed numbers (logN values) of adult (solid circle) and nymphal (empty circle) individuals belonging to the dominant family Cicadellidae identified in bimonthly surveys during 2009–2012.

and the dipteran Chironomidae with MAT was found to be negative and statistically significant ($P < 0.05$). Moreover, $\rho$ of the hemipteran Delphacidae and Cicadellidae and MCP were negative. Several families, including Aphidae, Empididae, and Mycetophilidae, had significant positive associations with MAT (Fig. 7B). According to the variance explained by MAT and MCP (Fig. 7B), these 2 climate factors couldn't solve the variance of 19 families obviously (only 20.79% of variance in the main matrix explained by predictors). $R^2$ of the dominant Chironomidae, Cicadellidae, Delphacidae, and Hypogastruridae families were low, despite the clearly negative coefficients of their correlation with MAT.

## DISCUSSION

This study conducted surveys on the eastern ridge of Mt. Shei at 3100 m, an elevation similar to that of Mt. Hohuan. On Mt. Shei, the primary dominant order of hexapods collected on YB was Collembola (43%). The previous study conducted on Mt. Hohuan reported that the hemipteran family Cicadellidae constituted 50% of the collected specimens and that few collembolans were collected. Nevertheless, Chironomidae can reach an abundance of up to 91% in the montane ponds of this mountain (Chen and Lin 1989; Lin et al. 2006). Environmental factors such as microhabitats are most likely the reason for the differences in the reported abundance of Cicadellidae. For example, Mt. Hohuan has a sporadic distribution of small ponds, but no such ponds were identified in the surveyed areas of Mt. Shei. In addition, in the present study, less than 1% of the collected hexapods belonged to the Coleoptera and Lepidoptera orders, and this scarcity could be attributed to the host plant (YB) itself, the collection method, and the surveyed locality of the upper montane area. Chen and Lin (1989) conducted a similar study on insects associated with YB at Mt. Hohuan at an elevation of approximately 3100 m. Their data revealed that few lepidopteran larvae were collected from YB using a sweeping net. However, many lepidopteran Noctuidae and Notodontidae were collected using a light trap at night. In addition, Chen et al. (2009) conducted a study in tropical Borneo and indicated that a sudden reduction in lepidopteran moths occurs at altitudes exceeding 3000 m.

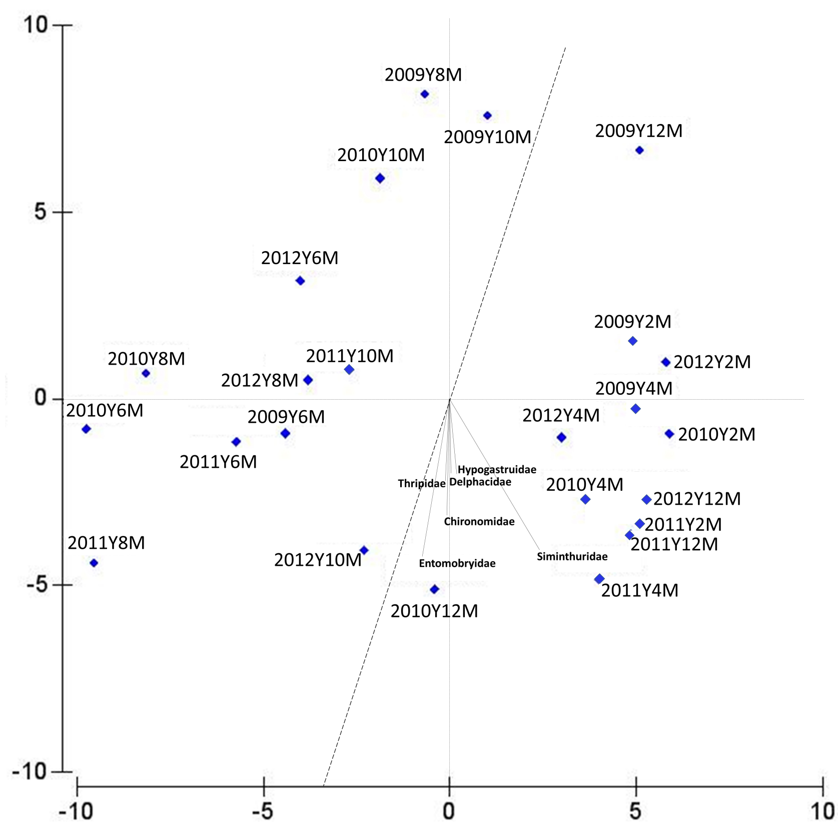


**Fig. 6.** Spatial ordination of hexapod compositions—determined through principal component analysis—identified in bimonthly surveys during 2009–2012. The dominant families with extremely low PC2 values (lower than -0.2) are listed (details provided in Table S4). The right and left areas present hexapods in the winter and summer groups, respectively.

