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碩士論文

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暖化操控對不同海拔的本土種紋白蝶、外來種紋白蝶及其蜜源植物的影響

Experimental warming impact on a native butterfly (*Pieris canidia*), an invasive butterfly (*P. rapae*), and their nectar plant (*Bidens pilosa* var. *radiata*) across altitude?

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摘要

授粉者可提供重要的生態系統服務。鑑於暖化可能改變授粉者及/或植物的生長與發育，進而影響不同環境梯度下的授粉者與植物之關係，本研究想探討1)暖化會如何影響授粉者與蜜源植物的生長與發育，2)暖化是否會影響授粉者與蜜源植物的授粉關係，3)暖化對授粉者和蜜源植物的影響是否會隨著海拔或本土種和外來種授粉者而變化，4)野外的授粉關係如何隨季節和海拔變化。本研究的物種包含大花咸豐草及兩種紋白蝶。大花咸豐草(*Bidens pilosa* var. *radiata*)是台灣近年來重要的外來入侵物種，已成為許多授粉者重要的蜜源植物，其中常見的授粉者包含了本土種的台灣紋白蝶(*Pieris canidia*)與外來種的紋白蝶(*P. rapae*)。為探討暖化對不同海拔的兩種紋白蝶與大花咸豐草的影響，本研究包含了實驗室暖化操控實驗以及野外調查。實驗室暖化操控實驗收集來自中海拔(~1000 m a.s.l.)和低海拔(~100 m a.s.l.)各三個地點的大花咸豐草種子和兩種紋白蝶雌蝶(使用 F1 做實驗)，分別利用三個生長箱調控溫度來記錄暖化對其生長與發育的影響(控制組、3℃暖化與 6℃暖化)。根據野外平均溫度資料，設置控制組溫度為 16.8℃(中海拔)或 22.8℃(低海拔)。野外調查則檢測紋白蝶的密度及大花咸豐草花朵的形質，是否會隨海拔及月分而改變。

研究結果顯示，暖化可對授粉者、植物、及兩者之交互關係造成影響，且此影響會隨海拔改變。首先，暖化可影響兩種授粉者(紋白蝶)的表現，然其結果受物種及海拔的影響 – 暖化會減少低海拔外來種紋白蝶的壽命與前翅長度，而暖化會對中海拔之本土種紋白蝶造成類似的影響。其次，暖化對蜜源植物(大花咸豐草)的影響亦隨海拔改變 – 暖化使中海拔大花咸豐草的開花時間提前、增加其開花數量，但減少其花朵的反射率。最後，暖化亦會影響授粉行為，然其結果受物種及海拔的影響 – 暖化增加了低海拔外來種紋白蝶的訪花頻率與覓食時間。野外調查顯示，紋白蝶的密度及大花咸豐草花朵的形質會隨海拔與月份改變。低海拔有較高的授粉者密度，而低海拔大花咸豐草(花蜜總糖量及反射率)和中海拔

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大花咸豐草(花蜜蔗糖量)在吸引力形質的表現上則各有優勢，而這些形質會隨月份而變化。以上的研究結果顯示，暖化可對這兩種紋白蝶(本土種vs. 外來種)造成不同的影響，而此影響及暖化對大花咸豐草的影響，皆會隨海拔改變。鑒於暖化對各授粉者物種(兩種紋白蝶)及海拔族群(中低海拔紋白蝶或大花咸豐草)的影響程度不同，暖化不但可能會改變現有本土種與外來種的生態系統服務，也可能會改變各海拔的授粉者與蜜源植物之間的交互關係，進而影響當地的動植物群聚。

關鍵字: 暖化、海拔、授粉、外來種、台灣紋白蝶、 紋白蝶、大花咸豐草

Abstract

Pollination is an important ecosystem service. Given that climate warming has reportedly affected the growth and development of pollinators and/ or plants, likely shifting current plant-pollinator interactions (e.g. mismatches) across spatial gradients (e.g. altitude or latitude), this study examines 1) how warming may affect the growth and development of pollinators and nectar plants (flowers), 2) whether warming will affect the interactions between pollinators and nectar plants, 3) whether the effects above, if any, will vary across altitude (spatially) and between native and invasive pollinators, and 4) how plant-pollinator interactions vary temporally across altitude in the field. This study examined a nectar plant and its two pollinators. *Bidens pilosa* var. *radiata*, a notorious invasive plant in Taiwan, has become an important nectar resource for many pollinators, including two common butterflies, the native *Pieris canidia* and invasive *P. rapae*. To understand warming impact on these butterflies and their nectar plants across altitude, this study included a laboratory experiment and field survey. The laboratory experiment collected the seeds of *B. pilosa* var. *radiata* and females of the two *Pieris* species (F1 for study) from three sites each at medium (~1000 m a.s.l.) and low altitude (~100 m a.s.l.). Species from medium or low altitude were each raised in three growth chambers (control temperature, 3^{o}C, and 6 ^{o}C warming); the control temperature for medium and low altitude was set at 16.8 ^{o}C and

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22.8 °C, respectively, based on field data. The field survey examined the population density of both *Pieris* and the flower traits of *B. pilosa* across altitude over months.

The results showed that warming impact on pollinators, plants, and their interactions varied with altitude. First, warming affected the native and invasive *Pieris* butterflies differently across altitude. In specific, warming reduced the adult longevity and forewing length of low-altitude invasive *P. rapae*, but of medium-altitude native *P. canidia*. Second, warming affected nectar plants (*B. pilosa*) differently across altitude. For example, warming facilitated flowering (earlier flowering and more flowers) and reduced flower reflectance in medium-altitude plants, but had no such effects on low-altitude plants. Third, warming also affected pollination activity differently between the two pollinators across altitude. For instance, warming increased the frequency and duration of flower visits by low-altitude *P. rapae*. In addition, the field survey showed that both *Pieris* and flower traits varied spatially (altitude) and temporally (months). Low altitude had a higher *Pieris* density; low-altitude *B. pilosa* plants (total sugar weight in flowers, flower reflection) and medium-altitude *B. pilosa* plants (sucrose concentration in flowers) might have a different strength in attracting pollinators. Many of these traits also varied with months. In summary, warming may differently affect the ecosystem service (a function of pollinator longevity and flower visit) provided by the two *Pieris* pollinators across

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altitude, and the different response of medium- and low-altitude plants to warming together suggests an upcoming shift in pollinator-plant interactions across altitude under climate warming, potentially shaping local plant-animal communities.

Keywords: climate warming, altitude, pollination, invasive species, *Pieris canidia, P. rapae, Bidens pilosa* var. *radiata*

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Introduction

The importance of pollination in ecosystems

A focal interest in modern ecology is to understand how environmental change will shape ecosystem services provided by species, communities or systems (Millennium Ecosystem Assessment 2005, Vanbergen and Insect Pollinators Initiative 2013). Pollination by animals, an example of critical ecosystem services, greatly benefits human beings and is regarded as one of the most important plant-animal mutualisms (Bronstein 1994, Kearns *et al.* 1998, Fontaine *et al.* 2005, Bascompte and Jordano 2007, Ollerton *et al.* 2011, Burkle *et al.* 2013, Revilla and Encinas-Viso 2015, Melathopoulos *et al.* 2015). For example, more than three quarters of angiosperms, or one third of major crops benefit from pollinators (Crepet 1984, Fontaine *et al.* 2005, Klein *et al.* 2007, Ollerton *et al.* 2011). Besides its important direct value (e.g. facilitating food production), pollination by animals also offers important indirect value, such as maintaining natural ecosystems via its close relationships with other species (Kremen *et al.* 2007).

Warming could have a big impact on plants and pollinators

Environmental changes, such as climate warming, can interrupt plant-pollinator interactions by affecting plants, pollinators, and/or their interactions (Burkle and

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Alarcón 2011, Hoover *et al.* 2012, Robbirt *et al.* 2014, Miller-Struttmann *et al.* 2015). For example, climate warming may alter plant phenology and morphology, leading to earlier flowering and increasing flower number (Anderson *et al.* 2012, Hoover *et al.* 2012, Van Etten and Brunet 2013, Høye *et al.* 2013, Scaven and Rafferty 2013, Bock *et al.* 2014, Wheeler *et al.* 2015). In addition, warming may also affect nectar volume, concentration, or plant seed production (consequently affecting plant dynamics) (Erickson and Markhart 2002, Hoover *et al.* 2012). As for pollinators, increasing temperature might influence the growth and development of pollinating insects, such as developmental acceleration, reduced body size, emergence advancement, etc. (Arroyo *et al.* 1985, Hegland *et al.* 2009, Karl and Fischer 2009, Forster *et al.* 2012, Kharouba *et al.* 2014, Kühsel and Blüthgen 2015).

Regardless of warming, the interaction between plants and pollinators could be affected by each other. For example, higher sucrose in nectar would increase the flower visits by bumble bees (Whitney *et al.* 2008), suggesting that sugar composition might affect the pollination activity by pollinators. On the other hand, pollinator activity might affect the seed reproduction of plants: higher pollinator activity could increase pollen transfer and increase plant reproduction success (Kearn *et al.* 1998, Inouye 2008, Zhang *et al.* 2014). As for warming impact, plants and pollinators may respond differently to warming (Kharouba and Vellend 2015), resulting in a

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phenology desynchronization and a temporal or spatial mismatch between plants and pollinators (Willmer 2012, Polce *et al.* 2014, Petanidou *et al.* 2014, Kudo 2014, Forrest 2015, Hindle *et al* 2015).

***Knowledge gap 1**: An integrated study is needed to understand how warming may affect plant and pollinator traits together.*

Although many studies have examined the response of plants and insects to warming separately (Bartomeus *et al.* 2011, Liu *et al.* 2012, Arroyo *et al*. 2013, Stuhldreher *et al.* 2014, Springate and Kover 2014, Bennett *et al.* 2015, Cochrane *et al.* 2015), there is a lack of studies that integrate most of important plant and pollinator traits together in the same system and investigate the potential correlations or interactions of these traits. This kind of integrated studies is critical to understand the real impact of climate warming on plant-pollinator communities, since the growth and development of plants (flowers) and pollinators, as well as plant-pollinator interactions, should be affected simultaneously by warming in the real world. In addition, this kind of integrated study will allow us to examine how a mismatch between plants and pollinators (due to different responses to warming) may feedback to a plant-pollinator community (Fagan *et al.* 2014).

Plant-pollinator interactions may commonly vary with environmental gradients

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To fully understand warming impact on plant-pollinator interactions in real world, it is necessary to study whether/how plant-pollinator interactions may vary temporally and/-or spatially (Malo and Baonza 2002, Olesen *et al.* 2008, Hoiss *et al.* 2015, Price *et al.* 2005, Cutler *et al.* 2015). While this important topic is less explored (Stenström *et al.* 1997, Devoto *et al.* 2005, Crimmins *et al.* 2010), it has been well known that other species interactions (e.g. plant-herbivore interactions) often vary with environmental gradients (e.g. altitude or latitude) (Pennings *et al.* 2009, Schemske *et al.* 2009, Ho and Pennings 2013, Shrestha *et al.* 2014, Rasmann *et al*. 2014), suggesting that plant-pollinator interactions may likely change with environmental gradients as well. This point of view is supported by a limited number of studies addressing altitudinal or latitudinal variations in plants, pollinators, or their interactions (De Frenne *et al.* 2011, Vandewoestijne and Van-Dyck 2011, Benadi *et al.* 2014, Nagano *et al.* 2014, Pellissier *et al.* 2014, Kuriya *et al.* 2015). For example, many plant species have later flowering date toward higher altitude (Frei *et al.* 2014a and 2014b), and most butterfly species also have later first flight date and increasing wing length toward higher altitude (Illán *et al.* 2012, Leingärtner *et al.* 2014). In addition, Zhao and Wang (2015) found that both floral traits and pollinator visit rate could vary with altitude, such as shorter sepal length and fewer bee visits at higher altitude.

Understanding plant-pollinator interactions across environmental gradients (e.g. altitude or latitude) will significantly improve our prediction in climate warming impact on plant-pollinator communities, especially when the same plant or pollinator species from different altitude or latitude may face different environmental challenges or respond inherently differently to the same degree of warming. For example, species or populations at higher altitude may face stronger environmental challenge under warming-induced range shifts because of the lack of suitable habitat at higher altitude (Roth *et al.* 2014, Costion *et al.* 2015). In addition, the same plant or pollinator species at different altitude or latitude may have adapted to local environment condition (temperature, photoperiod, resource, etc.) and/or evolved into various genotypes (Weber and Schmid 1998, Johansson *et al.* 2006, Zakharov and Hellmann 2008, Fischer and Karl 2010, Kingston *et al.* 2014). It is important to investigate whether these different populations or genotypes, if exist, may respond similarly or differently to climate warming, because these responses will reveal how plant-pollinator communities will shift under warming across altitude or latitude.

Knowledge gap 2*: how will warming affect current plant-pollinator interactions across environmental gradients (e.g. altitude)?*

Species responses to warming might varied with altitude (Deutsch *et al.* 2008, Karl and Fischer 2009, De Frenne *et al.* 2011, Brunet and Larson-Rabin 2012,

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Scheepens and Stöcklin 2013, Higgins *et al.* 2014, Yoshie 2014, Baldwin *et al.* 2014, Frel *et al.* 2014a and 2014b, Buckley *et al.* 2015, Bentz *et al.* 2016). While it is important to understand warming impact on plant-pollinator communities across environmental gradients, few studies have addressed this issue. It has been suggested that warming could decrease nectar volume per flower (Mu *et al*. 2015, Takkis *et al*. 2015), and pollinators may prefer warmer nectar resource (Norgate *et al*. 2010, Nicolson *et al.* 2013) and higher sucrose concentration (Tan *et al.* 2013, Williams *et al*. 2015). However, less is known about warming impact on plant- pollinator interactions across altitude or latitude (Kudo and Ida 2013). As mismatches between plants and pollinators have become a major concern under climate change (Rafferty *et al.* 2011, Xiao *et al*. 2015), filling up this knowledge gap will help answer whether and how the mismatches may vary with altitude or latitude.

Species invasions are common worldwide

Many communities have or will have both native and exotic (e.g. invasive) pollinators (Dlugosch and Parker 2008, Sanguinetti and Singer 2014). Although some studies suggested the negative impact of exotic/invasive pollinators on local ecosystems (Aizen *et al.* 2008, Shimamoto *et al.* 2011, Russo *et al.* 2014, Martyniuk *et al.* 2014), less is known about the interaction between native and invasive

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pollinator (Paini 2004, Thomson 2004, Roubik and Villanueva-Gutierrez 2009, Giannini *et al.* 2015). It is possible that native and exotic pollinators compete against each other, since native and exotic species may require similar abiotic and biotic resource, such as habitat and food resource, respectively (Hanna *et al.* 2014, Traveset and Richardson 2006, Riley and Dybdahl 2015). This competition may subsequently affect plant communities. For example, compared to native pollinators, exotic pollinators might spend more time on one inflorescence and produce a lower efficiency in cross pollination (Dupont *et al.* 2004). This lower cross-pollination might have a negative effect on native plants and in turn change the native plant and pollinator communities. Since the interaction between native and exotic pollinators can potentially change local communities, understanding this interaction is becoming an important issue in ecosystem management.

Knowledge gap 3: *how will warming affect the current status of native and exotic pollinators?*

While it has become increasingly important to understand both native and exotic pollinators in a community, a knowledge gap remains – how the current status of native and exotic pollinators will change under warming (Schweiger *et al.* 2010, Rader *et al.* 2013). Given that native and invasive species might respond differently to warming (Verlinden *et al.* 2014), it is important to examine if warming will shift the

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current balance and benefit native or exotic pollinators. In addition, a priority should focus on closely related native and exotic pollinators (e.g. congeneric), since exotic species are more likely to drive more phylogenetically related native species to local extinctions (Li *et al.* 2015).

Aims

To help fill up the knowledge gaps above, this study aims to understand warming impact on both native and invasive pollinators and their nectar plants across environmental gradients (i.e. altitude) (Fig. 1).

(1) Examine if warming will affect the growth and development of pollinators and nectar plants (flowers).

(2) Examine if warming will affect plant-pollinator interactions.

(3) Examine whether the warming effects above, if any, will vary across altitude.

(4) Examine if native and invasive pollinators may respond differently to warming across altitude.

(5) Besides spatial variation (altitude), how do plant-pollinator interactions vary temporally (e.g. seasonally) in the field?

To achieve these aims, this study examined one of the most common nectar plants (*Bidens pilosa* var. *radiata*) in subtropical Taiwan and two of its common

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pollinator species other than bees, the native *Pieris canidia* and invasive *P. rapae* butterflies, which are common butterflies in Taiwan (Liu and Yang 2010). To examine warming impact on the growth and development of both plants (flowers) and pollinators across altitude, this study included a factorial laboratory experiment, where species from two altitude origins (low and medium) were collected and grew under temperature treatments (ambient, 3 and 6 ^{o}C warming), which simulated the warming scenario by 2100 (IPCC 2007, 2013). To understand plant-pollinator interactions in the field over seasons, this study conducted field survey in flower traits (reflectance, nectar analysis), pollinator density, and flower visit by pollinators at both low and medium altitude.

Materials and Methods

Study system

Bidens pilosa var. *radiata* (Compositae) is among the most notoriously invasive plants in Taiwan (Chang *et al*. 2002, Jiang *et al.* 2003). It was introduced from north and tropical America to Taiwan after 1980s (Wu *et al.* 2004), serving as a nectar resource to bees. *B. pilosa* var. *radiata* is one of the three varieties of *B. pilosa* in Taiwan (the other two being *B. pilosa* var. *minor* and *B. pilosa* L. var. *pilosa* L.). *B. pilosa* var. *radiata* and *B. pilosa* var. *minor* are exotic species in Taiwan, but only *B. pilosa* var. *radiata* becomes invasive and seriously threatens the ecosystem (Peng *et al.* 1998, Hsu 2006, Hsu and Kao 2009, Hsu and Kao 2014, Huang 2014, Huang and Kao 2015). *B. pilosa* var. *radiata* is a perennial herb and produces flowers all year round, providing nectar and/or pollen as nutrient to most pollinators (Grombone-Guaratini *et al*. 2004, Li 2006, Liu and Yang 2010, personal observations). It is one of the most common nectar plants to both two *Pieris* in the field (Liu and Yang 2010; personal observations) and is widespread from low to medium altitude in Taiwan and especially common at low altitude (Huang 2008). One previous study showed that some traits of *B. pilosa* var. *radiata* varied with altitude (Huang 2008), which might hint a genetic difference across altitude (Deng 2003, Deng *et al.* 2005).

Pieris canidia and *P. rapae* (Lepidoptera: Pieridae) are common butterflies in

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lowland Taiwan, and reach high density from autumn-winter to spring (Li 2006, Li 2010, Lin 2015). *P. canidia* is native to Taiwan, but *P. rapae* is an invasive species likely with multiple invasions from Japan and China to Taiwan since 1960s (Li 2004). Larvae of two *Pieris* exploit Brassicaceae plants including both agricultural plants (e.g. *Brassica oleracea* var. *capitata*) and wild plants (e.g. *Rorippa indica*) (Chew and Renwick 1995). However, *Pieris* adults can pollinate wild plants, such as *Lantana camara* L., *B. pilosa* var. *radiata,* etc. (Liu and Yang 2010, personal observations).

Laboratory experimental design

To examine warming impact on the growth and development of nectar plants and pollinators across altitude, I conducted a laboratory experiment with a 2 species origins (low, medium altitude) x 3 temperature treatments (ambient, 3, 6 ^{o}C warming) design on each species, which were collected from three study sites (Taipei, Taoyuan and Nantou) at each altitude in general.

Seeds of *B. pilosa* var. *radiata* and individuals of adult *Pieris* were collected at low and medium altitude from three sites in 2013 and 2014 (Table 1). A total of 24 pots of *B. pilosa* var. *radiata* (8 replicates per study site) were grown in each growth chamber. Each pot was bagged with a mesh net to prevent accidental herbivore damage. In addition, 24 replicates of *P. rapae* (8 from each study site) and 24

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replicates of *P. canidia* (12 each from Taoyuan and Nantou) were reared in each growth chamber. *P. canidia* was not collected from Taipei due to low abundance at medium altitude.

Laboratory experimental procedure

Set-up

The low-altitude temperature treatments (growth chambers) were set at 22.8/20.4 °C, 25.8/23.4 °C and 28.8/26.4 °C (Fig. 2). The control temperature (22.8/20.4 °C) represented the average autumn-winter temperature from 3 sites (Data Bank for Atmospheric Research, October to December, 2003-2012), accordingly with the initial months of occurrence in *Pieris,* which were among few butterfly species feeding on *B. pilosa* var. *radiata* during winter in Taiwan (Liu and Yang 2010). The medium-altitude temperature treatments (growth chambers) were set at 16.8/14.4 °C, 19.8/17.4 °C and 22.8/20.4 °C (Fig. 2). The control temperature (16.8/14.4 °C) was set based on a 6°C reduction rate per 1000 meters increase in altitude (Jump *et al.* 2009). The warming treatment (3, 6 °C warming) for each altitude was set to simulate the warming scenarios by 2100, based on an IPCC prediction (IPCC 2007, 2013). The temperature treatment 22.8/20.4 °C (highest temperature treatment for medium altitude and lowest temperature treatment for low altitude populations) represented a common

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garden, which allowed us to investigate a potential genetic difference in populations across altitude. The temperature treatments below were presented only in day temperature for simplicity. In addition, each growth chamber was set at a constant relative humidity (70%) and a 12:12 photoperiod. The position of plants and caterpillars in a growth chamber were regularly rotated to account for the potential systematic errors of growth chamber.

B. pilosa var. radiata morphology and growth

I sowed *B. pilosa* seeds randomly in plastic containers (9cm in diameter and 5cm in height). The substrate of each pot was composed of 100g prewatered peat soil (type B2, Kekkilä, Finland), and mixed with 100ml water. Those containers were then put in growth chambers under experimental temperature treatments. After seedlings emerged, I transplanted each seedling to a larger pot (15.24 cm in diameter and 16 cm in height). The substrate of each pot was composed of 400g prewatered peat soil, and mixed with 400ml water. The plants were grown in growth chambers and watered 200 ml every two days.

To examine the impact of altitudinal origin and warming on plant performance, I measured weekly the plant vegetative traits (see Appendix A) and reproductive traits (flowering date and capitulum number). The first flowering date was recorded

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because a shift in flower phenology might cause a mismatch between plants and pollinators (Iler *et al.* 2013, Anderson 2013, CaraDonna *et al.* 2014). Capitulum number is one of the flower attractiveness to pollinators (Brunet *et al.* 2015); thus, I counted weekly and calculated total capitulum number at the end of experiment (for 5 months).

To understand *B. pilosa* production under different temperature treatments across altitude, I did artificial pollination, collected seeds (Fig. 3), and then measured seed traits (seed number, length and weight). Based on a previous study, *B. pilosa* flowers are incomplete protandry, and anther mature before stigma (Huang 2012, Huang and Kao 2014). When stigma of *B. pilosa* was matured, I collected fresh capitulum from campus of National Taiwan University (25°00' N, 121°32' E) and mixed pollen grains. I touched the mixed pollen three times with a cotton swab and put it on disk florets to make sure most flowers received pollens. After artificial pollination, I bagged the whole capitulum with a small mesh net in order to collect seeds later on. After seeds matured, I counted the seed number of each capitulum, and measured the mean seed length and weight in each pot. Mean seed length and weight were measured from 5 and 10 randomly selected seeds, respectively.

Flower reflectance

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To examine the impact of altitudinal origin and warming on plant attractiveness to pollinators, I measured the reflectance of ray florets (hereafter flower reflectance), which could reflect flower attractiveness to pollinators (Campbell *et al.* 2010, Koski and Ashman 2015). The capitulum not artificially pollinated were cut down, kept under low temperature to maintain freshness, and measured for their spectral reflectance within 24h to reduce potential water loss. The reflectance was recorded by a spectrometer (S2000, Ocean Optics Inc.), and I placed light probe 0.5cm above the middle of ray florets (Tso *et al.* 2002, Tso *et al.* 2004). All of the flower reflectance results were plotted from 300nm. Six wavelengths of flower reflectance (340nm, 380nm, 480nm 560nm and 620nm) were further analyzed because they represent the spectral sensitivity peak of *P. rapae* (Shimohigashi and Tominaga 1991, Qiu and Arikawa 2003a and 2003b).

Pieris morphology and growth

I collected adult butterflies from low and medium altitude in autumn 2013 for *P. canidia* and in spring 2014 for *P. rapae*. Adult *Pieris* were put in a cage (length: width: height=50 cm: 50 cm: 80 cm) with cabbage (Brassica oleracea var. *capitata* L.) as host plants in green house. I provided *B. pilosa* var. *radiata* flowers as nectar resource every two days. After female *Pieris* laid eggs on host plants, I used the newly hatched caterpillars in the following laboratory experiment.

To examine the impact of altitudinal origin and warming on pollinator performance, I measured the *Pieris* growth and development traits (body weight, development time, head width (4th instar) and adult forewing length) from the first instar to adult stage. Larvae grew in plastic containers (9 cm in diameter and 5 cm in height) with a mesh on top until becoming pupae (details in Appendix B). After becoming pupae for one day, pupae were weighted and then removed from the original container to a new one to avoid the failure of eclosion, with the pupal period recorded. After becoming adults for 12hs, *Pieris* were measured for their forewing length. Females and males were separated in different cages to avoid mating. All cages were put back to growth chambers, and the adult longevity was observed. The adult density of each cage was no more than five individuals to avoid strong competition. *B. pilosa* flowers, collected from the campus of National Taiwan University (25°00' N, 121°32' E), were supplied every two days as nectar resource to *Pieris* adults. After adults died, they were kept in triangle paper bags and dried at 40°C for three days at least. I measured the adult dry weight and then calculated adult fresh weight based on the correlation between dry and fresh body weight (Lin 2015).

Interaction between Pieris and B. pilosa var. radiata

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To examine the impact of altitudinal origin and warming on plant-pollination interaction, I recorded the flower-visiting behavior (frequency and duration) of *Pieris* on *B. pilosa* under different temperature treatment. I collected twenty capitulum of *B. pilosa* from National Taiwan University (25°00' N, 121°32' E), and kept the *B. pilosa* and each *Pieris* adult in the center of a cage under each temperature treatment (growth chamber) of this study. I recorded the time period of staying and feeding on flowers for each *Pieris* individual during 20 minutes of observation. I conducted one to two observation trials per individual, depending on its longevity.

This article focuses on plant flower traits, pollinator traits, and their relationships. Therefore, the results of plants vegetative growth traits and larval growth traits will be listed in appendix.

Field experimental design

To examine the spatial and temporal variation in plants and pollinators in the field, I also conducted field surveys at different altitude (low, medium) across months in three study sites (Taipei, Taoyuan and Nantou) in 2014 and 2015. The field surveys examined: (1) If the attractiveness of *B. pilosa* plants to pollinators (i.e. capitulum number, flower reflectance, sugar composition) would be different across altitude and months. (2) If the interaction between *B. pilosa* and pollinators (pollinators density,

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flower visit) would be different across altitude and months.

To examine the potential impact of environmental factor (e.g. mean temperature, humidity and diurnal temperature variation) on plant-pollinator interactions in the field, I collected the weather data since 2014 from three study sites using WatchDog B-series button logger (Spectrum Technologies, Inc.) (details in Appendix D).

Field experimental procedure

Capitulum number

To examine the impact of altitudinal origin on flower attractiveness to pollinators in the field, I counted capitulum number at low and medium altitude (each with three study sites) in four months (January, April, July and October 2014). A total of 18 replicates of capitulum number (6 replicates per study site) were counted at each altitude for each month.

Flower reflectance

The protocol to measure field flower reflectance is similar to that in the laboratory experiment. Samples were collected at both altitudes from two study sites (Taoyuan and Nantou) in four months (January, April, July and October, 2014). I kept the samples under low temperature (cooler) to maintain freshness and measured the

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flower reflectance within 24hrs. The mean reflectance was calculated from three capitulum per plant, and I plotted reflectance figures from 300nm. The six major wavelengths for *Pieris* were analyzed over altitude and months. A total of 18 replicates of mean flower reflectance (6 replicates per study site) were measured at each altitude for each month.

Sugar composition in nectar

To examine the impact of altitudinal origin on sugar composition, I collected capitulum from the three study sites at each altitude in three months (March, August and October 2014). This study analyzed nectar because it provides pollinator energy resource and could reflect flower attractiveness to pollinators. The samples were kept under low temperature (cooler) to maintain freshness. The sample from Nantou in August was excluded because of an accident. Sugar, including glucose, fructose and sucrose (Baker and Baker 1983, Nicolson and Thomburg 2007), were be analyzed, and then I calculated the proportion and weight per capitulum for each type of sugar. The sugar volume, quality and concentration were measured with High-Performance Anion-Exchange Chromatography with Pulsed Amperometric Detection (HPAEC-PAD, details in Appendix C). A total of 18 replicates of sugar composition (6 replicates per study site) were measured at each altitude for each month.

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Pollinator density

To examine the impact of altitudinal origin on plant-pollination interactions in the field, I conducted pollinator density observations at both altitudes from two study sites (Taoyuan and Nantou) in three months (January, March, and August) in 2014 or 2015. I observed areas around 3 x 3 m^2 with *B. pilosa* flower coverage over 70% for 30 minutes on sunny days during 9:00 - 15:00. The pollinator group (bee, butterfly, others) and abundance were recorded. The abundance of bees was recorded every 5 minutes due to their high activity, which made counting other pollinators difficult at the same time. One area at each altitude per site in August and three areas at each altitude per site in January and March were conducted.

Statistical analysis

Laboratory experiment

This study examined the impact of warming and altitude origin on plant and pollinator performance with GLMM (Generalized linear mixed models). Plant growth traits (e.g. height, leaf number) were analyzed with temperature treatment (ambient, 3, 6 ^{o}C warming) and species origin (low, medium altitude) as fixed factors, site as random factor, week as a repeated factor, and plant individual as a subject. Flower

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reflectance under six major wavelengths was analyzed by MANOVA (Multivariate Analysis of Variance), with temperature and species origin as factors. Other plant traits (e.g. flowering date, biomass) were analyzed by GLMM with temperature treatments and species origin as fixed factors, and site as a random factor. The pollinator traits (e.g. body weight, forewing length) were analyzed by GLMM with temperature treatments, species origins, species identity (native, invasive species) as fixed factors, and site as a random factor. *Pieris* visit rate was analyzed by logistic regression, with temperature treatments, species origins, and species identity as fixed factors and site as a random factor. All analyses above were conducted using SAS 9.4 (SAS Institute Inc., Cary, NC, USA).

Field survey

Pollinator density and capitulum number were analyzed by GLMM, with species origins (low, medium altitude) and month (or season) as fixed factors, and site as a random factor. Flower reflectance was analyzed by MANOVA, with species origin and month as fixed factors and site as a random factor. Flower attractiveness (e.g. nectar content) within a site was analyzed by GLM, with species origin and month as factors. All analyses above were conducted using SAS 9.4.

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Results

Warming effect on plant growth and development across altitude

Reproductive trait - flower

Warming effect on plant vegetative traits (Table A1) and reproductive traits (Table 2) varied with altitude. Warming advanced flowering date and capitulum number in medium-altitude, but did not do so in low-altitude plants (Fig. 4). *B. pilosa* from both altitudes showed no difference in flowering date or capitulum number in the common garden experiment (i.e. 22.8 ^{o}C, capitulum number, P =0.1717; flowering date, P =0.2267).

Reproductive trait- seed

Warming had a different effect on seed number, length, and weight (Table 3, Fig. 5). Warming (3^{o}C only) increased seed production by 90% in medium-altitude *B. pilosa*, but warming decreased that by 45-61% in low–altitude plants (Fig. 5a). *B. pilosa* from both altitudes showed no difference in common garden experiment (Fig. 5a, P =0.7676). Differently, warming (3^{o}C only) reduced seed length by 12% in medium-altitude plants, but had no effect on low-altitude plants. *B. pilosa* from medium altitude had longer seed length than those from low altitude in common garden experiment (Fig. 5b, P =0.0222). As for seed weight, either warming or plant

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origin (altitude) had no effect (Fig. 5c, warming, *P*=0.6868; plant origin, *P* =0.9860).

Warming effect on pollinator growth and development across altitude

Pieris rapae

Warming impact on the pupal and adult body weight of *P. rapae* varied with altitude (Table 4, Fig. 6). In specific, warming had no effect on medium-altitude *P. rapae* but decreased the pupal weight of low-altitude *P. rapae* by 37% (Fig. 6a). The pupal weight of *P. rapae* from both altitudes showed no difference in common garden experiment (Fig. 6a, *P* =0.8444). Warming had no effect on the adult weight of medium-altitude *P. rapae* but decreased that of low-altitude *P. rapae* by 40% (Fig. 6b). The adult weight of *P. rapae* from both altitudes showed no difference in common garden experiment (Fig. 6b, *P* = 0.3629).

Warming affected the larval period, pupal period, and adult period of *P. rapae* (Table 5, Fig. 7). In specific, warming reduced the larval period of medium- and low-altitude *P. rapae* by up to 62 and 45%, respectively (Fig. 7a). Warming also reduced the pupal period of medium- and low-altitude *P. rapae* by up to 54 and 22%, respectively (Fig. 7b). However, warming did not affect and reduced (19%) the adult period of medium- and low-altitude *P. rapae*, respectively. In common garden experiments, low-altitude *P. rapae* had a longer larval period than medium-altitude

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ones (larval period, *P* <0.0001; pupal period, *P* =0.5464; adult period, *P* =0.1884).

Warming also affected the morphology (wing length) of *P. rapae*, while this effect varied with altitude (Table 6, Fig. 8). In specific, warming did not affect and reduced (14%) the forewing length of medium- and low-altitude *P. rapae*, respectively. The adult forewing length of *P. rapae* from both altitudes showed no difference in common garden experiment (Fig. 8, *P* =0.4967).

Pieris canidia

Warming impact on the pupal and adult body weight of *P. canidia* varied with altitude (Table 4, Fig. 6). In specific, warming decreased the pupal weight of medium- and low-altitude *P. canidia* by 14 and 11%, respectively (Fig. 6a). In common garden experiment, medium-altitude *P. canidia* had heavier pupal weight than low-altitude ones (Fig. 6a, *P* =0.0023). Warming decreased the adult weight of medium- and low-altitude *P. canidia* by 19 and 21%, respectively (Fig. 6b). In common garden experiment, medium-altitude *P. canidia* had heavier adult weight than low-altitude ones (Fig. 6b, *P*=0.0070).

Warming affected the larval period, pupal period, and adult period of *P. canidia* (Table 5, Fig. 7). In specific, warming reduced the larval period of medium- and low-altitude *P. canidia* by up to 29 and 28%, respectively (Fig. 7a). Warming also

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reduced the pupal period of medium- and low-altitude *P. canidia* by up to 38 and 16%, respectively (Fig. 7b). However, warming reduced (24%) and did not affect the adult period of medium- and low-altitude *P. canidia*, respectively. In common garden experiments, low-altitude *P. canidia* had a longer larval and pupal period than medium-altitude ones (larval period, P <0.0001; pupal period, P =0.0012; adult period, P =0.1164).

Warming also affected the morphology (wing length) of *P. canidia,* while this effect varied with altitude (Table 6, Fig. 8). In specific, warming reduced the forewing length of medium- and low-altitude (3°C only) *P. canidia* by 6% and 5%, respectively. The adult forewing length of *P. canidia* from both altitudes showed no difference in common garden experiment (Fig. 8, P =0.0758).

Native vs. invasive pollinators

As for pupal and adult weight, the native *Pieris* was usually heavier than the invasive *Pieris,* but warming impact may vary with species and altitude (Table 4, Fig. 6). For example, warming reduced the difference between the native and invasive *Pieris* in pupal weight at medium altitude, but increased the difference at low altitude (Fig. 6a). Warming reduced the difference between the native and invasive *Pieris* in adult weight at medium altitude, but did not affect the difference at low altitude (Fig.

6b).

As for the larval, pupal, and adult period, the native *Pieris* had longer larval period but shorter pupal period than the invasive *Pieris,* but warming impact may vary with species and altitude (Table 5, Fig. 7). For example, warming reduced the difference between the native and invasive *Pieris* in larval period at medium altitude, but increased the difference at low altitude (Fig. 7a). Warming did not affect the difference between the native and invasive *Pieris* in pupal period at medium altitude, but reduced the difference at low altitude (Fig. 7b).

As for forewing length, medium-altitude native *Pieris* had longer forewing length than the invasive *Pieris* under ambient or warming treatment. However, low-altitude native *Pieris* only had longer forewing length than the invasive *Pieris* under 3 ^{o}C warming treatment (Table 6, Fig. 8)

Warming effect on plant-pollinator interactions across altitude

Warming impact on flower-visiting behavior of Pieris on B. pilosa var. radiata in the laboratory

Warming could affect the flower-visiting rate, visit duration, and feeding duration of *Pieris* in laboratory experiments. As for the flower-visiting rate of *Pieris* on *B. pilosa*, warming did not affect and increased that of medium- and low-altitude *P.*

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rapae from, respectively (Table 7, Fig. 9). Warming increased (3^{o}C only) and did not affect the flower-visiting rate of medium- and low-altitudes *P. canidia*, respectively. The flower-visiting rate of *P. rapae* or *P. canidia* showed no difference across altitude in common garden experiment (*P. rapae, P* =0.5015; *P. canidia, P* =0.2990). Warming did not affect the difference between native and invasive *Pieris* at both altitudes.

As for the flower-visiting duration, warming overall did not affect that of both *Pieris* (Table 7, Fig. 10a). However, warming ($3\ ^{o}$C only) decreased that of medium-altitude *P. rapae* on *B. pilosa*. In addition, warming increased that of medium-altitude *P. canidia* on *B. pilosa* but had no effect on low-altitude ones. The flower-visiting duration of *P. rapae* and *P. canidia* showed no difference across altitude in common garden experiment (*P. rapae, P* =0.2547; *P. canidia, P* =0.7906). Furthermore, warming reduced the difference in flower-visiting duration between native and invasive *Pieris* at medium altitude, but had no effect at low altitude.

As for feeding duration, warming increased that of low-altitude *P. rapae* on *B. pilosa*, but had no effect on medium-altitude *P. rapae* or both low- and medium-altitude *P. canidia* (Table 7, Fig. 10b). The feeding duration of *P. rapae* and *P. canidia* showed no difference across altitude in common garden experiment (*P. rapae, P* =0.7781; *P. canidia, P* =0.2478). In addition, warming increased the difference in feeding duration between native and invasive *Pieris* at low altitude but had no effect at medium altitude (Fig. 10b).

Flower attractiveness (reflectance) of B. pilosa var. radiata in the laboratory

Warming impact on flower reflectance under the six wavelengths varied with altitude (Table 8, Fig. 11). Warming decreased and did not affect the flower reflectance of *B. pilosa* from medium and low altitude, respectively (Fig. 11a, b). Low-altitude flowers had higher reflectance than medium-altitude ones in common garden treatment (Fig. 11c, *P*<0.0001).

Spatial (altitude) and temporal variations in the field

Flower traits of B. pilosa var. radiata

The flower traits of *B. pilosa* (capitulum number, flower reflectance, disk florets weight, and sugar content), which could be related to plant attractiveness to pollinators varied spatially and temporally in my field study.

Capitulum number recorded from the field (Ho *et al.* unpublished data) showed a spatial and temporal variation (Fig. 12; altitude, *P* =0.1376; season, *P* <0.0001; altitude*season, *P* <0.0001). Low-altitude *B. pilosa* had higher capitulum number than medium-altitude ones in winter. At medium altitude, there were more capitulum in fall than in spring, summer and winter. At low altitude, there were more capitulum

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in fall and winter than in summer. However, the patterns were different across sites (Fig. A5).

Flower reflectance also varied spatially and temporally (Table 9). Generally, the flower reflectance of field *B. pilosa* showed a similar pattern to that in the laboratory experiment. Low-altitude *B. pilosa* had higher flower reflectance than medium-altitude ones in the field (Fig. 13, *P*=0.0497). Low-altitude *B. pilosa* had higher flower reflectance than medium-altitude ones in summer and fall, but had no difference across altitude in spring and winter (Table 9, Fig. 14). At medium altitude, higher flower reflectance was observed in summer than in spring and fall. Similarly, at low altitude, higher flower reflectance was observed in summer than in spring, fall and winter (Fig. 15).

Flower weight was also measured in this study, since it might be related to sugar volume (Herrer 1985, Galletto and Bernardello 2004.). Both whole flower weight (*P*= 0.2899) and disk florets weight (*P*= 0.4719) had no difference across altitudes in general (Fig. 16). However, flower weight varied with months: flowers were heavier in October than March and August (whole flower weight, *P*< 0.0001; disk flower weight, *P*<0.0001). In specific, medium-altitude *B. pilosa* had higher whole flower weight in October than in March and August, and low-altitude *B. pilosa* had higher whole flower weight in March and October than in August (Fig. 16a).

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Medium-altitude *B. pilosa* had higher disk florets weight in October than in March and August, but low-altitude *B. pilosa* had higher disk florets weight in October than August (Fig. 16b). The patterns were different across sites (Fig. A6).

Sugar content also had varied spatially and temporally (Table 10). Generally, nectar analysis showed that the sugar content of field *B. pilosa* varied with altitude (Fig. 17). In specific, low-altitude *B. pilosa* had higher glucose content than medium-altitude ones (*P* =0.0017), but medium-altitude *B. pilosa* had higher sucrose content (*P* =0.0084) (Fig. 17a). As for the sugar weight per flower, low-altitude *B. pilosa* had more glucose, fructose and total sugar than medium-altitude ones (glucose, *P* <0.0001; fructose, *P* <0.0001; sucrose, *P* =0.1496; total sugar, *P* =0.0003) (Fig. 17b). However, the sugar content varied with altitude and months. As for the spatial variation in Taoyuan (Fig. 18), low-altitude *B. pilosa* had higher fructose and sucrose proportion than medium-altitude ones in October and August, respectively. And the pattern was same for fructose and sucrose weight per flower. However, low-altitude *B. pilosa* had less glucose proportion than medium-altitude ones in October and August. As for the temporal variation at low-altitude, higher glucose proportion was observed in March and October than August, and higher sucrose proportion was observed in August than March and October. At medium altitude, higher glucose proportion was observed in October than in March and August, higher fructose proportion was

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observed in March and August than in October, and higher sucrose proportion was observed in August than in March and October. The patterns in sugar weight per flower were similar to those in sugar proportion. However, the patterns in sugar content varied across sites (Fig. 18, Fig. 19).

Pollinator density

Pollinator density survey in the field showed that butterflies (*Pieris* mainly) were important pollinators besides bees (Table 11, Fig. 20). *Pieris* abundance (including passing and visiting individuals) in *B. pilosa* area varied spatially and temporally. As for the spatial variation, *Pieris* density was higher at low altitude than medium altitude in January and March, but not in August. As for the temporal variation, *Pieris* density was higher in March and August than in January at medium altitude, but higher in March than in January and August at low altitude.

Total butterfly abundance varied spatially and temporally as well. As for the spatial variation, total butterfly density was higher at low altitude than medium altitude in January and March, but not in August. As for the temporal variation, total butterfly density was higher in August than in January and March at medium altitude, but higher in March than in January and August at low altitude.

Bee density varied spatially and temporally. As for the spatial variation, bee

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density was higher at low altitude than medium altitude in January and March but not in August. As for the temporal variation, bee density was similar across months at low altitude, but higher in March and August than January at medium altitude. Overall, total pollinator density (bees+ butterflies+ others) was higher at low altitude than medium altitude in January and March, but not in August. Total pollinator density was similar across months at low altitude, but higher in March and August than in January at medium altitude.

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Discussion

Summary

This study has these major findings: 1) Warming impact on plants, pollinators, and their interactions might differ across altitude. 2) Warming may lead to a mismatch between plants and pollinators, since warming mostly affected the performance of adult *Pieris* from low altitude, but the flower traits of *B. pilosa* from medium altitude. 3) Warming impact on the native and invasive pollinators differed. In specific, the native *P. canidia* would be more sensitive to warming than the invasive *P. rapae* at medium altitude, but invasive *P. rapae* would be more sensitive to warming than native *P. canadia* at low altitude. 4) Warming impact on plants and pollinators could be a function of both plasticity and genetic difference across spatial gradients. 5) The field survey showed that both *Pieris* and *B. pilosa* traits varied spatially (altitude) and temporally (months) in the field.

Warming impact on nectar plants, pollinators, and their interactions varies with altitude

Nectar plants

The flower traits of *B. pilosa* (capitulum number and flower reflectance) could be related to plant attractiveness to pollinators in this study. Since warming impact on

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the flower and seed traits of plants (*B. pilosa*) differed across altitude, warming may have an altitude-dependent consequence on plant reproduction (Fig. 21). For example, warming increased the capitulum number of medium-altitude plants (i.e. increased flower display to pollinators (Strauss 1997, Brunet *et al.* 2015)), but had no effect on low-altitude plants. Warming reduced the flower reflectance of medium-altitude plants and likely lowered their attractiveness to pollinators, based on a positive correlation between flower reflectance and attractiveness to pollinators (Rae and Vamosi 2013, Song *et al.* 2015), but warming had no effect on low-altitude plants. Since flower reflectance could be affected by a change in anthocyanin content, distribution, or epidermal cell shape (Anderson *et al.* 2013, Papiorek *et al.* 2014), future studies can examine whether warming changes flower reflectance by affecting these structure factors.

Given that warming caused conflicting effects on the attractiveness of medium-altitude plants, it will require a real pollination study to understand the net effect of warming. While this study (artificial pollination) did not test how warming impact on flower attractiveness to pollinators would subsequently affect seed production, this study did reveal direct warming impact on seed production. For instance, warming decreased the seed production (i.e. seed number) of low-altitude *B. pilosa* plants, but warming (3^{o}C only) increased that of medium-altitude plants.

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The results in this study help advance our understanding in warming impact on nectar plants. For example, previous studies showed negative impact of warming on flower number and nectar volume, but positive impact on flowering date (i.e. advancement) (Saavedra *et al*. 2003, Liu *et al.* 2012, Mu *et al.* 2015, Whittington *et al.* 2015). This study actually suggests that many of these warming effects could be altitude dependent. In addition, previous studies suggested that the response of plant reproductive traits to warming could be plastic (Van Etten and Brunet 2013, Anderson *et al.* 2013, Frei *et al.* 2014a, Cranston *et al.* 2015, Pajoro *et al.* 2016). This study further shows that these responses should be a function of both plasticity and genetic difference (i.e. genotypes across altitude). Finally, a previous study showed that *B. pilosa* from different altitudes had no difference in leaf chlorophyll content and seed weight (Huang *et al.* 2015), but this study demonstrates that medium-altitude *B. pilosa* could have higher leaf chlorophyll content than low-altitude ones, in common garden.

Pollinators

Warming impact on the forewing length of pollinators (*Pieris*) differed across altitude, and this may have an altitude-dependent consequence on pollination service (Fig. 21). Previous studies have suggested a positive correlation between butterfly

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forewing length and flight distance (Greenleaf *et al.* 2007, Ducatez *et al.* 2012, Skórka *et al.* 2013, Shi *et al.* 2015, Blanken *et al.* 2015). This study showed that warming reduced the forewing length of both low- and medium-altitude *P. canidia*, potentially shortening their flight distance from both altitudes. However, warming only reduced the forewing length of low-altitude *P. rapae*, potentially shortening the flight distance of low- but not medium-altitude *P. rapae*. Since *B. pilosa* needs pollens from different flowers for cross-pollination (Huang *et al.* 2012), pollinators with longer flight distance may facilitate *Bidens* pollen exchange and successful pollination. Therefore, *B. pilosa* might face reduced pollination service from the native *P. canidia* at both altitude under warming (i.e. due to shorter forewings) and from the invasive *P. rapae* at low altitude under warming.

Warming impact on *Pieris* adult period (longevity) varied with species and altitude, suggesting species- and altitude-dependent warming impact on pollination service (Fig. 21). Longer pollinator longevity might benefit nectar plants because pollinators could provide longer pollination service and increase pollination efficiency. This study showed that warming reduced the adult period of medium-altitude *P. canidia*, potentially decreasing its pollination service. Warming, however, reduced the adult period of low-altitude *P. rapae.*

Interestingly, while *Pieris* adults can serve as beneficial pollinators to many

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plants, *Pieris* larvae are major agricultural pests worldwide. In this study, warming reduced the larval period of *Pieris* from both altitudes but decreased adult period of *P. canidia* and *P. rapae* from medium- and low-altitude, respectively. Thus, warming might reduce *Pieris* larvae damage to crops and *Pieris* adults' pollination service to plants simultaneously. However, this prediction is based on an assumption that shorter life cycle will not lead to more *Pieris* generations per year, unlike the case where more generations of herbivores in a growth season cause more threat to plant in the long term (Gomi *et al.* 2007, Altermatt 2010, Martín-Vertedor *et al.* 2010). The life tables of low- and medium-altitude *Pieris* were included in Table A5 and A6.