The diversity index values obtained in this study exhibit a fluctuating pattern, with most values being higher in warmer periods (*i.e.*, June, August, and October). The low sample diversity in the other seasons may be due to sudden decreases in temperature and rain. For example, before the survey was conducted on December 16, 2019, the temperature had suddenly decreased from 7°C to 2°C, and this was accompanied by precipitation (Table S1). Chen and Lin (1989) reported that nonhomogeneously distributed patterns of insect fauna on YB may affect sample collection. The diversity indices measured in their study were noted to be slightly higher than those measured in the present study. For example, Chen and Lin (1989) derived average evenness indices of 0.7 and 0.8, which are higher than those (0.6 and 0.7) measured in warmer months in the present study.

The present study demonstrated that temperature is a major factor influencing the hexapod composition and dynamics on montane YB in Taiwan. The Collembolla, Hemiptera, and Hymenoptera orders had the highest abundance, and their characteristics might also be associated with the composition and dynamics of Mt. Shei hexapods. The number of individuals from the Hemiptera order, which comprises generally larger hexapods, was the most stable, with more than 100 individuals collected during each sampling event, including those conducted in winter (Figs. 1 and 2). This might be because herbivorous Auchenorrhyncha and Sternorrhyncha can sustain themselves with Gramineae as a food source (Stinson and Brown 1983). Regular, dynamic patterns were identified for the surveyed parasitic Hymenoptera. Fewer than 10 individuals were collected in winter, whereas approximately 100 individuals were collected in summer (Fig. 2). The Pearson correlation coefficients reveal that the regular pattern of Hymenoptera might be associated with seasonal fluctuations in temperature or with the abundance (Fig. S5) of the preferred parasitic host of hemipterans (Symonds and Elgar 2013). Hymenoptera, for which 30 families were identified, was more diverse than Collembola and Hemiptera, for which 5 and 11 families were identified, respectively. Dramatic fluctuations in abundance were discovered for the tiny apterous Collembola (Fig. 2, Fig. S1). More than 1500 collembolan individuals were acquired in the August 2011 survey, whereas no or fewer than 10 individuals were collected in several other surveys