Putting warming impact on adult period and forewing length together, this study suggests a negative impact of warming on the pollination service of *P. canidia* at medium altitude, since warming decreased the adult period and forewing length. However, the overall impact of warming on *P. rapae* is not that straightforward, since warming decreased the adult period and forewing length of low-altitude *P. rapae* but increased the feeding duration, which might compensate the negative impact of warming.

The results in warming impact on *Pieris* were similar to many previous studies, which have shown that warming had negative effects on the body weight, development and adult forewing length of butterflies (Kingsolver 2000, Stevens 2004,

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Kingsolver *et al.* 2012, Stuhldreher *et al.* 2014, Barton *et al.* 2014, Bauerfeind and Fischer 2014). For example, warming could increase the developmental rate and reduce the pupal weight of *P. rapae* (Whitney-Johnson *et al.* 2005). Also, previous studies suggested that larger body size of pollinators had lower visitation rate (Stout 2000, Vivarelli *et al.* 2011), but higher pollination efficiency (O'Neill and O'Neill 2010, Luo *et al.* 2012, Pearce *et al.* 2012, Willmer and Finlayson 2014). Accordingly in this study, warming decreased the body size (forewing length) and increased the visitation rate of low-altitude *P. rapae*.

Plant-pollinator mismatch

Because plants and pollinators had a different response to warming across altitude (Fig. 22), warming might lead to a mismatch in plant-pollinator communities across altitude and then impede associated ecosystem service (pollination). For example, warming advanced flowering date and increased capitulum number in medium-altitude plants, but decreased adult period in medium-altitude *P. canidia*. Therefore, this positive and negative warming impact on plants and pollinators, respectively, can result in a plant-pollinator mismatch at medium altitude. Furthermore, this plant-pollinator mismatch varied across altitude, since warming did not affect flower traits and the adult period of *P. canidia* at low altitude.

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Previous studies have suggested either one of these points: 1) Plants were sensitive to warming (i.e. advanced flowering date), whereas pollinators might not (Rafferty and Ives 2011, Petanidou *et al.* 2014). 2) Pollinators were sensitive to warming, whereas plants might not (Miller-Struttmann *et al.* 2015). 3) Both plants and pollinators were affected by warming but responded differently in the direction or degree (Gordo and Sanz 2005). Thus, warming would increase the mismatch between plants and pollinators (Memmott *et al.* 2007, Schweiger *et al.* 2008, Kudo 2014). The results of this study suggest that warming can affect associated plants and pollinators differently and likely lead to a plant-pollinator mismatch, which is altitude-dependent in this study system. Although some studies argued that warming might not cause a plant-pollinator mismatch due to higher biodiversity (Burkle and Alarcón 2011, Bartomeus *et al.* 2013), the prominent role of *B. pilosa* and *Pieris* in this study system should make mismatch, if happens, obvious.

Native vs. invasive pollinators

Invasive species are widespread in the world and threaten native species, and this study found that native and invasive may respond differently to warming across altitude. The results of this study call for an attention that warming may shift the current balance between native and invasive pollinators because they might have a

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different sensitivity to a temperature increase. For example, at low altitude, warming decreased the adult period of invasive *Pieris* but did not affect that of native *Pieris*. Thus, low-altitude invasive *Pieris* might be more sensitive to warming than native *Pieris*. However, the pattern was opposite at medium altitude. Medium-altitude native *Pieris* might be more sensitive to warming than the invasive *Pieris*, given that warming decreased the adult period of the native *Pieris* only. In addition, the direction of warming impact on the difference between the native and invasive *Pieris* can vary across altitude. For example, warming decreased the difference in pupal weight between the native and invasive *Pieris* at medium altitude, but increased the difference at low altitude (Fig. 6a).

Intraspecific genetic variation

Warming impact on nectars plants and pollinators could be a function of both plasticity and genetic difference across spatial gradients. This study shows many plastic responses to warming in plant flower traits (Fig. 4) or pollinator traits (Fig. 6). This study also suggests that the responses to warming in plants (Fig. 5b) or pollinators (e.g. *P. canidia* in Fig. 6) could have a genetic basis, supported by our common garden experiment with low- and medium-altitude populations (Table 12). For example, medium-altitude plants had higher quantity (e.g. plant height, leaf number, biomass), higher quality (chlorophyll content), and lower flower reflectance than low-altitude ones in common garden, suggesting a genetic difference in populations across altitude. As for pollinators, medium-altitude *P. canidia* had heavier body weight (pupal and adult) but shorter larval and pupal period than low-altitude ones. Similarly, medium-altitude *P. rapae* had heavier body weight (2nd, 3rd and 4th) but shorter larval period than low-altitude ones. The results highlight the need to consider both genetic difference and plasticity in plants and pollinators under climate change (Karl *et al.* 2008, Vergeer and Kunin 2013, Barton *et al.* 2014, Kooyers *et al.* 2015).

Spatial and temporal variation in nectar plants and pollinators in the field

The flower traits of *B. pilosa* measured in study could be related to plant attractiveness to pollinators; pollinator traits measured in this study could be related to pollination success. Therefore, the spatial (altitude) and temporal (month) variation in flower and pollinator traits observed in the field suggests dynamic plant-pollinator interactions in natural communities (Medan *et al.* 2002, Debieu *et al.* 2013, Ranjitkar *et al.* 2013, Preite *et al.* 2015)..

Plant and pollinator interactions vary spatially (altitude)

Investment on flower attractiveness can increase plant reproductive success through higher pollinator activity (Celedón-Neghme *et al.* 2007, Kimball 2008, Blaauw and Isaacs 2014, Dötterl *et al.* 2014, Brodie *et al.* 2015). This study found that low- and medium-altitude plants might have a different strength or strategy to attract pollinators. For example, low-altitude *B. pilosa* had higher flower reflectance (both laboratory experiment and field survey) and total sugar weight than medium-altitude ones, suggesting that low-altitude *B. pilosa* are more attractive in these traits. However, medium-altitude *B. pilosa* had higher sucrose concentration than low-altitude ones. Since higher sucrose concentration could mean better flight fuel for pollinators (Willers *et al.* 1987, O'Brien 1999) and enhance the reproduction of male pollinators (Watanabe and Hirota 1999), medium-altitude *B. pilosa* with higher sucrose concentration seem to be better nectar source to pollinators.

The different strength or strategy in flower attractiveness across altitude in this study might explain why some flower attractiveness traits increase or decrease with altitude in other studies. For example, flower attractiveness might increase (e.g. flower size, UV spectrum) or decrease (e.g. flower number, flowering date) with altitude (Suárez et al. 2009, Fan and Yang 2009, Maad *et al.* 2013, Teixido and Valladares 2015, Koski and Ashman 2015). Given that a trade-off may exist among traits, such as the case for flower size and number (Pélabon *et al.* 2013), an investigation in the trade-off among multiple traits will help clarify the underlying mechanisms for flower trait

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variation.

As for pollinator density, total *Pieris* density and total pollinator density were higher at low than medium altitude, suggesting stronger plant-pollinator interactions and higher pollination success at low altitude. The result is consistent with previous studies, where pollinator visitation rate was higher at low altitude than higher altitude (Totland 2001, Zhao and Wang 2015).

Plant and pollinator interactions vary temporally (month)

Plant-pollinator interactions varied with month in this study system (Fig. 23). In spring (March), low-altitude *B. pilosa* flowers had higher glucose, fructose, total sugar weight and pollinator density but lower sucrose than medium-altitude ones. In summer (August), low-altitude *B. pilosa* flowers had higher reflectance and sucrose than medium-altitude ones. In fall (October), low-altitude *B. pilosa* flowers had higher reflectance, glucose, fructose and total sugar weight than medium-altitude ones. In winter (January), low-altitude *B. pilosa* flowers had higher capitulum number and pollinator density than medium-altitude ones.

The strength and weakness of this study

This study helps advance our understanding in plant-pollinator interactions

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across spatial and temporal gradients under current climate or upcoming climate warming, by conducting both laboratory experiments and field surveys, and examining plant and pollinator trait associations/variations in the same system. This study also helps reveal some contrasting responses to warming between native and invasive pollinators, suggesting an upcoming ubiquitous change in most ecosystems, which commonly have both pollinators. Due to logistics, this study, however, does not examine the nectar composition in *B. pilosa* flowers grown under different temperature (growth chamber) and use these flowers for pollinator visitation experiments. In addition, this study does not examine potential interactions (e.g. competition) between the focal plant/pollinator species and others.

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Conclusions

This study shows that the warming impact on plants, pollinators, and their interactions can vary with altitude, likely leading to plant-pollinator mismatch, shaping local plant-animal communities, and impeding ecosystem service. The altitudinal dependence of warming impact on plants or pollinators could be due to the plasticity and/ or genetic effects of species. In addition, warming can affect native and invasive pollinators differently, likely shifting plant-pollinator interactions in this study system. Given that species invasion is common, it is important to investigate if this shift (due to different responses in native vs. invasive pollinators) will be the new norm worldwide under climate warming. Finally, the study shows the field dynamics in plants and pollinators, both of which could vary spatially (altitude) and temporally (months) in nature.

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Table 1. Study sites

The species collected from both low (~100 m a.s.l) and medium (~1000 m a.s.l) altitude of three study sites (Taipei, Taoyuan and Nantou) in 2013 and 2014.

Study site	**Elevation**	**Longitude**	**Latitude**	**Species**
Hwa-Jiang (Taipei)	81m	121°29' E	25°02' N	*B. pilosa* var. *radiata* *P. rapae*
Tatunshan (Taipei)	1093m	121°31' E	25 °10' N	*B. pilosa* var. *radiata* *P. rapae*
Shiyizhi old trail (Taoyuan)	175m	121°16' E	24 °50' N	*B. pilosa* var. *radiata* *P. canidia* *P. rapae*
Dongyanshan (Taoyuan)	925m	121°24' E	24 °49' N	*B. pilosa* var. *radiata* *P. canidia* *P. rapae*
Erbawan old trail (Nantou)	158m	120°37' E	23 °48' N	*B. pilosa* var. *radiata* *P. canidia* *P. rapae*
Xitou (Nantou)	1128m	120°47' E	23 °40' N	*B. pilosa* var. *radiata* *P. canidia* *P. rapae*

Table 2. Warming impact on *B. pilosa* var. *radiata* flower traits across altitude

The plant flower traits (capitulum number and flowering date) were recorded under 3 temperature treatments (control, 3^{o}C and 6 ^{o}C warming) across altitude (low and medium) and analyzed with GLMM. The P values were given, and bold value represented a significant difference (p<0.05).

Plant traits	**Factors**			
	N	**Altitude**	**Temperature**	**Alt.*Temp.**
Capitulum number	144	0.4780	0.1772	**0.0047**
Flowering date	58	0.2444	0.0612	**0.0021**

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Table 3. Warming impact on *B. pilosa* var. *radiata* seed traits across altitude

The plant seed traits (seed number/ capitulum, seed length and weight) were measured under 3 temperature treatments (control, 3°C and 6 °C warming) across altitude (low and medium) and analyzed with GLMM. The P values were given, and bold value represented a significant difference ($p<0.05$).

Plant traits	**N**	**Factors**		
		Altitude	**Temperature**	**Alt.*Temp.**
Seed number	97	**0.0005**	0.0614	**0.0085**
Seed length	97	0.0971	**0.0045**	0.2516
Seed weight	62	0.6868	0.5750	0.3827

Table 4. Warming impact on *Pieris* weight at each life stage across altitude

The body weight of species (*P. canidia, P. rapae)* from larvae to adult was measured under 3 temperature treatments (control, 3°C and 6 °C warming) across altitude (low and medium) and analyzed with GLMM. The P values were given, and bold value represented a significant difference ($p<0.05$).

				Factors				
***Pieris* stage**	**N**	**Species**	**Temperature**	**Altitude**	**Sp.*Temp.**	**Sp.*Alt.**	**Temp.*Alt.**	**Sp.*Temp. *Alt.**
2nd instar	215	**<0.0001**	**<0.0001**	0.5383	0.0544	**0.0018**	**0.0018**	**0.0012**
3rd instar	336	**<0.0001**	**0.0033**	0.2107	**<0.0001**	**0.0053**	0.1883	0.2471
4th instar	327	**<0.0001**	**0.0472**	0.7697	**0.0133**	**0.0235**	0.8774	0.5733
5th instar	313	**<0.0001**	0.1555	0.0597	**0.0315**	0.2918	0.4983	0.7960
Pupa	293	**<0.0001**	**<0.0001**	**<0.0001**	0.2726	**0.0105**	**0.0421**	**0.0006**
Adult	277	**<0.0001**	**<0.0001**	**<0.0001**	0.0949	**0.0093**	0.1656	**0.0204**

Table 5. Warming impact on the duration of each life stage in *Pieris* across altitude
The stage period of species (*P. canidia*, *P. rapae)* was recorded under 3 temperature treatments (control, 3^{o}C and 6 ^{o}C warming) across altitude (low and medium) and analyzed with GLMM. The P values were given, and bold value represented a significant difference ($p<0.05$).

***Pieris* stage**		**Factors**						
	N	**Species**	**Temperature**	**Altitude**	**Sp.*Temp.**	**Sp.*Alt.**	**Temp.*Alt.**	**Sp.*Temp. *Alt.**
Larva	292	**0.0258**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Pupa	284	**0.0058**	**<0.0001**	**<0.0001**	**0.0270**	0.7336	**<0.0001**	0.1791
Adult	275	0.0729	0.0631	**0.0003**	0.3922	**0.0104**	0.6110	0.1976

Table 6. Warming impact on *Pieris* forewing length across altitude

The forewing length of species (*P. canidia, P. rapae)* was measured under 3 temperature treatments (control, 3^{o}C and 6^{o}C warming) across altitude (low and medium) and analyzed with GLMM. The P values were given, and bold value represented a significant difference ($p<0.05$).

***Pieris* forewing length**	**Factors**							
	N	**Species**	**Temperature**	**Altitude**	**Sp.*Temp.**	**Sp.*Alt.**	**Temp.*Alt.**	**Sp.*Temp. *Alt.**
	275	**<0.0001**	**0.0028**	**<0.0001**	0.8685	0.0580	0.2006	**0.0109**

Table 7. Warming impact on the flower-visiting behavior of *Pieris* on *B. pilosa* var. *radiata* across altitude
The behavior of species (*P. canidia, P. rapae)* was recorded under 3 temperature treatments (control, 3°C and 6 °C warming) across altitude (low and medium) and analyzed with logistic regression and GLMM. Individual was put in a small cage with flower of *B. pilosa* and observed 20 minutes in the growth chamber. The P values were given, and bold value represented a significant difference (p<0.05).

	Factors							
***Pieris* visit behavior**	**N**	**Species**	**Temperature**	**Altitude**	**Sp.*Temp.**	**Sp.*Alt.**	**Temp.*Alt.**	**Sp.*Temp. *Alt.**
Visit rate	225	0.5521	**0.0404**	0.1857	0.0862	0.5426	0.0880	**0.0420**
Visit duration	225	0.6597	0.1432	0.4409	0.2832	0.0750	0.2832	**0.0166**
Feeding duration	225	0.1589	**0.0024**	**0.0367**	0.2244	**0.0041**	**0.0135**	**0.0215**

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Table 8. Warming impact on *B. pilosa* var. *radiata* flower reflectance across altitude
Ray florets of reflectance was measured by spectrometer under 3 temperature treatments (control, 3^{o}C and 6^{o}C warming) across altitude (low and medium) and analyzed with MANOVA. The results compared with the six major wavelengths to *Pieris*. The P values were given, and bold value represented a significant difference ($p<0.05$).

		Factors						
	N	**Wavelength**	**Temperature**	**Altitude**	**W.*Temp.**	**W.*Alt.**	**Temp.*Alt.**	**W.*Temp. *Alt.**
Flower reflectance	51	**<0.0001**	**<0.0001**	**<0.0001**	0.4723	**0.0398**	**<0.0001**	0.4428

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Table 9. Field pattern in *B. pilosa* var. *radiata* flower reflectance across altitude and season (months)

Ray florets of reflectance was measured by spectrometer which was collected at altitude (low and medium) with season (spring, summer, fall and winter) and analyzed with MANOVA. The results compared with the six major wavelengths to *Pieris*. The P values were given, and bold value represented a significant difference (p<0.05).

					Factors			
	N	**Wavelength**	**Season**	**Altitude**	**W.*Sea.**	**W.*Alt.**	**Sea .*Alt.**	**W.*Sea. *Alt.**
Flower reflectance	96	**<0.0001**	**<0.0001**	**0.0497**	**0.0197**	0.7793	**<0.0001**	0.4495

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Table 10. Field pattern in *B. pilosa* var. *radiata* flower sugar content across altitude and months
Flower of sugar (percentage and weight per flower) was measured by HPAEC-PAD. The samples were collected at two altitudes (low and medium) with month (March, August and October), and analyzed with GLM. The result separated by site due to the sugar in August from Nantou medium altitude was excluded. The P values were given, and bold value represented a significant difference ($p<0.05$).

	Factors					
	Taoyuan N=36			**Nantou N=24**		
Sugar content	**Altitude**	**Month**	**Alt.*Mon.**	**Altitude**	**Month**	**Alt.*Mon.**
Glucose%	**0.0059**	**<0.0001**	**0.0183**	**<0.0001**	**<0.0001**	**<0.0001**
Fructose%	0.0516	**0.0339**	**0.0004**	0.2115	**<0.0001**	0.2602
Sucrose%	**0.0294**	**<0.0001**	**<0.0001**	**0.0002**	**<0.0001**	**0.0024**
Glucose weight	**0.0071**	**<0.0001**	0.1410	**<0.0001**	**0.0008**	0.1455
Fructose weight	**0.0009**	**<0.0001**	**0.0286**	**<0.0001**	**<0.0001**	0.6925
Sucrose weight	0.1047	**<0.0001**	**0.0421**	**0.0161**	**<0.0001**	**0.0325**
Total sugar weight	**0.0024**	**<0.0001**	0.0814	**0.0001**	**<0.0001**	0.5140

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Table 11. Field pattern in pollinator density across altitude and months
The observation was conducted at two altitudes (low and medium) with month (January, March and August), and analyzed with GLMM. The category included the bee, butterfly and other (each pollinator category included passing and feeding individual). The P values were given, and bold value represented a significant difference (p<0.05).

Pollinators	**Factors**		
	Altitude	**Month**	**Alt.*Mon.**
Passing bee	**0.0002**	0.2767	**0.0016**
Passing butterfly	**<0.0001**	**<0.0001**	**0.0008**
Passing *Pieris*	0.1989	**0.0006**	0.1138
Passing total	**<0.0001**	**<0.0001**	**<0.0001**
Feeding bee	**<0.0001**	**0.0006**	**0.0001**
Feeding butterfly	**<0.0001**	**<0.0001**	**<0.0001**
Feeding *Pieris*	0.2932	**<0.0001**	**<0.0001**
Feeding total	**<0.0001**	**<0.0001**	**<0.0001**
Total bee	**<0.0001**	0.0845	**0.0203**
Total butterfly	**<0.0001**	**<0.0001**	**<0.0001**
Total *Pieris*	**0.0079**	**<0.0001**	**0.0016**
Total pollinator	**<0.0001**	**<0.0001**	**<0.0001**

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Table 12. Plant (*B. pilosa*) and *Pieris* traits in common garden.

	Traits	**Trend**
Plant	Height	M>L
	Leaf number	M>L
	CHL	M>L
	Leaf toughness	L>M
	Total biomass	M>L
	Above-ground biomass	M>L
	Seed length	M>L
	Flower reflectance	L>M
P. rapae	2nd body weight	M>L
	3rd body weight	M>L
	4th body weight	M>L
	Larval period	L>M
P. canidia	2nd body weight	M>L
	3rd body weight	L>M
	Pupal weight	M>L
	Adult weight	M>L
	Larval period	L>M
	Pupal period	L>M

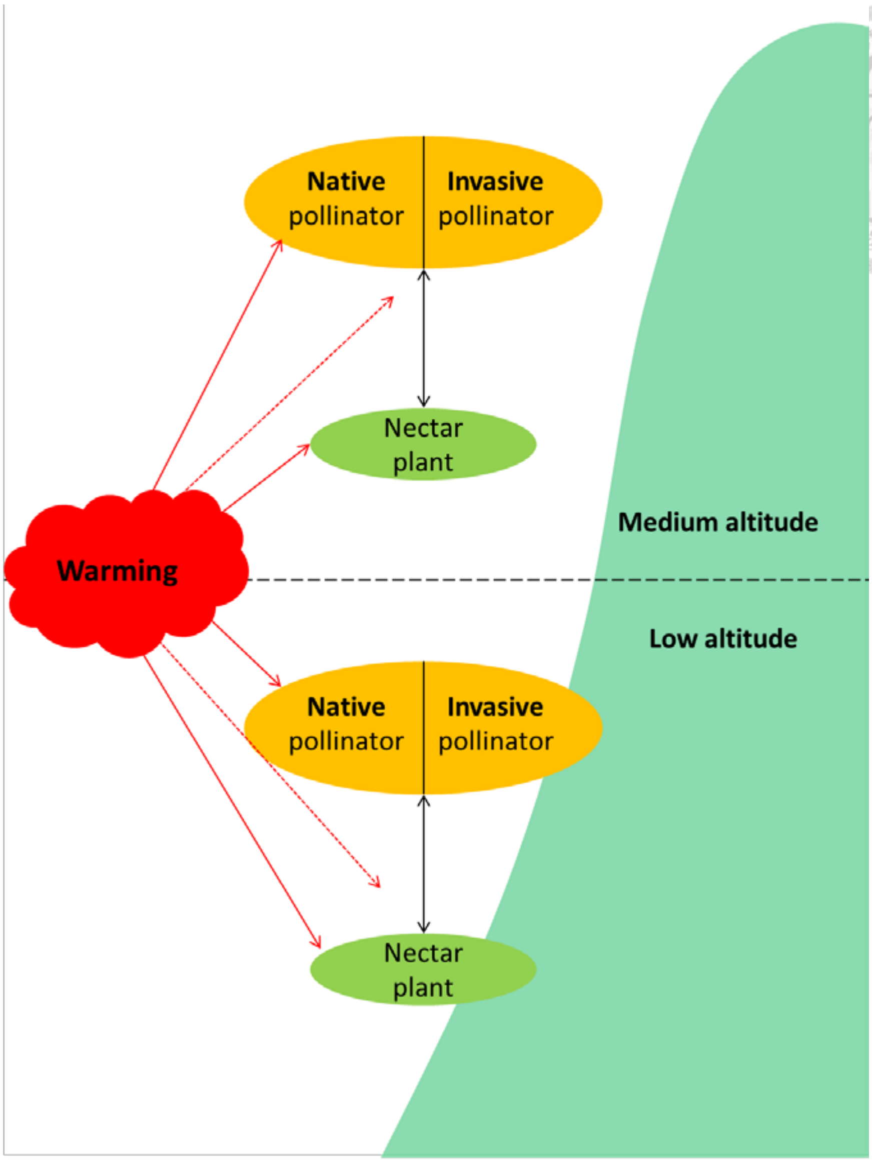

Fig. 1 Concept map
This study aimed to investigate the warming impact on the native and invasive pollinator and their common nectar plant across altitude (i.e. populations originally from low or medium altitude).

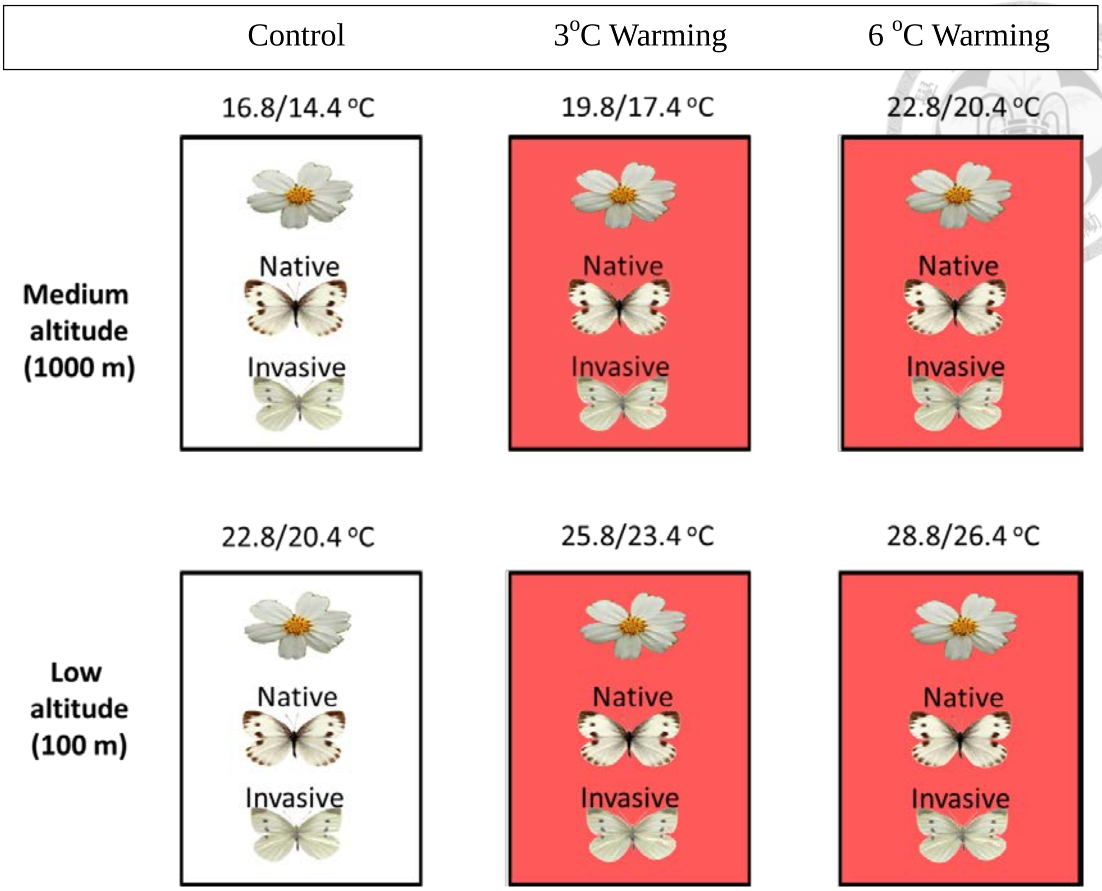

Fig. 2 Laboratory design

Pollinators and plants collected from medium and low altitude were raised in three temperature treatments (control, 3°C warming and 6 °C warming). The control temperature was set as 16.8°C and 22.8°C for medium and low altitude, respectively.

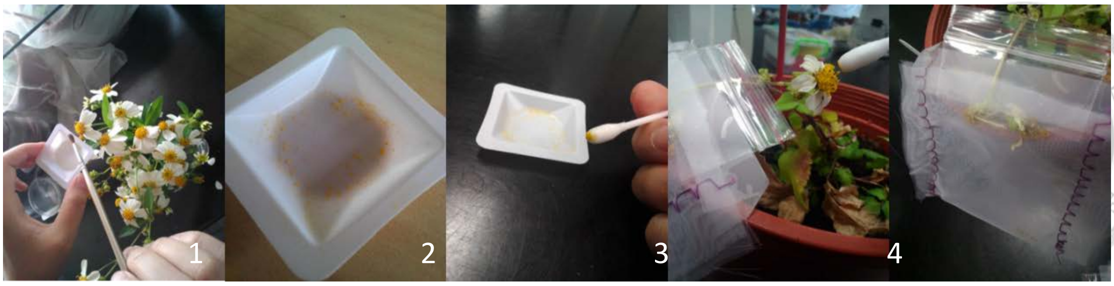

Fig. 3 The protocol of artificial pollination

(1) Collected pollen from fresh capitulum, (2) mixed all of the pollen, (3) used a cotton swab to touch the mixed pollen, (4) touched on opened disk florets of an experimental plant and (5) covered a mesh bag on the capitulum

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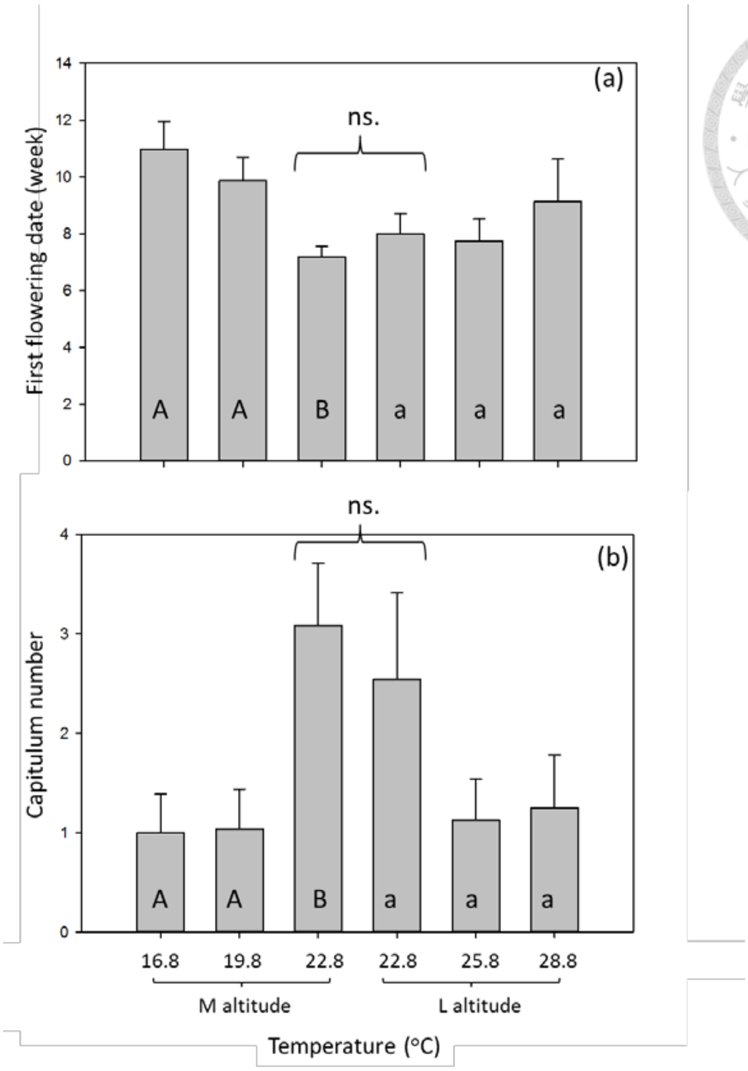

Fig. 4 Warming impact on *B. pilosa* var. *radiata* flower traits across altitude
Warming impact on *B. pilosa* first flowering date (a), and capitulum number (b). Plants from medium and low altitude were grown in three temperature treatment (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively.
(mean ± SE values were given; ns. : represented no significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C); capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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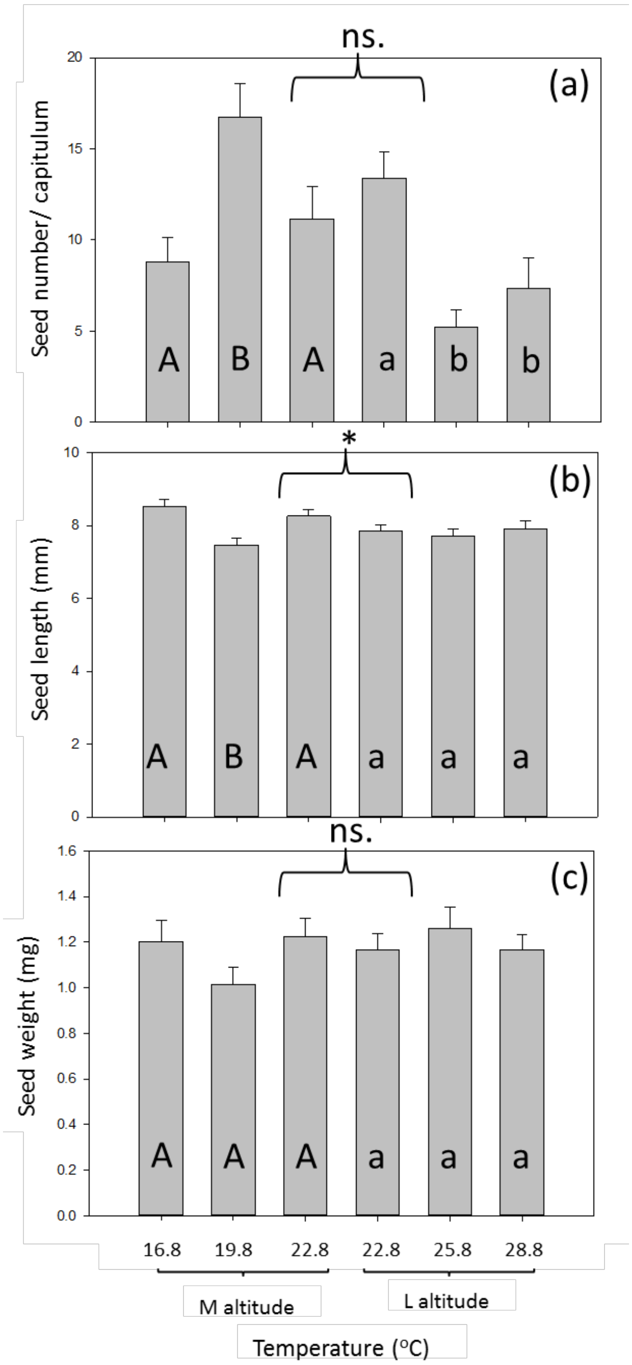

Fig. 5 Warming impact on *B. pilosa* var. *radiata* seed trait across altitude

Warming impact on seed number per capitulum (a), seed length (b) and seed weight (c) across altitude. Plants from medium and low altitude were grown in three temperature treatment (control, 3°C warming and 6 °C warming). The control temperature was set as 16.8°C and 22.8°C for medium and low altitude, respectively.

(mean ± SE values were given; ns. : represented no significant difference between altitudes in common garden treatment (i.e. 22.8 °C), *: represented a significant difference between altitudes in common garden treatment; capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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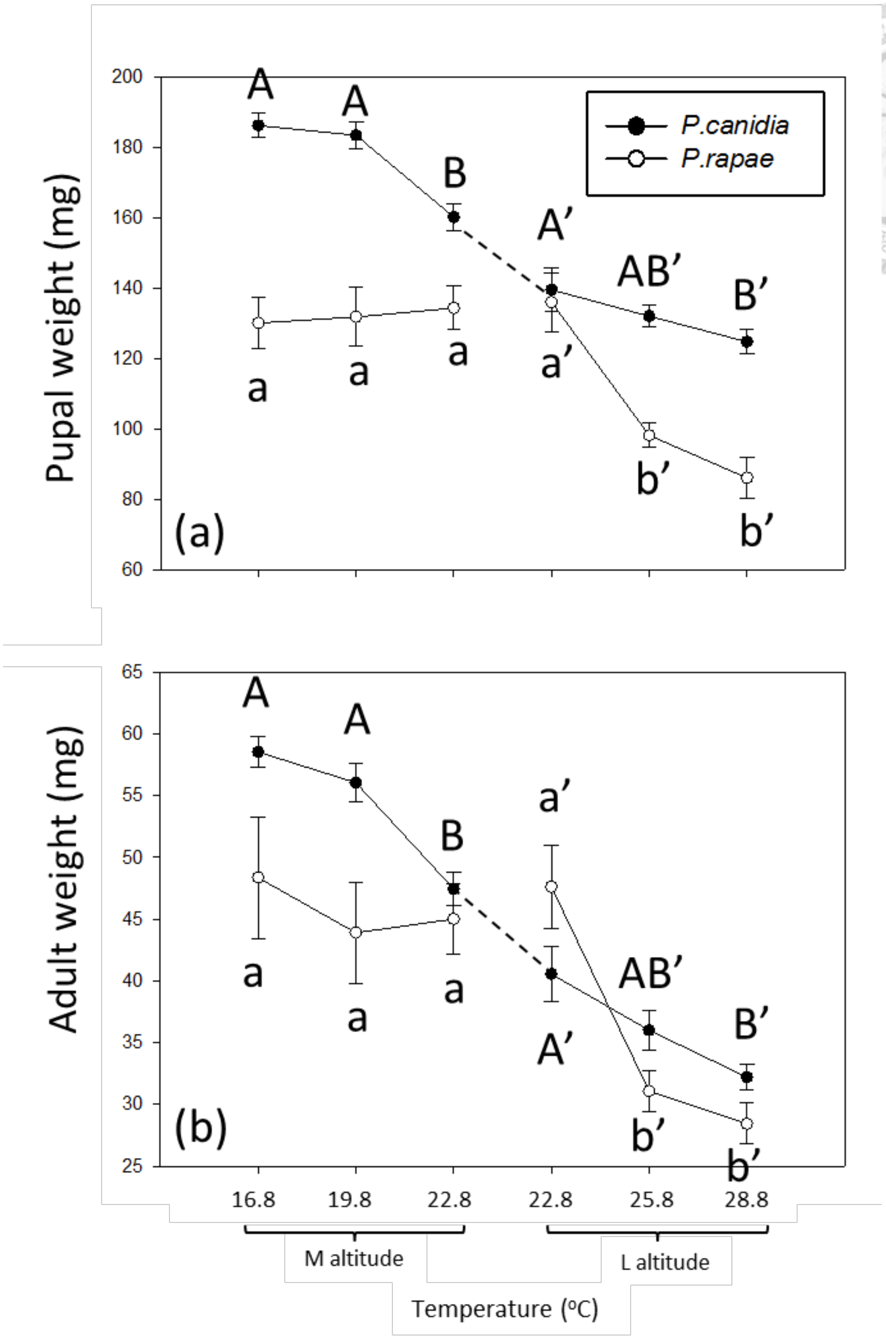

Fig. 6 Warming impact on *Pieris* weight at each life stage across altitude
Pollinators from medium and low altitude were reared in three temperature treatments (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively. *P. canadia* and *P. rapae* are indicated with black and white circle, respectively.
(mean ± SE values were given; dash line : represented a significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C), capitalized letters: represented the comparison of *P. canadia*, small letters: represented the comparison of *P. rapae*, the letters with prime represented the low-altitude *Pieris* and same alphabets mean no significant difference between treatments)

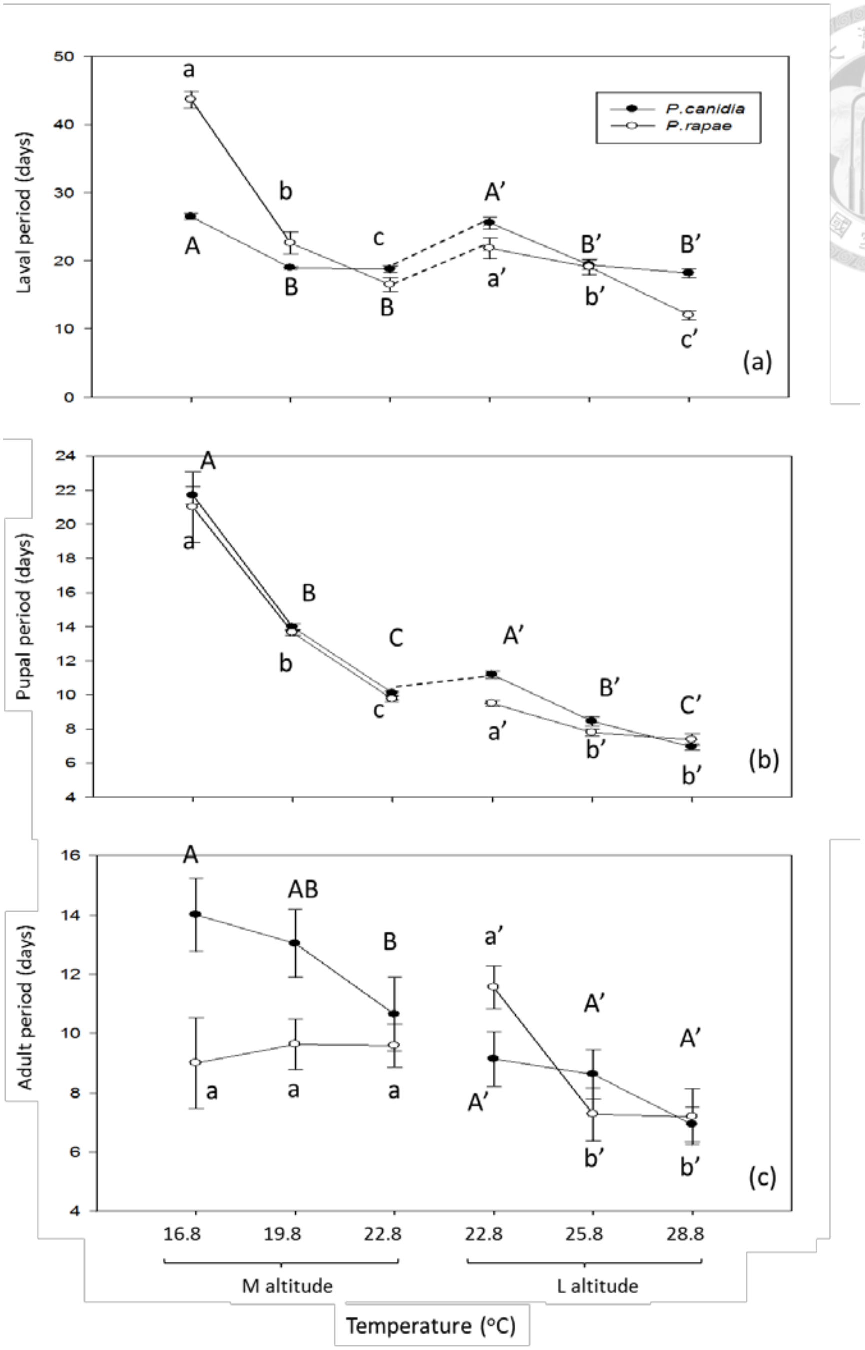

Fig. 7 Warming impact on the duration of each life stage in *Pieris* across altitude

Pollinators from medium and low altitude were reared in three temperature treatments (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively. *P. canadia* and *P. rapae* are indicated with black and white circle, respectively.

(mean ± SE values were given; dash line : represented a significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C), capitalized letters: represented the comparison of *P. canadia*, small letters: represented the comparison of *P. rapae*, the letters with prime represented the low-altitude *Pieris* and same alphabets mean no significant difference between treatments)

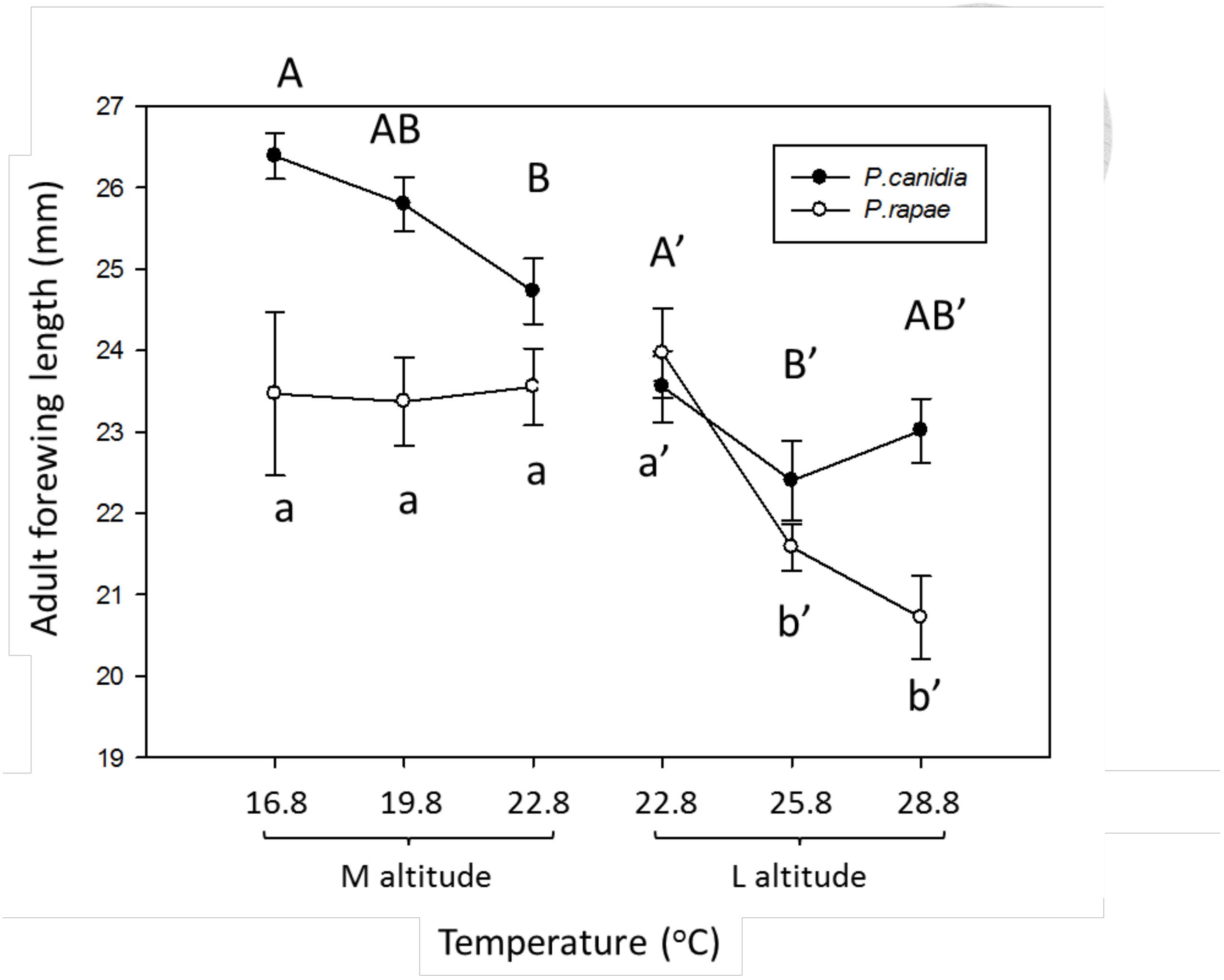

Fig. 8 Warming impact on *Pieris* forewing length across altitude

Pollinators from medium and low altitude were reared in three temperature treatments (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively. *P. canadia* and *P. rapae* are indicated with black and white circle, respectively.