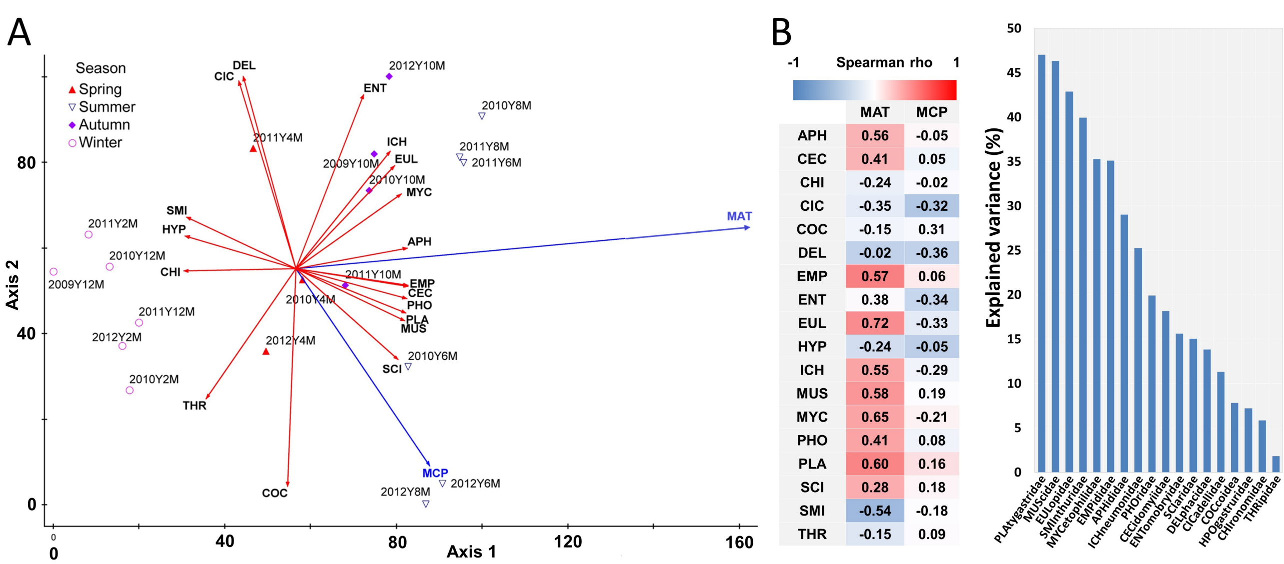


**Fig. 7.** Redundancy analysis (RDA) of hexapod families identified in bimonthly surveys during 2009–2012. (A) RDA revealed that the explained variance derived on the first (X) and second (Y) axes for the first 19 families in the two principal components (*i.e.*, PC1 and PC2) were 0.773 and 0.227, respectively. Triplot revealed the association between hexapod compositions at the family level and monthly average temperature (MAT) and monthly cumulative precipitation (MCP). Families are indicated by red arrows, and climatic factors are indicated by blue arrows. Samples collected in spring (April), summer (June and August), fall (October), and winter (December and February) are indicated by red triangles, empty triangles, diamonds, and circles, respectively. The eigenvalues on the first and second axes were 0.262 and 0.194, respectively. The arrow lengths and directions correspond to the variance explained by the climatic factors. The directions of the arrows indicate whether the magnitude of the variance explained by the climatic factors increased. The perpendicular distances between the family and climatic variable axes (or arrows) in the plot reflect their correlations; the smaller the distance is, the stronger the correlation is. (B) Spearman's Pearson correlation coefficients between the individuals of 19 hexapod families and two climate factors. The values for each family are presented in a gradient of blue to red to represent the families' expected correlations with the climatic factors. The values in the blue bars indicate the explained variance by the climatic factors for each family. The first three capital letters of family name in panel B were used in place of the full name of each family.

(Fig. S1, Table S3). Temperature and microhabitats might have major effects on collembolan development. For example, the numbers of individuals belonging to the dominant Sminthuridae and Entomobryidae families surveyed in this study were comparable (Fig. 1); individuals of the Sminthuridae family were mainly found in winter, whereas those of the Entomobryidae family were mostly found in summer (Fig. S4). The reason why no collembolans were collected in some surveys remains unclear. Nevertheless, several factors, such as precipitation and microhabitats, might have influenced their abundance. For example, rainfall occurred on or several days before the surveys conducted on October 14 and December 16, 2009, and June 17, August 3, and October 2, 2010 (Table S1, Table S3). Furthermore, several microhabitat factors, such as vegetation type and spatial size, have been reported to affect the development of the tiny Collembola (Coulson et al. 2000; Yeh et al. 2012).

In the montane areas of Taiwan, adult hexapods are most abundant in the warmer seasons (from June to October), and most hexapods overwinter in the larval stage (Chen and Lin 1989; Yeh et al. 2012). In the present study, however, abundance of some hexapod families was not low in winter (Fig. S4). Adults of the species belonging to the dominant Chironomidae, Cicadellidae, Delphacidae, Entomobryidae, and Sminthuridae families were discovered to be abundant year round. Several families, particularly those of coleopterans and large dipteran flies, such as Calliphoridae, Empididae, Muscidae, Syrphidae, and Tachinidae, could only be found in summer. A small abundance during the winter months was noted for only a few families, including Derodontidae and Phyrganeidae. Spearman analysis revealed that the coefficients of the correlation of Empididae and Muscidae with MAT were high (Fig. 7B). The multivariate analyses using PCA (Fig. 6), NMDS (Fig. S2), and UPGMA (Fig. S3) were helpful to figure out the spatial orientations or the assemblages for the collected individuals of each hexapod famiy of the bimonthly surveys during 2009–2012. They have different mathematical algorithms and statistical procedures. The similar results provided by these multivariate analysis tools were helpful in figuring out the assemblages of the survey data. Accordingly, in the multivariate analyses, this study excluded species found only in winter from the hexapod community comprising the winter group. PCA revealed that the families that tended to be dominant in winter contributed the most to the composition of the winter group (Fig. 5, Fig. S4). The coefficients obtained from the PCA indicated that families with divergent eigenvalues lower than -0.2 in PC2 may have contributed to the development of a pseudo-winter group (Table S4). According to the results of the triplot analysis in RDA, the proportion of the explained variance for the whole year indicated that the abundance of the dominant Chironomidae, Cicadellidae, Delphacidae, and Hypogastruridae families was not high, although the coefficients of their correlation with MAT were clearly negative (Fig. 7B). The hexapod families with eudominant, dominant, and subdominant abundance levels all year in the surveyed areas had key ecological functions for YB phytocoenosis, while the ecological effects of hexapod families with lower abundance levels, such as Dermaptera, Neuroptera, and Trichoptera, required further justification (Table 1).