(mean ± SE values were given; capitalized letters: represented the comparison of *P. canadia*, small letters: represented the comparison of *P. rapae*, the letters with prime represented the low-altitude *Pieris* and same alphabets mean no significant difference between treatments)

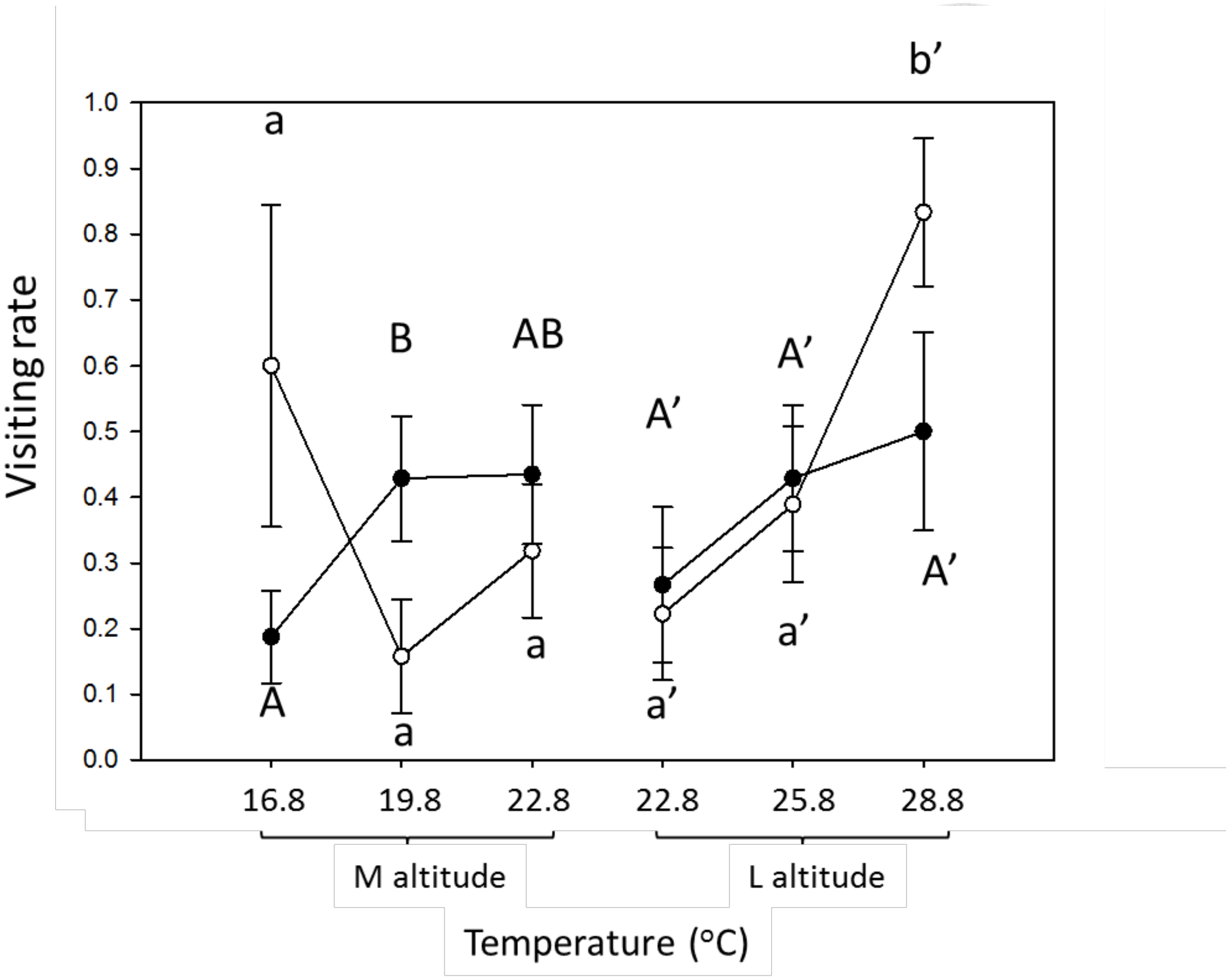

Fig. 9 Warming impact on flower-visiting rate of *Pieris* on *B. pilosa* across altitude Pollinators from medium and low altitude were reared in three temperature treatments (control, 3^{o}C warming and 6 ^{o}C warming). *Pieris* visit was recorded for 20 minutes. The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively. *P. canadia* and *P. rapae* are indicated with black and white circle, respectively.
(mean ± SE values were given; capitalized letters: represented the comparison of *P. canadia*, small letters: represented the comparison of *P. rapae*, the letters with prime represented the low-altitude *Pieris* and same alphabets mean no significant difference between treatments)

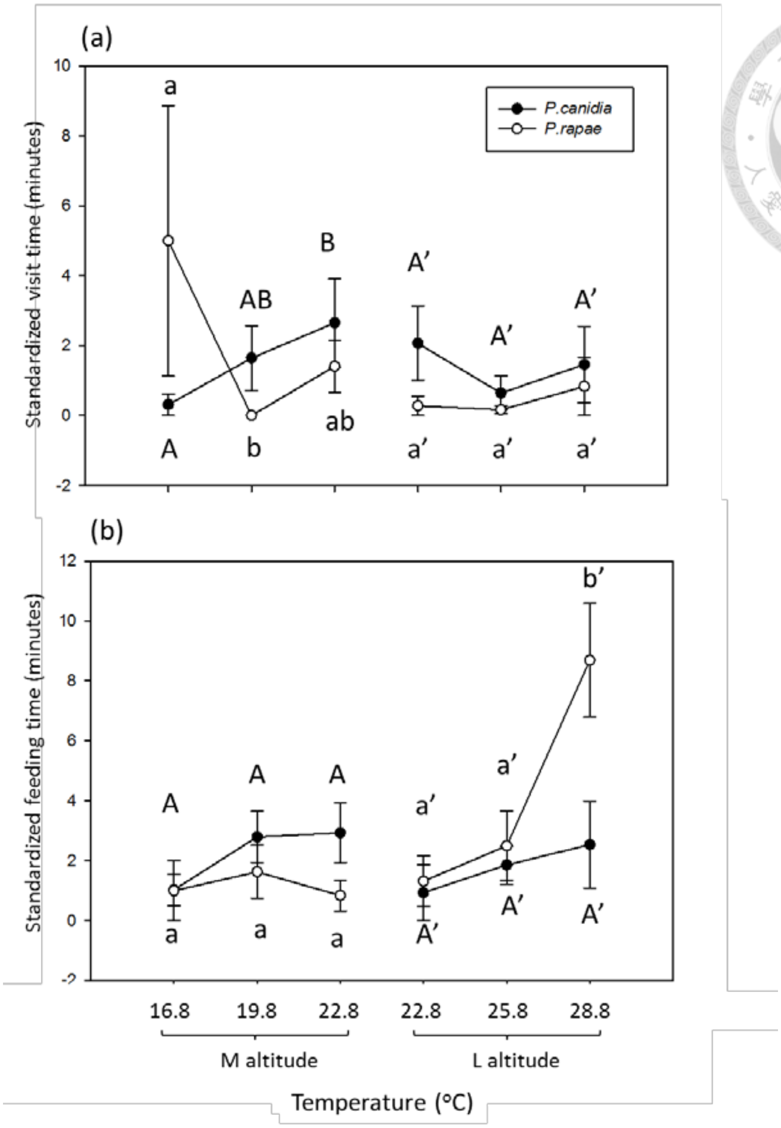

Fig. 10 Warming impact on flower-visiting behavior of *Pieris* on *B. pilosa* across altitude

Pollinators from medium and low altitude were reared in three temperature treatments (control, 3°C warming and 6 °C warming). *Pieris* visit was recorded for 20 minutes. The control temperature was set as 16.8°C and 22.8°C for medium and low altitude, respectively. *P. canadia* and *P. rapae* are indicated with black and white circle, respectively.

(mean ± SE values were given; capitalized letters: represented the comparison of *P. canadia*, small letters: represented the comparison of *P. rapae*, the letters with prime represented the low-altitude *Pieris* and same alphabets mean no significant difference between treatments)

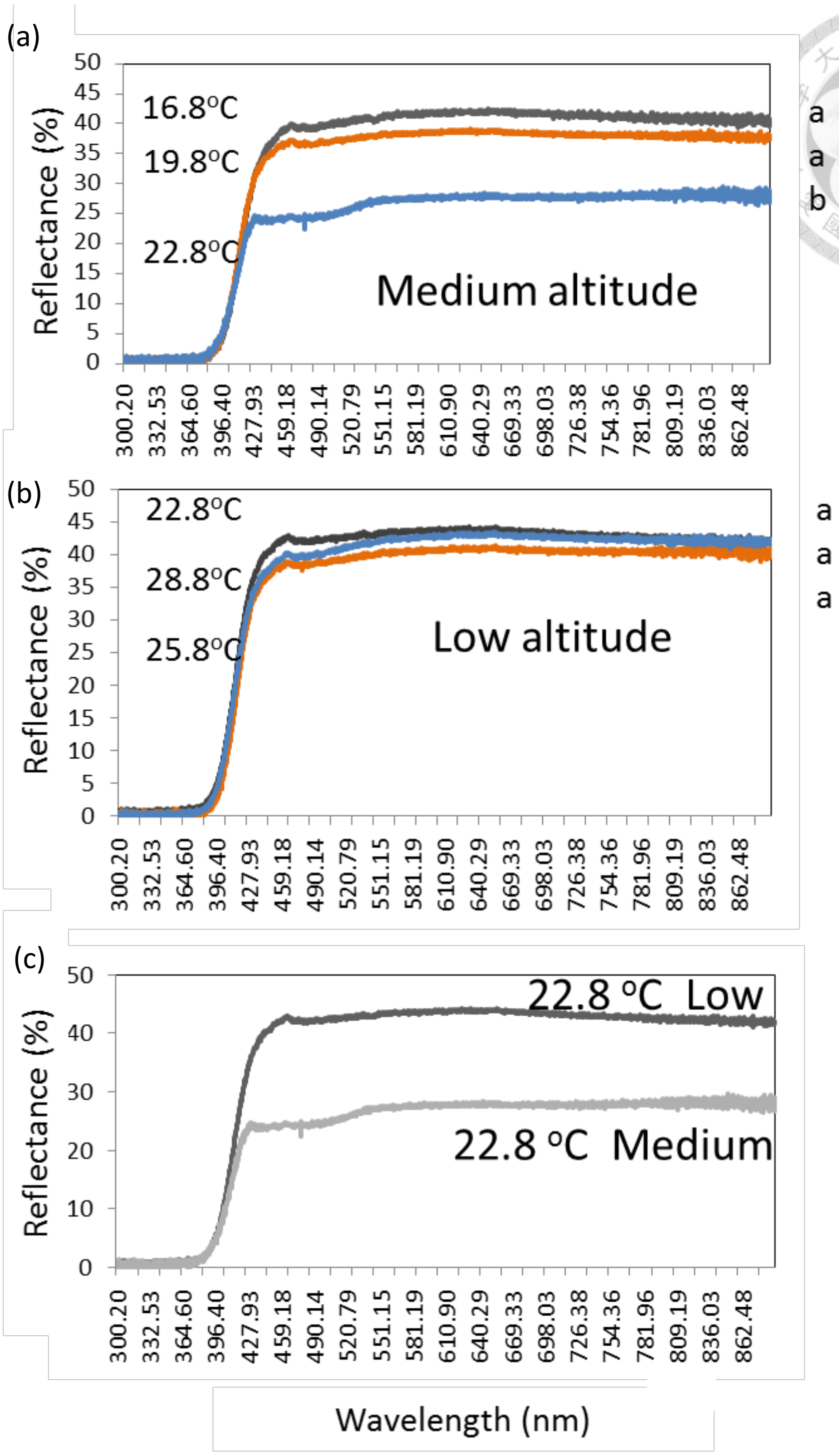

Fig. 11 Warming impact on *B. pilosa* var. *radiata* flower reflectance across altitude
Plants from medium and low altitude were grown in three temperature treatment (control, 3°C warming and 6 °C warming). The control temperature was set as 16.8°C and 22.8°C for medium and low altitude, respectively. Flower reflectance was measured in medium-altitude plant (a) and low-altitude plant (b); the gray line, orange line and blue line were the control treatment, 3°C warming and 6 °C warming from both altitudes, respectively. Lower figure was a comparison between altitudes in common garden (c), dark line represented low-altitude plants and light line represented medium-altitude plants.
(small letters: represented the comparison of *B. pilosa* from each altitude)

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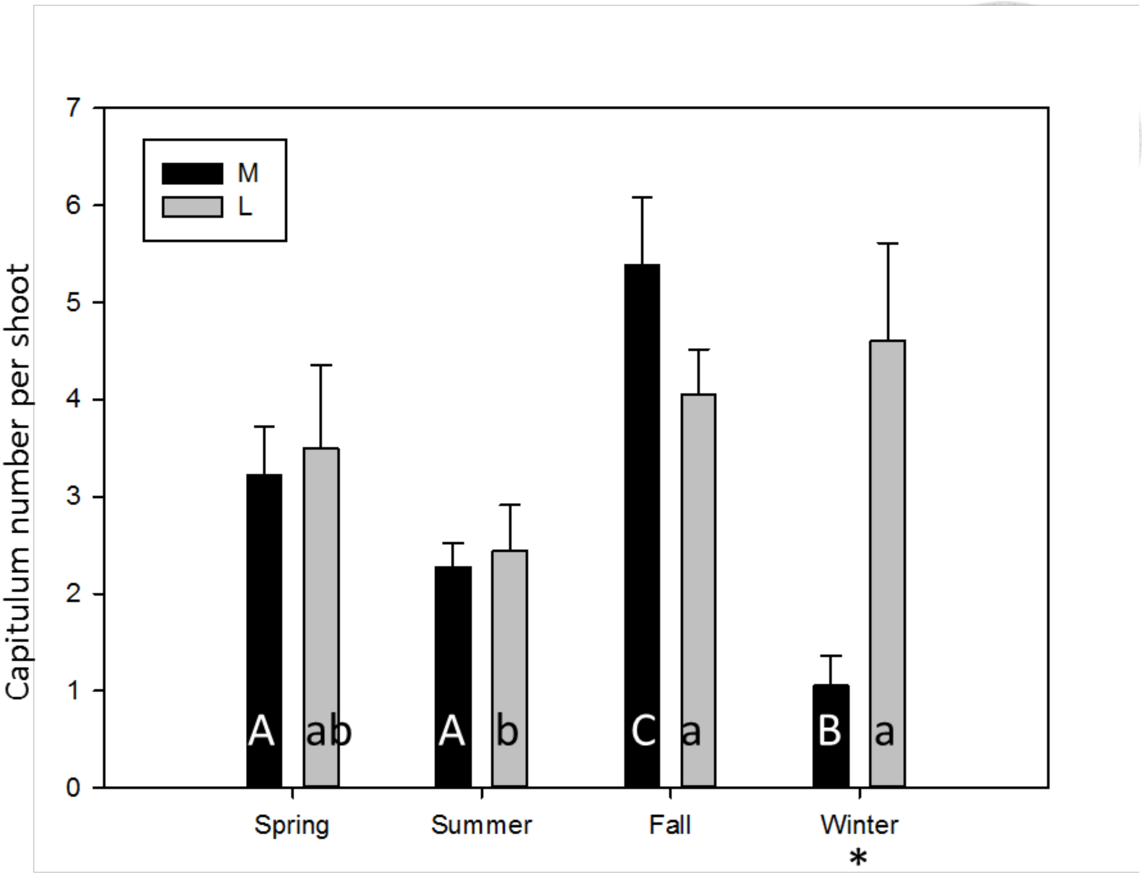

Fig. 12 Field pattern in *B. pilosa* var. *radiata* capitulum number across altitude and season (months)

Capitulum number was recorded at medium and low altitude across season (mean ± SE values were given; *: represented a significant difference between altitudes across season, capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

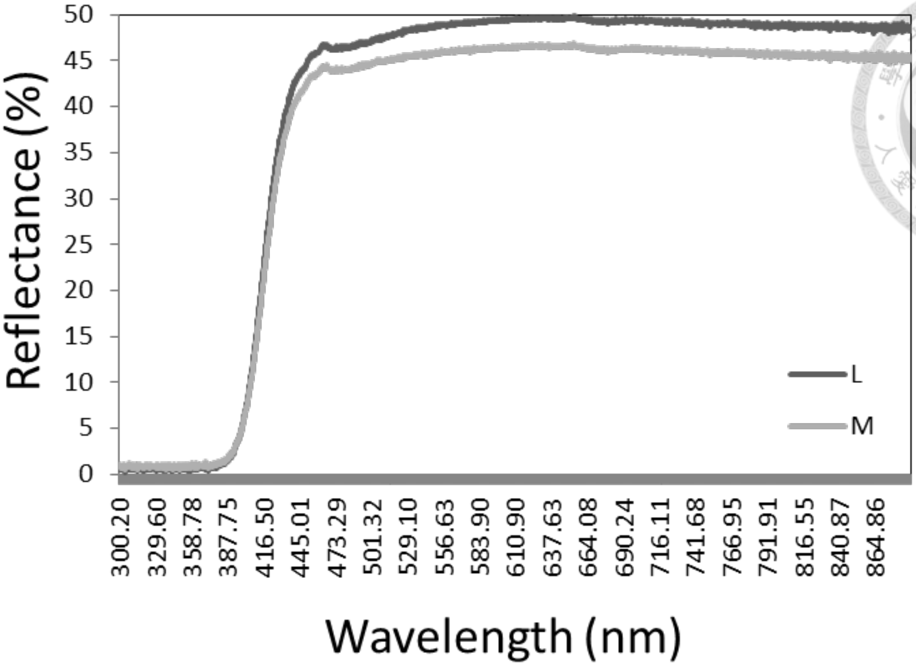

Fig. 13 Field pattern in *B. pilosa* var. *radiata* flower reflectance across altitude
The flowers were collected from field and compared reflectance with low and medium altitude. (dark line represented flower reflectance in low-altitude plants and light line represented flower reflectance in medium-altitude plants)

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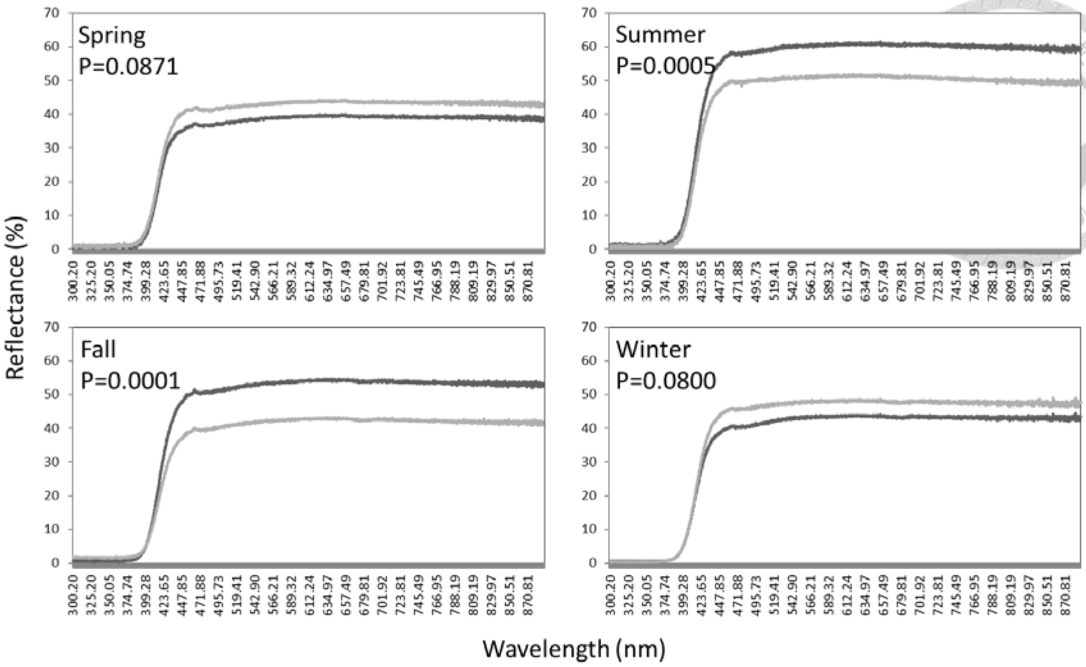

Fig. 14 Field pattern in *B. pilosa* var. *radiata* flower reflectance across altitude and season (months)

The plants of flower reflectance were measured at medium and low altitude across season. The comparison between altitudes in each season, dark line represented flower reflectance in low-altitude plants and light line represented flower reflectance in medium-altitude plants.

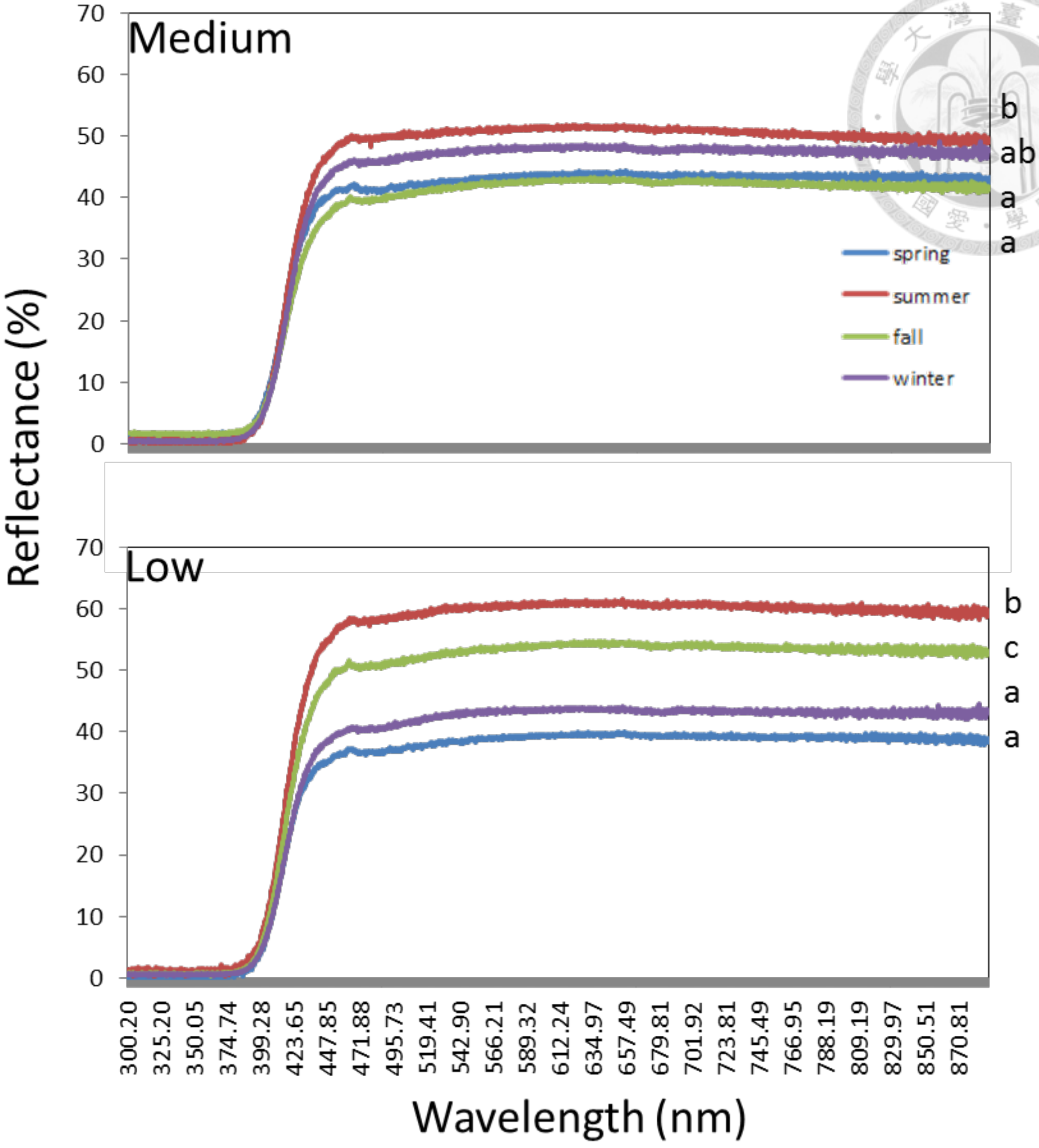

Fig. 15 Field *B. pilosa* var. *radiata* flower reflectance across season (months)
The plants of flower reflectance were measured at medium altitude and low altitude across season.
(different color line represented plant collected from different season, small letters: represented the comparison between medium-altitude plant or between low-altitude plant and same alphabets mean no significant difference)

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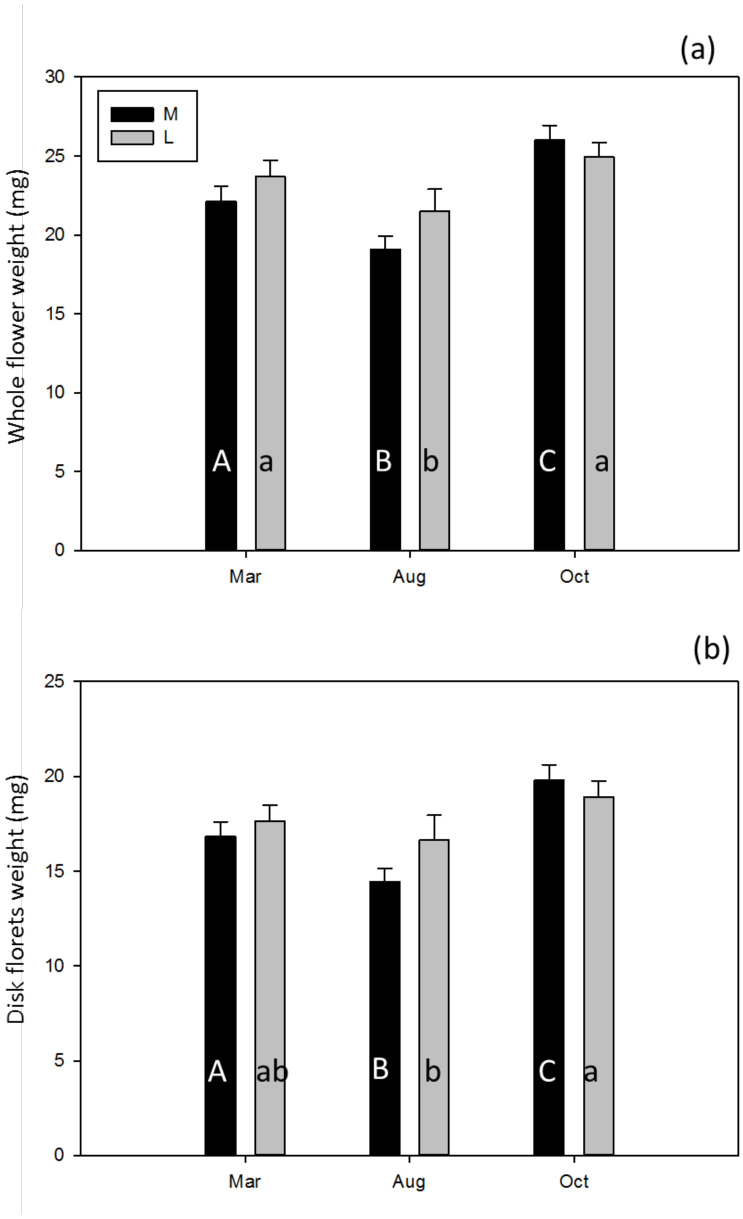

Fig. 16 Field pattern in *B. pilosa* var. *radiata* flower weight across altitude and month
Flower was collected at medium and low altitude across month and weight whole flower per capitulum (included disk florets and receptacle) (a), and only disk florets per capitulum(b).

(mean ± SE values were given; capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

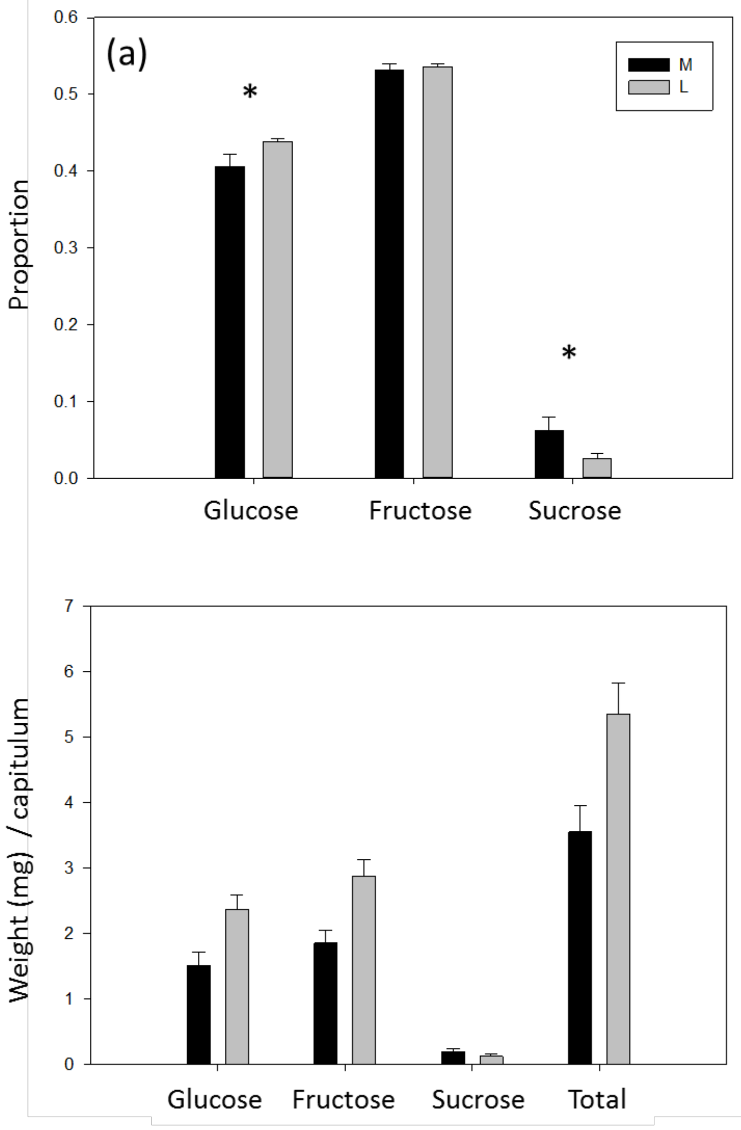

Fig. 17 Field pattern in *B. pilosa* var. *radiata* sugar content across altitude
Sugar was collected from medium- and low-altitude flower and analyzed sugar proportion (a) and weight of sugar content per flower.
(mean ± SE values were given; *: repreasented a siginificant difference between altitudes)

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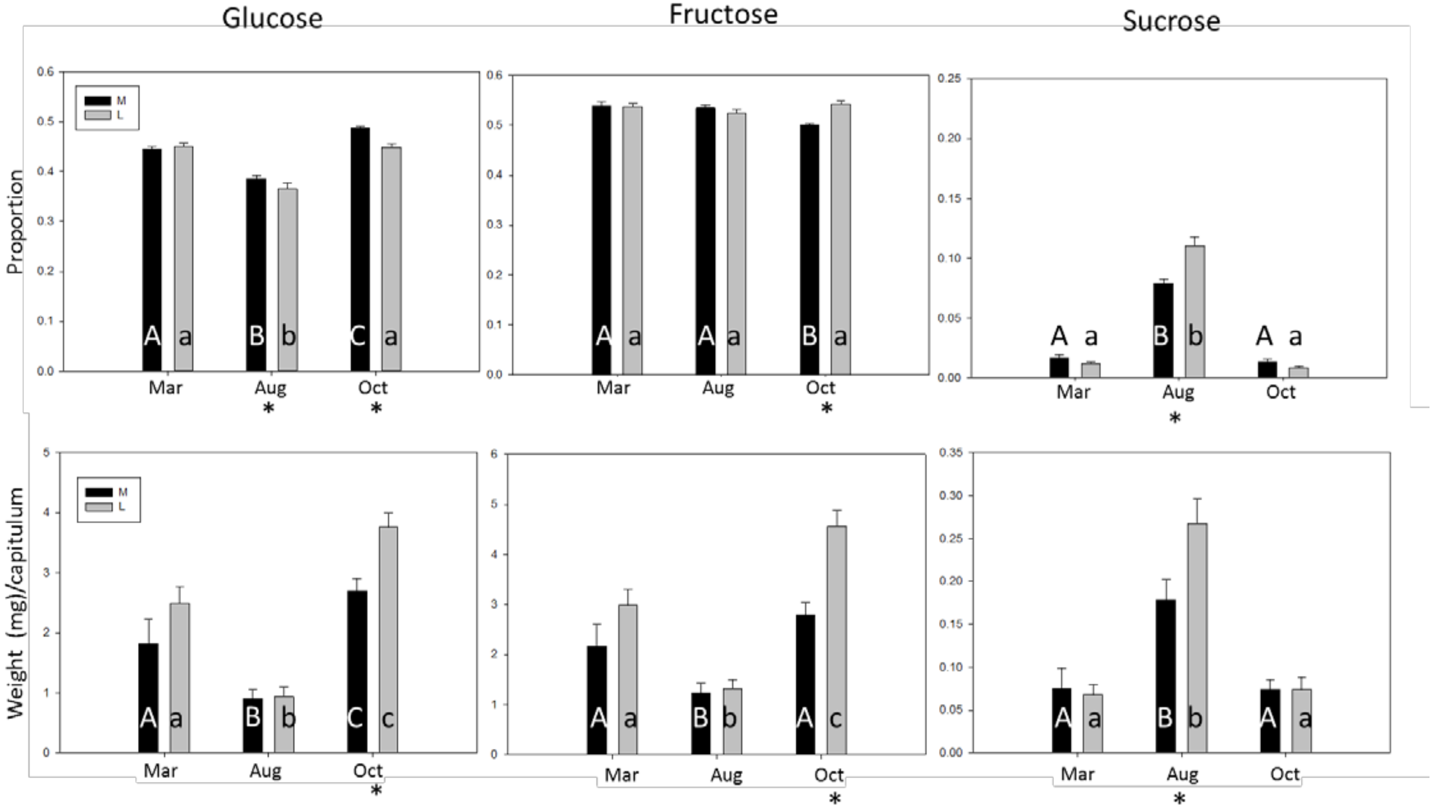

Fig. 18 Field pattern in *B. pilosa* var. *radiata* sugar content across altitude and months in Taoyuan

Sugar was collected from medium- and low-altitude plants across month. Upper three figures are the proportion of each sugar content, and lower three figures are the weight of sugar content per flower.

(mean ± SE values were given; *: represented a significant difference between altitudes across month, capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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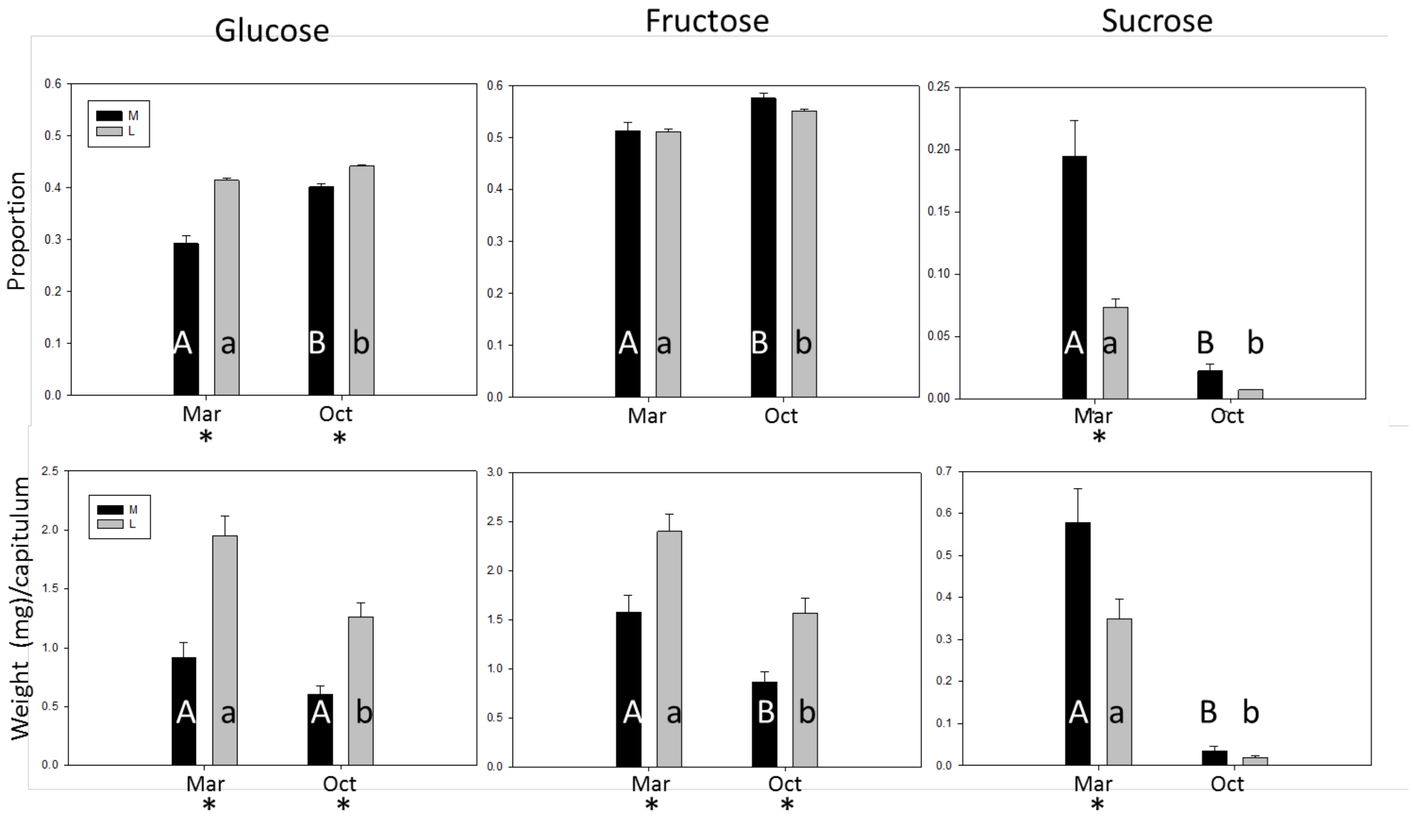

Fig. 19 Field pattern in *B. pilosa* var. *radiata* sugar content across altitude and months in Nantou

Sugar was collected from medium- and low-altitude plant across month. Upper three figures are the proportion of each sugar content, and lower three figures are the weight per flower of each sugar content.

(mean ± SE values were given; *: represented a significant difference between altitudes across month, capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

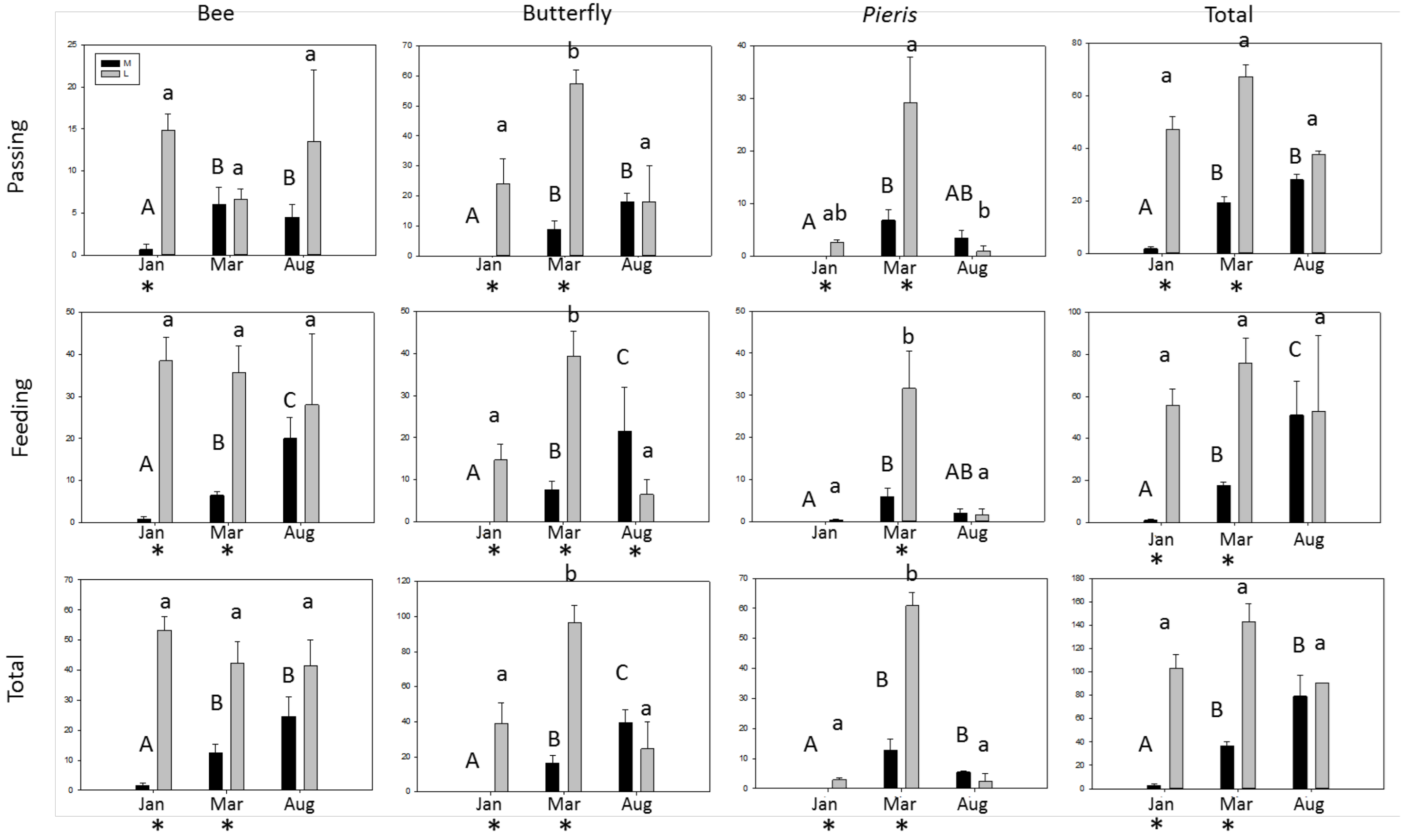

Fig. 20 Field pattern in pollinator density across altitude and months

Observation on 3x3 m^2 *B. pilosa* var. *radiata* from medium and low altitude during 30 minutes, recorded the pollinator to three categories (bees, butterflies and others) and two behaviors (passing and feeding).

(mean ± SE values were given; *: represented a significant between altitudes across month; capitalized letters: represented the comparison of medium-altitude pollinators, small letters: represented the comparison of low-altitude pollinators, same alphabets mean no significant difference between treatments)

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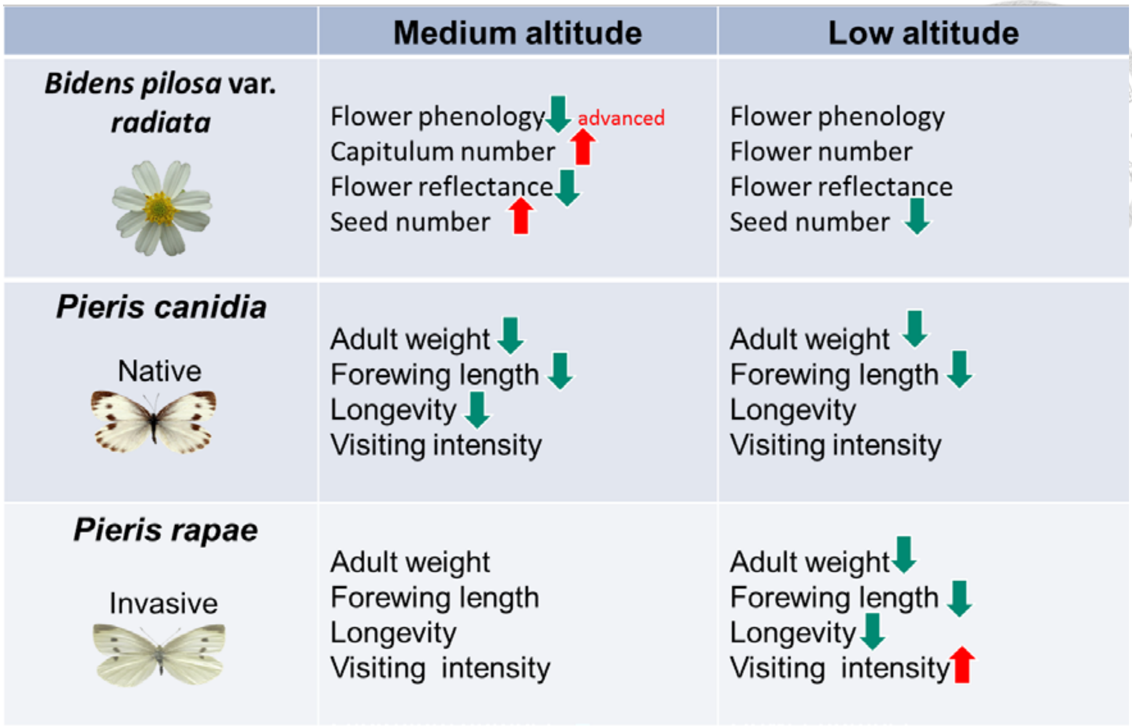

	Medium altitude	**Low altitude**
Bidens pilosa* var. *radiata	Flower phenology↓ advanced Capitulum number ↑ Flower reflectance↓ Seed number ↑	Flower phenology Flower number Flower reflectance Seed number ↓
Pieris canidia Native	Adult weight ↓ Forewing length ↓ Longevity ↓ Visiting intensity	Adult weight ↓ Forewing length ↓ Longevity Visiting intensity
Pieris rapae Invasive	Adult weight Forewing length Longevity Visiting intensity	Adult weight↓ Forewing length ↓ Longevity↓ Visiting intensity↑

Fig. 21 Summary
The simple figure gave a brief summary for warming impact on plant and pollinator across altitude. Warming advanced the flowering, increased capitulum and seed number but decreased flower reflectance of medium-altitude *B. pilosa*. Warming decreased the adult weight, forewing length and adult period of medium-altitude native *Pieris*. Warming decreased the seed number of medium-altitude *B. pilosa*. Warming decreased the adult weight and forewing length of low-altitude *Pieris*, but decreased the adult period and increased the feeding duration of low-altitude invasive *Pieris*.

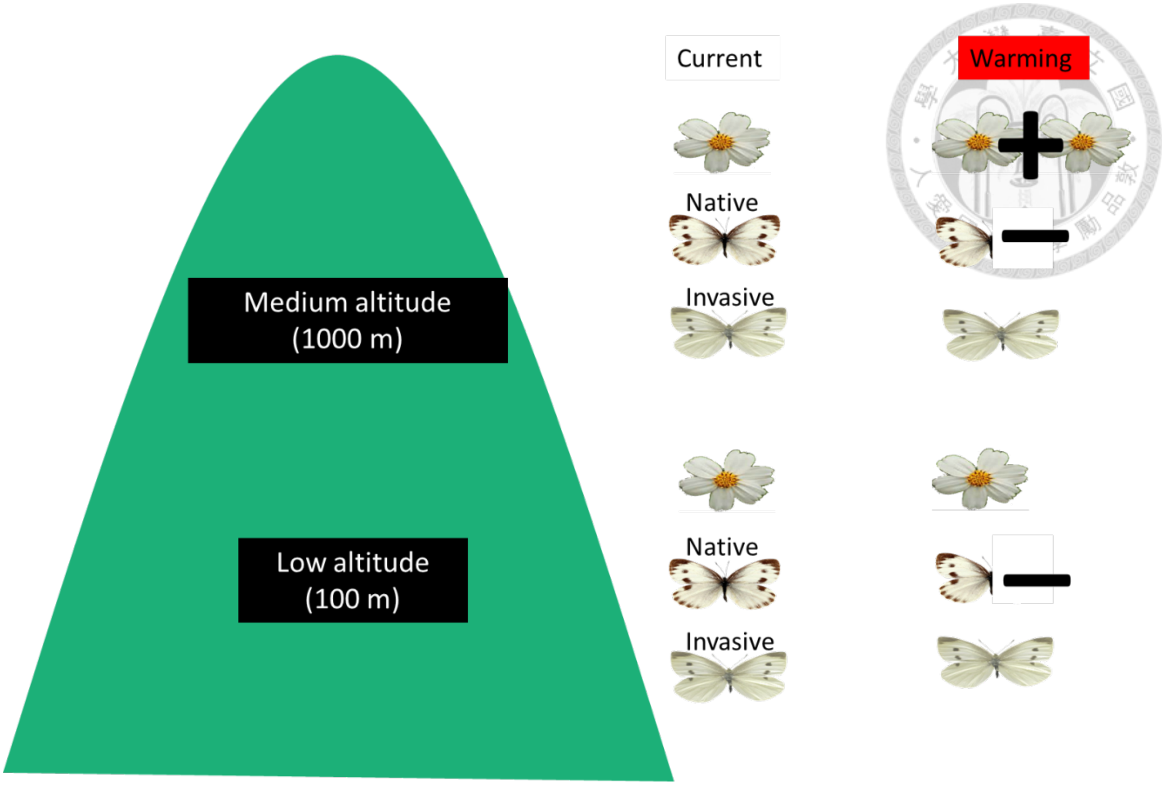

Fig. 22 Mismatch occurred under warming
The figure gave a potential mismatch under warming. For example, warming would take advantage to *B. pilosa* var. *radiata* (e.g. increase capitulum number) but take disadvantage to native *P. canidia* (e.g. decreased adult period) at medium altitude. Thus, the mismatch might occur between plant and pollinator.at medium altitude.

	Spring (March)		Summer (August)		Fall (October)		Winter (January)	
reflectance			L>M		L>M			
Capitulum number							L>M	
Flower weight								
Sur% (tao/nan)		M>L	L>M	▨			▨	
Sur W (tao/nan)		M>L	L>M	▨			▨	
Total W (tao/nan)		L>M		▨	L>M	L>M	▨	
Total *Pieris*	L>M				▨			
Total pollinator	L>M				▨		L>M	

Fig. 23 Plants and pollinators varied with altitude and season (months)
Field survey was conducted at medium and low altitude across month. Empty column represented no difference between altitudes. Gray column represented no field survey in this month.