## CONCLUSIONS

A systematic study of hexapod fauna is crucial for the documentation of biota adaptation in high-elevation areas, in which warm growing seasons are short. Both biotic and abiotic factors are vital for diversified hexapod adaptation to YB, the dominant phytocoenosis of montane areas in Taiwan. In this study, hexapods belonging to 113 families and 11 orders were acquired. The hexapods developed mostly in warmer seasons, and 90% of the individuals belonged to the dominant orders Collembola, Hemiptera, and Hymenoptera. The surveyed hexapods were divided into two major family groups according to survey season (*i.e.*, summer and winter groups) through multivariate analysis. However, a few insect families were found only in winter. This pseudo-winter group might actually comprise individuals from several dominant families that are present all year but appear to be more abundant in winter. Temperature and ordinal characteristics were determined to be major factors affecting the composition and dynamics of the hexapods on montane YB on Mt. Shei. Hemiptera, which feeds on YB, has a stable abundance of individuals that appear mostly in the nymphal stage in winter. The dynamic pattern of the parasitic hymenopteran wasps was closely correlated with seasonal fluctuations in temperature or insect abundance. In addition, the abundance of the tiny apterous Collembola fluctuated dramatically and was considerably affected by temperature, precipitation, and microhabitat factors.

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**Authors' contributions:** CLT and WBY collected the specimens; TH and WBY designed the research; HYL, TH, and WBY identified hexapods; TH and HYL generated and analyzed the results; and TH, CLT, and WBY interpreted the results and wrote the paper. All authors contributed, read and approved the final manuscript.

**Competing interests:** All authors declare no competing interests.

**Availability of data and materials:** The datasets generated during and/or analyzed during the current study are available from the supplementary data files as well as from corresponding author on reasonable request.

**Consent for publication:** All authors agree with the content of this article and with its publication as submitted.

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## Supplementary materials

**Table S1.** Daily temperature, humidity, and precipitation in the survey area on Mt. Shei. The red shading indicates the bimonthly survey day. (download)

**Table S2.** List of all 11 orders along with the numbers of individuals belonging to each of the 113 families. (download)

**Table S3.** Pertinent information for the hexapod collection in the survey area on Shei Moutain in 2009-2012. (download)

**Table S4.** Eigenvalues derived from the principal component analysis of the morphospecies of each hexapod family. (download)

**Fig. S1.** Individuals belonging to the dominant families Cicadellidae (diamond), Entomobryidae (triangle), and Sminthuridae (circle) as identified in the bimonthly surveys during 2009–2012. (download)

**Fig. S2.** Spatial distribution of the insect families identified in all surveys during 2009–2012, as determined through nonmetric multidimensional scaling analysis. The similarities between the group patterns and statistical results are displayed. (download)

**Fig. S3.** Hierarchical clustering analysis based on the unweighted pair-group average method for hexapod families identified in all bimonthly surveys during 2009–2012. The summer group, winter group, and the similarities between clusters are displayed. (download)

**Fig. S4.** Relative abundance of the dominant hexapod families—as determined through principal component analysis—identified in surveys during 2009–2012. The size of the circle below each panel is proportional to the number of individuals collected. (A) Cicadellidae, (B) Entomobryidae, (C) Sminthuridae, (D) Chironomidae, and (E) Delphacidae. (download)

**Fig. S5.** Numbers of individuals in the Hymenoptera (triangle), Insecta (square), and Hemiptera (gray circle) families identified during 2009–2012. Temperature is presented in empty circles. The Pearson correlation coefficients (*r*) of Hymenoptera, Insecta, and Hemiptera with Temperature are displayed. (download)