Appendix

Appendix A: Plant vegetative growth traits

Methods

To examine the impact of altitudinal origin and warming on plant performance, I measured weekly the plant vegetative growth traits (plant height, leaf size, leaf number and leaf chlorophyll content). Plant height was measured from soil surface to the top of leaf. I measured the leaf length and width for three (2nd to 4th from bottom of plant) opened leaves, and calculated the leaf size by formula of ellipse area (abπ, a and b are half of length and width). I calculated the mean leaf size per plant. Each ternate was as one leaf and I counted the number of ternate per plant. Chlorophyll content was measured for three (2nd to 4th from bottom of plant) opened leaves by chlorophyll meter (Chlorophyll Meter SPAD-502), and I calculated the mean chlorophyll content per plant

Before finishing the experiment, I did the destructive measurements (leaf toughness and plant biomass). After fifth month since I sowed the plant which due to most pot was senescent, I measured two to three of the leaf toughness with penetrometer (Chatillon DFEII) and calculated mean leaf toughness per plant. I cut down the plant from the soil surface to divide the plant into above ground and below ground. Both above and below ground of plant were dried at 40 ^{o}C oven for three days at least and weighted the plant biomass.

The seeds collected by artificial pollination were grown in different temperature treatment in order to examine the seed germination.

Results

Warming alone or its interaction with other factors (altitude, weeks) significantly

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affected plant growth, suggesting that warming was an important factor and its effects could vary with altitude over time (Table A1). For example, warming increased the height of medium- and low-altitude plants by 74% and 38 %, respectively (Fig. A1(a, e)). Note that medium-altitude plants were higher than low-altitude ones under the same temperature (i.e. common garden; 22.8 ^{o}C), suggesting a genetic difference in plants across altitude (Fig. A1(i), *P* =0.0005). As for leaf number, warming increased that of medium-altitude plants by 19%, but had no effect on low-altitude plants (Fig. A1(b, f)). Note that medium-altitude plants had more leaves than low-altitude plants in common garden (Fig. A1(j), *P* =0.0017). As for chlorophyll content, warming increased that of medium-altitude plants by 7%, but had no effect on low-altitude plants (Fig. A1(d, h)). Note that medium-altitude plants had higher chlorophyll content than low-altitude plants in common garden (Fig. A1(l), *P* =0.0068). As for leaf size, warming increased that of medium-altitude plants by 22%, but had no effect on low-altitude plants (Fig. A1(c, g)), and plant origin (altitude) did not affect leaf size in common garden (Fig. A1(k), *P* =0.3696).

Leaf toughness and plant biomass, both destructive measurements, were examined when plants were about five-month old. As for leaf toughness, warming decreased that of medium-altitude plants by 30%, but warming (3^{o}C only) actually increased that of low-altitude plants (Table A2, Fig. A2). Plant origin (altitude) did not affect leaf toughness in common garden (*P* =0.2288).

Plant biomass was collected after leaf toughness and divided into above-ground and below-ground biomass (Table A3, Fig. A3). As for total biomass, warming increased that of medium-altitude plant by 46% but had no effect on low-altitude plants. Note that medium-altitude plants had higher total biomass than low-altitude plants in common garden (Fig. A3a, *P* =0.0173). As for above-ground biomass,

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warming overall did not have a strong effect, while warming increased that of medium-altitude plant by 99% but had no effect on low-altitude plants. Note that medium-altitude plants had higher above ground biomass than low-altitude plants in common garden (Fig. A3b, *P* =0.0021). As for below-ground biomass, warming had no effect on medium-altitude plants but decreased that of low-altitude plants by 45%. Note that above ground biomass had no difference across altitude in common garden (Fig. A3c, *P* =0.4804).

The seed of medium-altitude *B. pilosa* under different temperature treatments did not germinate. However, seeds of low-altitude *B. pilosa* under different temperature treatments had 8-50% germination rate.

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Appendix B: Pieris larval stage

Methods

Each newly hatched larva was put in one plastic container (9 cm in diameter and 5 cm in height) with a mesh on the top. Each larva was fed with fresh cabbage (*Brassica oleracea* var. *capitata* L.) as their host plant because *Pieris* used Cabbage as their host plant during autumn to spring which corresponded to the experimental temperature setting. All of the cabbage was grown at the same place to maintain the similar leaf quality, and I selected randomly the leaf of each plant to fed larvae every two days.

I measured the first instar weight by gathering ten individual to get the mean weight for larvae. I weighed larvae for each individual from second to fifth instar every two days, especially weighted when they became the next instar. After larvae entered 5th instar, I collected their old skin and measured the head width (4th instar). Besides, I also recorded the pupation and eclosion date which can calculate the larval period, pupal period and adult period.

Results

Pieris rapae

Warming impact on the larval weight of *P. rapae* varied with altitude (Table 4, Fig. A4). This study continuously measured the body weight of *Pieris* larvae. Warming increased the 2nd weight of medium-altitude *P. rapae* by 63%, but had no effect on low-altitude ones. Warming increased the 3rd weight of medium- and low-altitude *P. rapae* by 67% and 57%, respectively. Warming increased the 4th weight of medium- and low-altitude *P. rapae* by 21 and 31%, respectively. Warming did not affect the 5th weight of both medium- and low-altitude *P. rapae*. In common garden experiments, low-altitude *P. rapae* had heavier 2nd, 3rd and 4th body weight than medium-altitude ones (2nd, *P* <0.0001; 3rd, *P* =0.0001; 4th, *P* =0.0062). Warming and altitude origin did not affect the head width of *P. rapae* (4th instar) (Table A4).

Pieris canidia

Warming impact on the larval weight of *P. canidia* varied with altitude (Table 4, Fig. A4). Warming had no effect on the 2nd weight of medium-altitude *P. canidia*, but increased low-altitude ones by almost 2 folds. Warming decreased the 3rd weight of medium-altitude *P. canidia* by 23%, but had no effect on low-altitude ones. Warming had no effect on the 4th weight of both medium- and low-altitude *P. canidia*. Warming (3°C) increased the 5th weight of medium-altitude *P. canidia*, but had no effect on low-altitude ones. In common garden experiments, low-altitude *P. canidia* had lighter 2nd and heavier 3rd instar weight than medium-altitude ones. (2nd, *P* =0.0166; 3rd, *P* =0.0180). Warming and altitude origin did not affect the 4th head width of *P. canidia* (Table A4).

Native vs. invasive

While native *Pieris* had heavy larval weight than invasive *Pieris* (Table 4, Fig. A4). As for larval weight, the native *Pieris* was usually heavier than the invasive *Pieris*, but warming impact on their larval weight may vary with species and altitude. For example, warming increased the difference between the native and invasive *Pieris* in 2nd instar weight at low altitude, but did not do so at medium altitude (Fig. A4). Warming decreased the difference between the native and invasive *Pieris* in 3rd and 4th instar weight at both altitudes. However, warming increased the difference between the native and invasive *Pieris* in 5th instar weight at both altitudes. Native *Pieris* had larger head width than invasive *Pieris* (4th instar) (Table A4).

Appendix C: Flower analysis

Sugar

For nectar content experiments, I collected *B. pilosa* flowers from field at low and medium altitude. Fresh capilulum were lyophilized and stored in the -20 ^{o}C refrigerator to avoid enzyme activity. Due to higher individual difference of sugar volume between flowers, the capitulum was separated the disk florets and receptacle in order to had higher efficiency to abstract the nectar. The flower was weight and calculated the ratio of disk florets and whole flower (both of disk florets and receptacle). The disk florets was distributed randomly to the receptacle based on the ratio and put in a 50ml centrifuge tube together. Added 5ml 85 ^{o}C purified water and covered the top. Put the tube in shaker incubator with 50 ^{o}C shook 7 minutes with 150 rpm. Put in centrifuge with 4000 rpm for 3 minutes, and then abstracted in 50ml volumetric flask. Repeated the method above for 4 times to get the 20ml totally and qualified to 50ml and mixed. The mixture was put in 15ml centrifuge tube and frozen in refrigerator to tested by HPAEC-PAD (ICS3000, Thermo Scientific™ Dionex™ , California Sunnyvale, USA).

Appendix D: Weather information

The weather data collected from field during sugar analysis had varied spatially and temporally. As for the spatial variation in Taoyuan (Fig. A8), both mean temperature and diurnal temperature variation were higher at low altitude than medium altitude in March, August and October. Humidity was higher at medium altitude than low altitude in August and October. As for the temporal variation at low altitude, temperature and temperature variation were higher in August. At medium altitude, temperature was higher in August, and temperature variation was similar across months. Humidity had no difference across month at both medium and low altitude. The patterns in weather varied across sites (Fig. A9).

In addition, the weather data collected from field during pollinator density observation also had varied spatially and temporally. (Fig. A10). As for the spatial variation, mean temperature was higher at low altitude than medium altitude in January, March and August. Diurnal temperature variation was higher at low altitude than medium altitude in August. Humidity was higher at medium altitude than low altitude in January, March and August. As for the temporal variation at both medium and low altitude, temperature and humidity was higher in August and March, respectively. Diurnal temperature variation had no difference across month at both medium and low altitude.

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Table A1. Warming impact on *B. pilosa* var. *radiata* growth traits across altitude

Plant vegetative growth traits (plant height, leaf number, leaf size and chlorophyll content) were measured weekly under 3 temperature treatments (control, 3^{o}C and 6 ^{o}C warming) across altitude (low and medium) and analyzed with repeated measures ANOVA. The P values were given, and bold value represented a significant difference ($p<0.05$).

Plant traits	**Factors**							
	N	**Altitude**	**Temperature**	**Week**	**Alt.*Temp.**	**W.*Alt.**	**W.*Temp.**	**W.*Alt.* Temp.**
Height	144	**0.0092**	**<0.0001**	**<0.0001**	**0.0038**	0.2846	**<0.0001**	**0.0067**
Leaf number	144	**0.0055**	**0.0097**	**<0.0001**	0.0695	**<0.0001**	**0.0031**	**0.0010**
Leaf size	144	**0.0228**	0.0987	**<0.0001**	**0.0256**	**0.0138**	**0.0326**	**<0.0001**
CHL	144	**0.0138**	**0.0047**	**<0.0001**	0.0601	**0.0004**	**<0.0001**	**0.0382**

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Table A2. Warming impact on *B. pilosa* var. *radiata* leaf toughness across altitude
The leaf toughness was measured under 3 temperature treatments (control, 3°C and 6 °C warming) across altitude (low and medium) and analyzed with GLMM. The leaf toughness was collected at end of experiment. The P values were given, and bold value represented a significant difference ($p<0.05$).

		Factors		
Plant traits	**N**	**Altitude**	**Temperature**	**Alt.*Temp.**
Leaf toughness	126	0.4556	**<0.0001**	**0.0016**

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Table A3. Warming impact on *B. pilosa* var. *radiata* plant biomass across altitude
The plant biomass was measured under 3 temperature treatments (control, 3^{o}C and 6 ^{o}C warming) across altitude (low and medium) and analyzed with GLMM. The plant biomass was measured at the end of experiment. The P values were given, and bold value represented a significant difference ($p<0.05$).

Plant traits	**N**	**Factors**		
		Altitude	**Temperature**	**Alt.*Temp.**
Total	139	0.4020	0.1345	0.1265
Above-ground	139	0.3509	**0.0003**	**0.0471**
Below-ground	139	**0.0002**	**0.0410**	0.0673

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Table A4. Warming impact on *Pieris* head width across altitude

The 4th head width of species (*P. canidia, P. rapae)* was measured under 3 temperature treatments (control, 3^{o}C and 6 ^{o}C warming) across altitude (low and medium) and analyzed with GLMM. The P values were given, and bold value represented a significant difference ($p<0.05$).

					Factors			
***Pieris* 4th head width**	**N**	**Species**	**Temperature**	**Altitude**	**Sp.*Temp.**	**Sp.*Alt.**	**Temp.*Alt.**	**Sp.*Temp. *Alt.**
	311	**<0.0001**	0.4507	0.8143	0.7331	0.4733	0.3172	0.8718

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Table A5. Stage specific life table of *P. rapae*

Temp.	Life stage	# survival	# died	Mortality	Mortality rate for each stage	Average days
medium						
16.8	Larva	3	21	0.875	7	44
	Pupa	3	0	0	0	21
	Adult	3	0	0	0	9
19.8	Larva	20	4	0.167	0.2	23
	Pupa	20	0	0	0	14
	Adult	19	1	0.042	0.053	10
22.8	Larva	24	0	0	0	17
	Pupa	24	0	0	0	10
	Adult	24	0	0	0	10
low						
22.8	Larva	22	2	0.083	0.091	22
	Pupa	22	0	0	0	10
	Adult	22	0	0	0	12
25.8	Larva	24	0	0	0	19
	Pupa	24	0	0	0	8
	Adult	22	2	0.083	0.091	7
28.8	Larva	16	8	0.333	0.5	12
	Pupa	16	0	0	0	7
	Adult	16	0	0	0	7

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Table A6. Stage specific life table of *P. canidia*

Temp.	Life stage	# survival	# died	Mortality	Mortality rate for each stage	Average days
medium						
16.8	Larva	32	2	0.059	0.063	27
	Pupa	32	0	0	0	22
	Adult	32	0	0	0	14
19.8	Larva	30	2	0.063	0.067	19
	Pupa	29	1	0.031	0.035	14
	Adult	29	0	0	0	13
22.8	Larva	29	5	0.147	0.172	19
	Pupa	29	0	0	0	10
	Adult	28	1	0.029	0.036	11
low						
22.8	Larva	26	10	0.278	0.385	26
	Pupa	25	1	0.028	0.04	11
	Adult	25	0	0	0	9
25.8	Larva	33	3	0.083	0.091	19
	Pupa	31	2	0.056	0.065	9
	Adult	29	2	0.056	0.069	9
28.8	Larva	33	3	0.083	0.091	18
	Pupa	31	2	0.056	0.065	7
	Adult	38	3	0.083	0.079	7

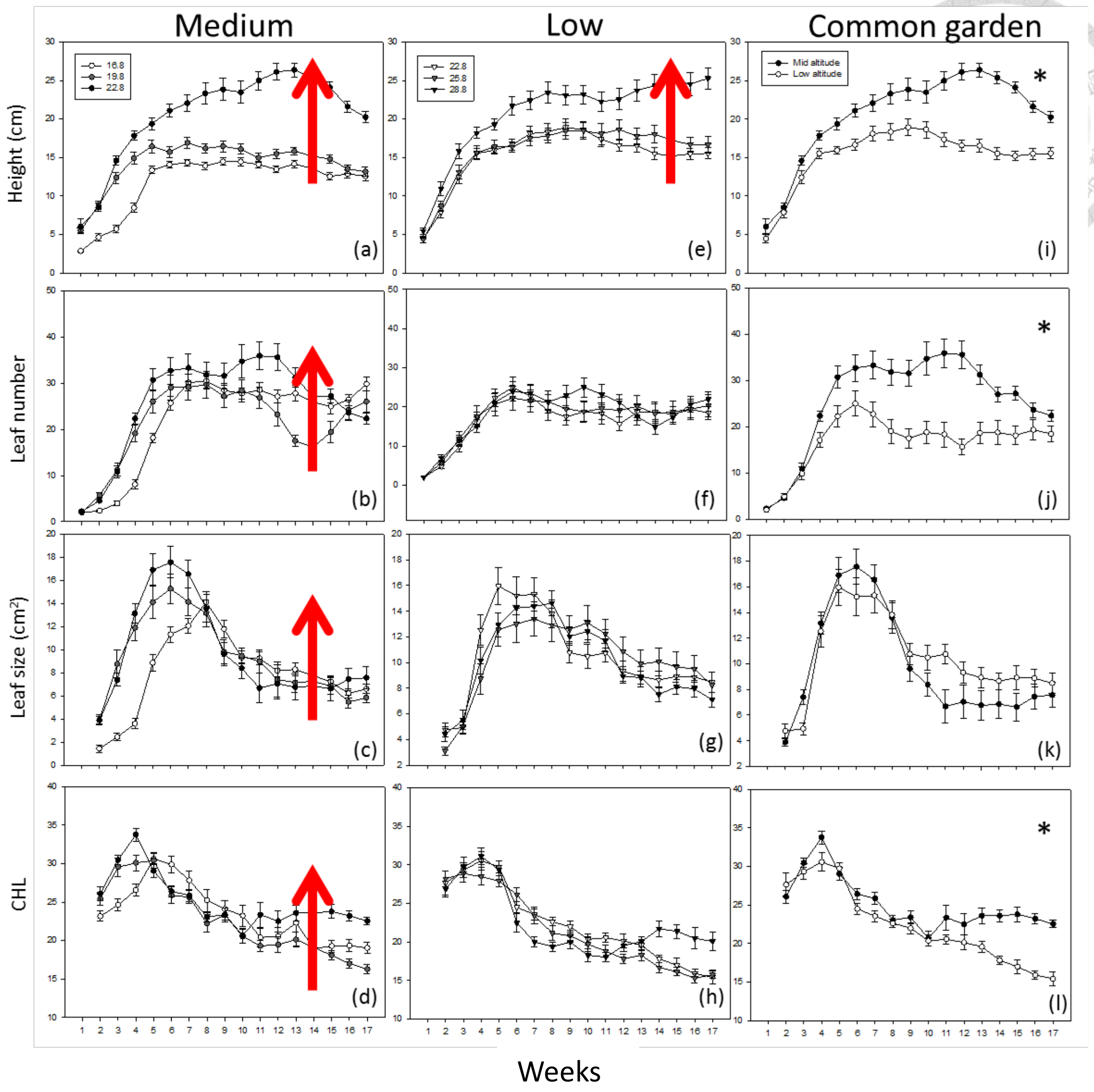

Fig. A1 Warming impact on *B. pilosa* var. *radiata* growth traits across altitude
Plants from medium and low altitude were grown in three temperature treatment (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively. Plant traits were measured weekly from medium- and low-altitude plant. Plant height, leaf number, leaf size and chlorophyll content (CHL) varied with temperature across altitude. Left three figures was medium-altitude plants (fig. 1a-d), middle three figures was low-altitude plants (fig. 1e-h) and right three figures was plants in common garden (fig.1 i-l).
(mean ± SE values were given; *: represented a significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C); arrows: represented a significant difference to warming)

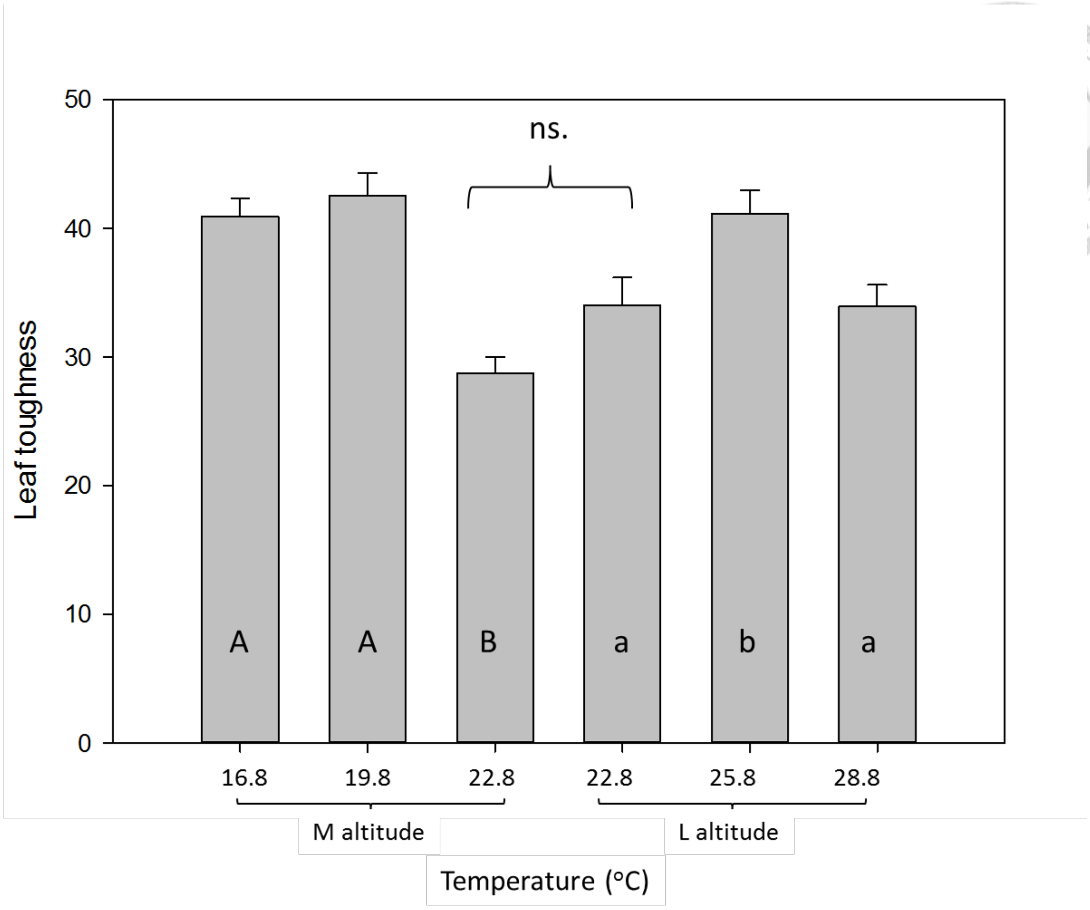

Fig. A2 Warming impact on *B. pilosa* var. *radiata* leaf toughness across altitude

Leaf toughness was measured until the fifth month. Plants from medium and low altitude were grown in three temperature treatment (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively.

(mean ± SE values were given; ns. : represented no significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C); capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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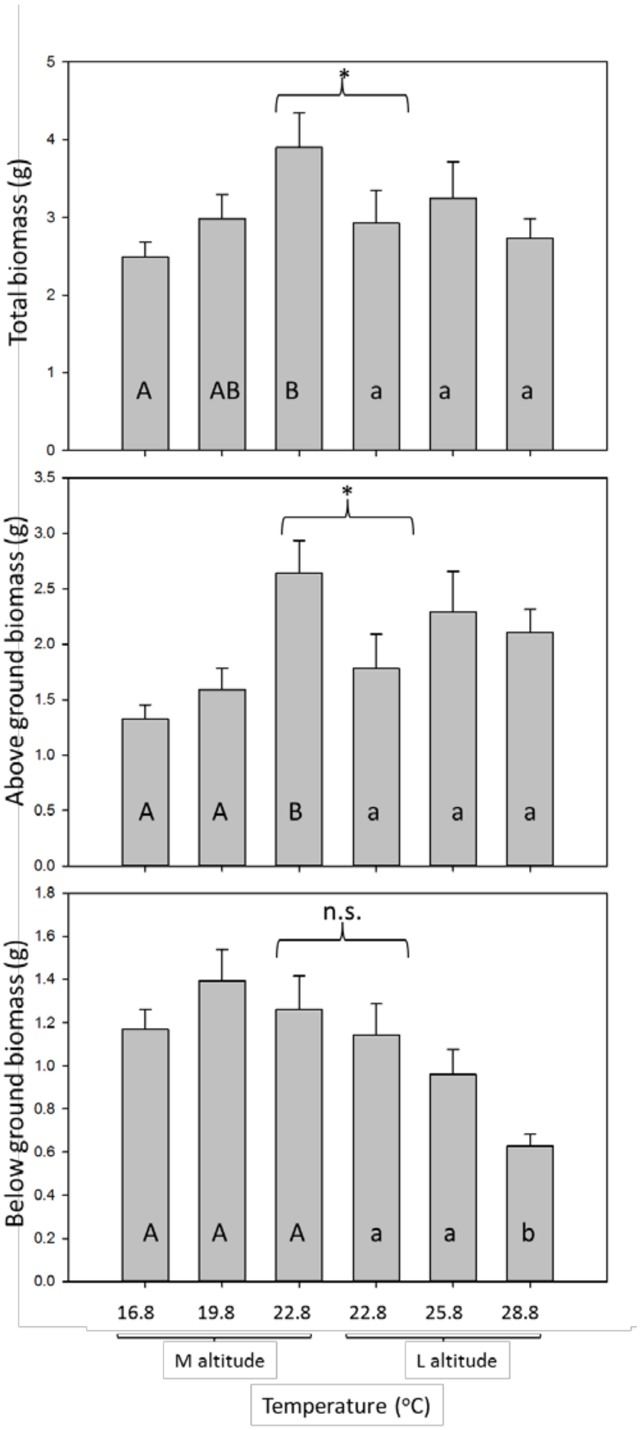

Fig. A3 Warming impact on *B. pilosa* var. *radiata* plant biomass across altitude

Plant biomass was collected until the fifth month and divided by above and below ground. Plants from medium and low altitude were grown in three temperature treatment (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively.

(mean ± SE values were given; ns. :represented no significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C), *: represented a significant difference between altitudes in common garden treatment; capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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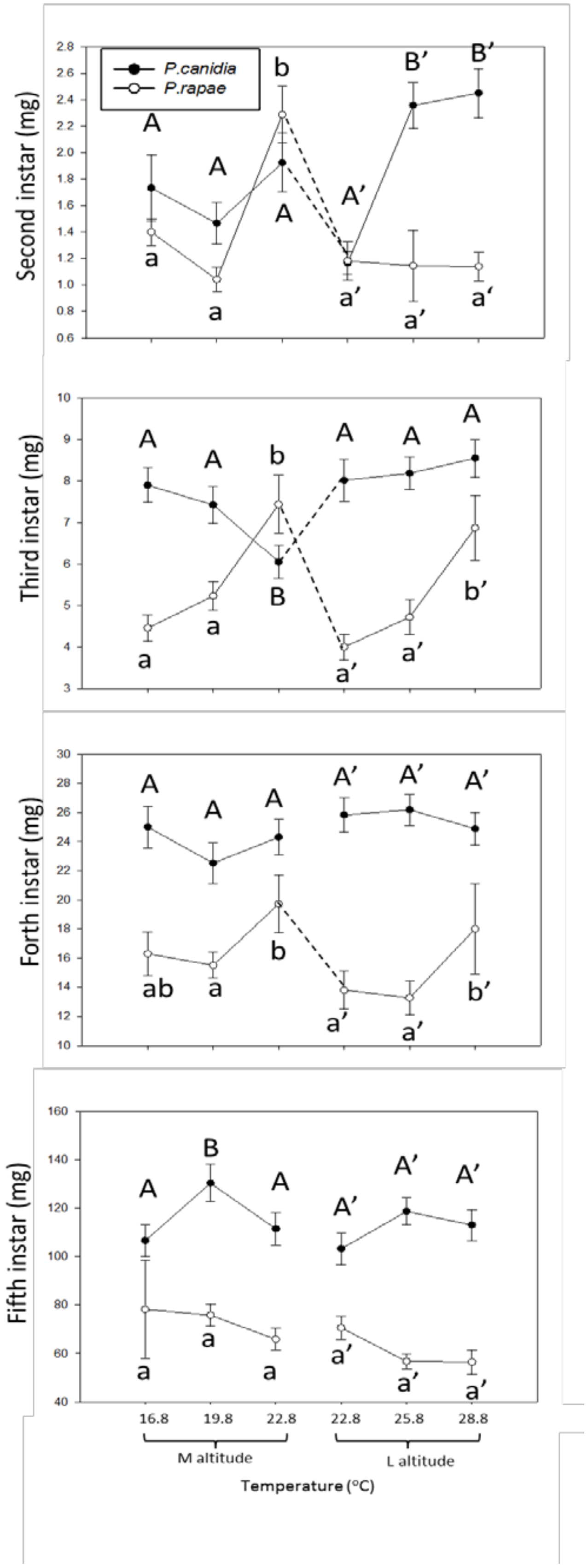
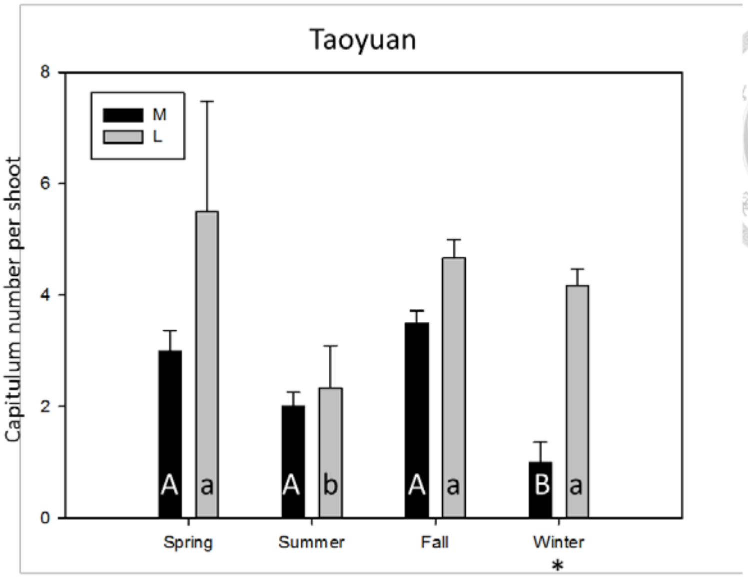


Fig. A4 Warming impact on *Pieris* larva weight at each life stage across altitude

Caterpillar of pollinator from medium and low altitude reared in three temperature treatments (control, 3^{o}C warming and 6 ^{o}C warming). The control temperature was set as 16.8^{o}C and 22.8^{o}C for medium and low altitude, respectively. *P. canadia* and *P. rapae* are indicated with black and white circle, respectively.

(mean ± SE values were given; dash line : represented a significant difference between altitudes in common garden treatment (i.e. 22.8 ^{o}C), capitalized letters: represented the comparison of *P. canadia*, small letters: represented the comparison of *P. rapae*, the letters with prime represented the low-altitude *Pieris* and same alphabets mean no significant difference between treatments)



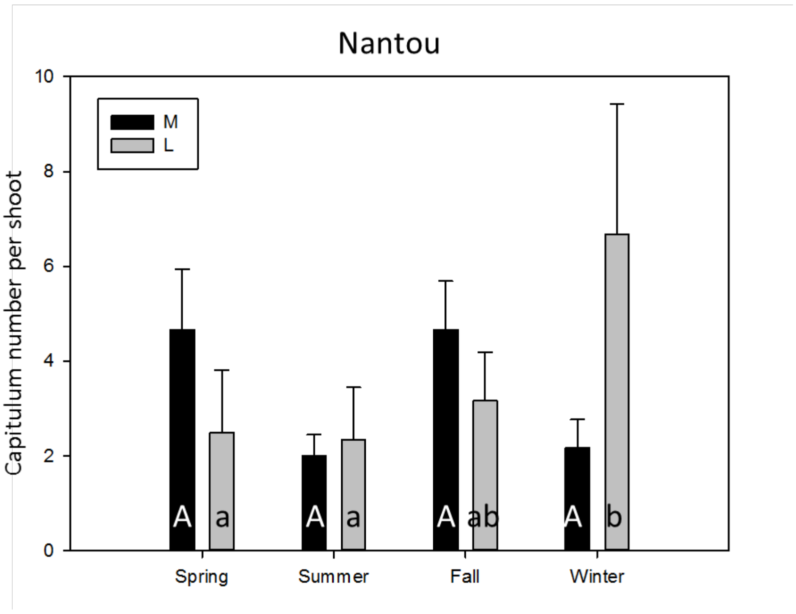


Fig. A5 Field pattern in *B. pilosa* var. *radiata* capitulum number across altitude and season (months)

Capitulum number was recorded at medium and low altitude across season in Taoyuan and Nantou.

(mean ± SE values were given; *: represented a significant difference between altitudes across season, capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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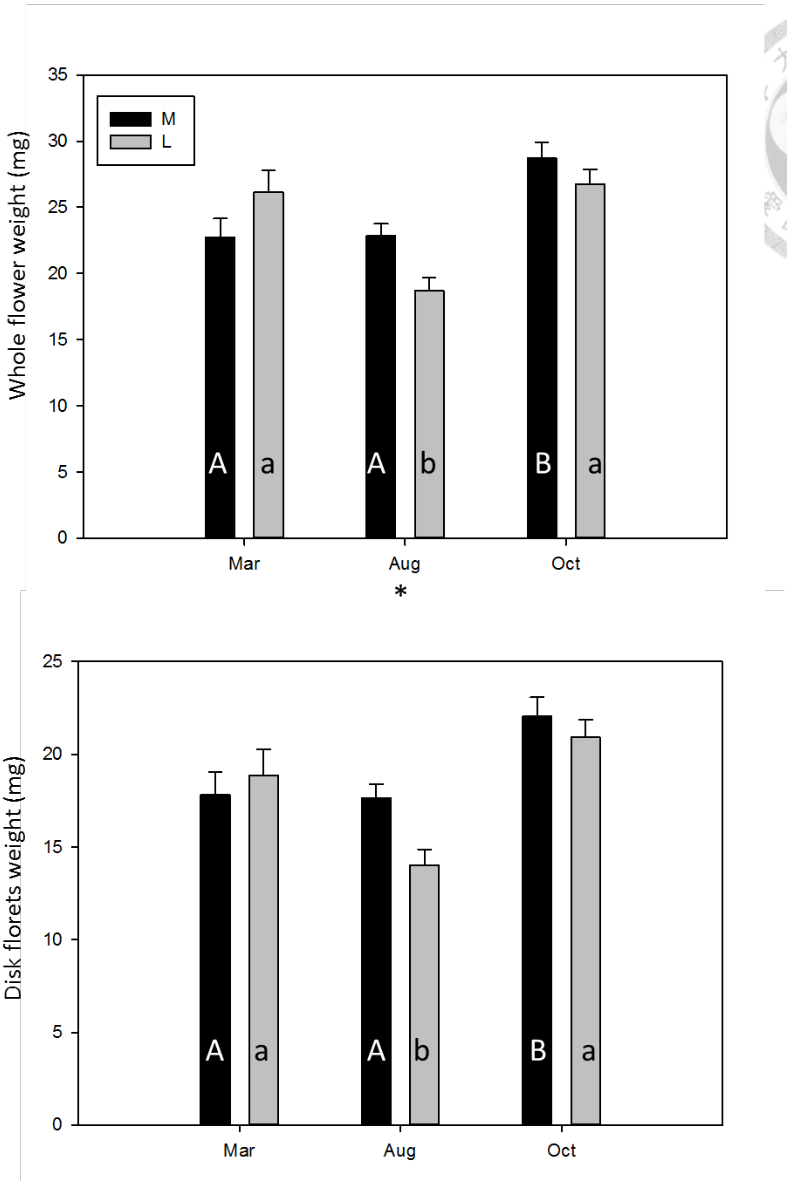

Fig. A6 Field pattern in *B. pilosa* var. *radiata* flower weight across altitude and months in Taoyuan

Flower was collected at medium and low altitude across month, and weighted whole flower weight per capitulum and disk florets weight per capitulum.

(mean ± SE values were given; *: represented a significant difference between altitudes across month; capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

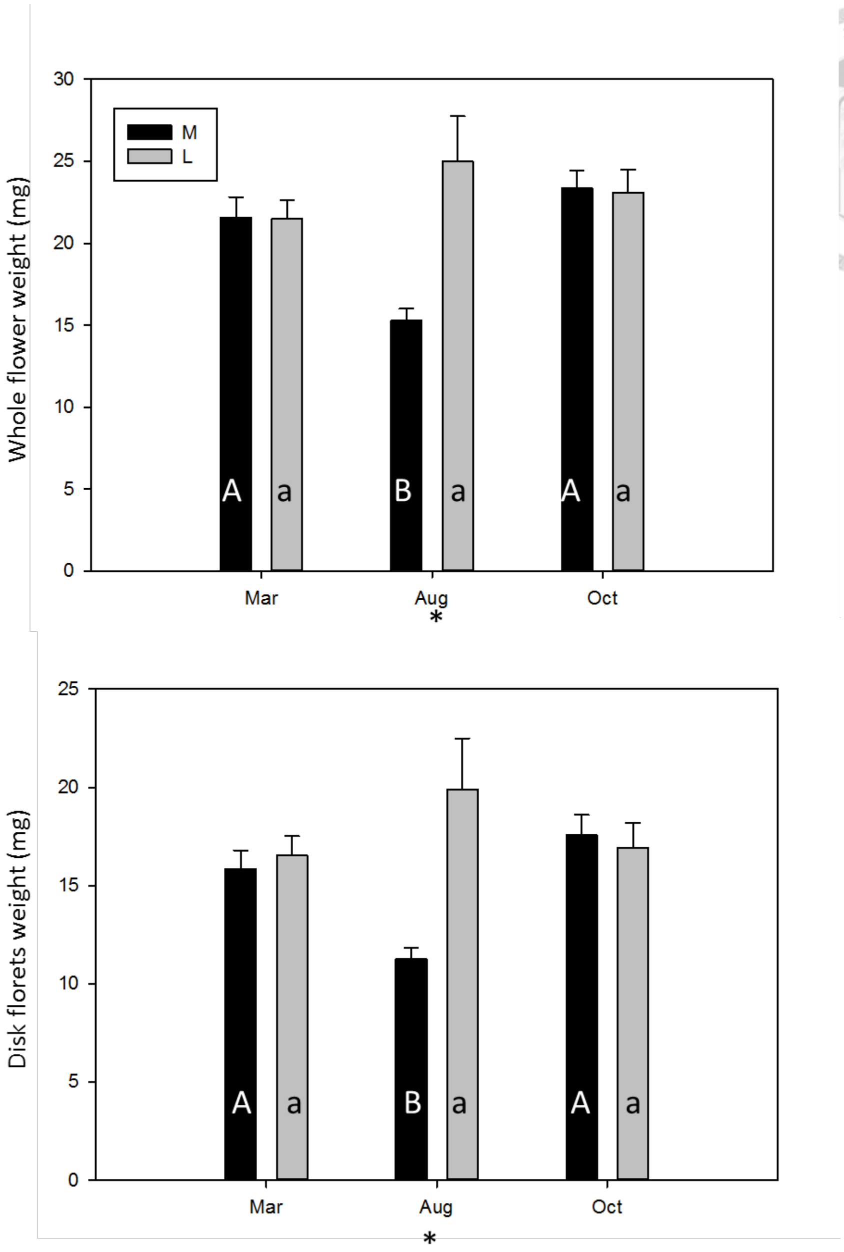

Fig. A7 Field pattern in *B. pilosa* var. *radiata* flower weight across altitude and months in Nantou

Flower was collected at medium and low altitude across month, and weighted whole flower weight per capitulum and disk florets weight per capitulum.

(mean ± SE values were given; *: represented a significant difference between altitudes across month; capitalized letters: represented the comparison of medium-altitude plants, small letters: represented the comparison of low-altitude plants, same alphabets mean no significant difference between treatments)

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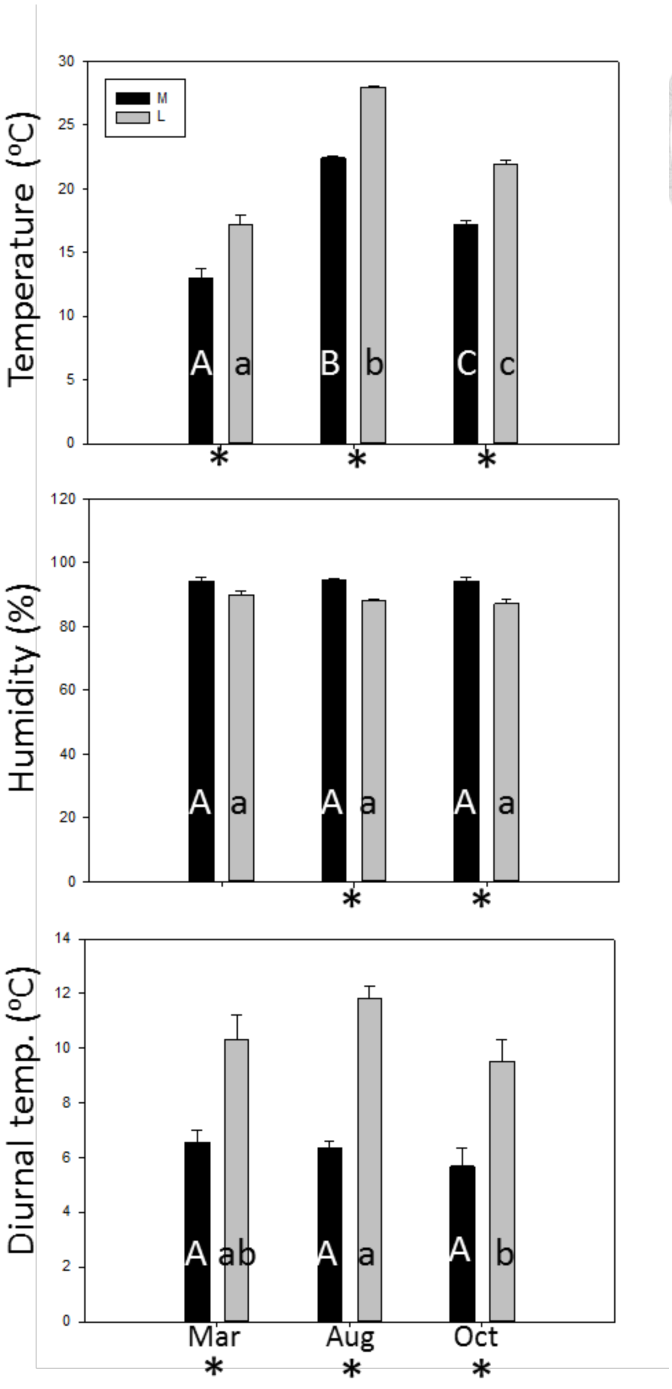

Fig. A8 Weather information during sugar collection in Taoyuan
The weather data was recorded at medium and low altitude with month in Taoyuan for temperature, humidity and diurnal temperature variation.
(mean ± SE values were given; *: represented a significant difference between altitudes across month, capitalized letters: represented the comparison of medium-altitude weather, small letters: represented the comparison of low-altitude weather, same alphabets mean no significant difference)

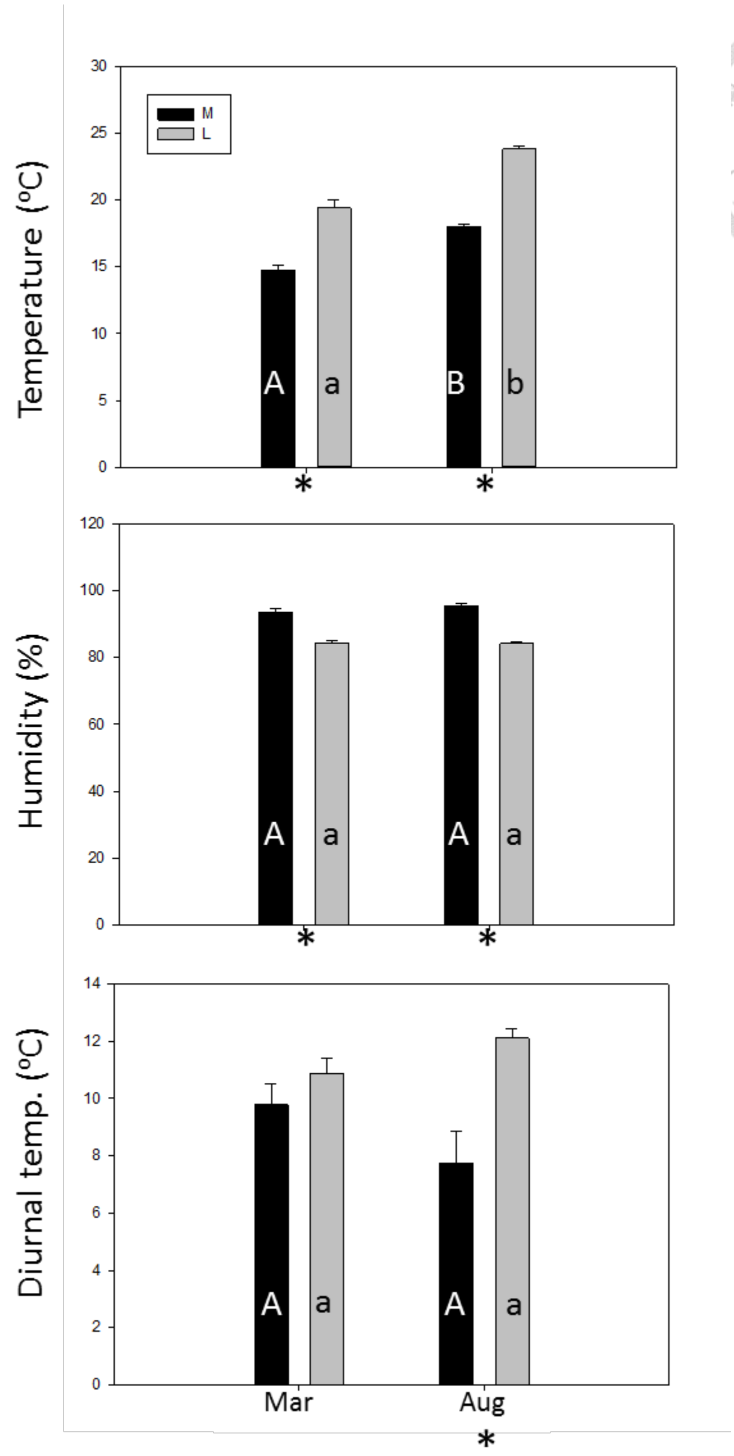

Fig. A9 Weather information during sugar collection in Nantou

The weather data recorded at medium and low altitude with month in Nantou for temperature, humidity and diurnal temperature variation.

(mean ± SE values were given; *: represented a significant difference between altitudes across month, capitalized letters: represented the comparison of medium-altitude weather, small letters: represented the comparison of low-altitude weather, same alphabets mean no significant difference)

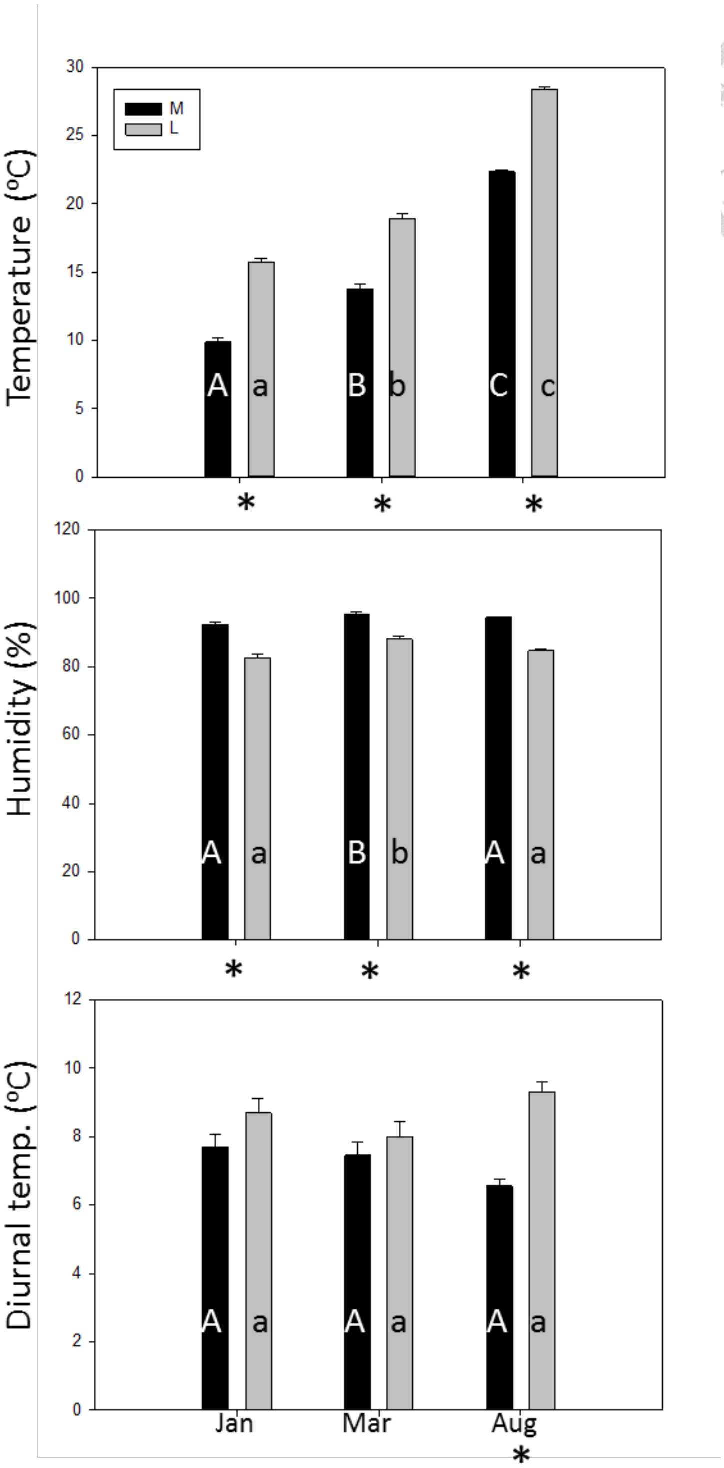

Fig. A10 Weather information during pollinator density observation
The weather data was collected from medium and low altitude with month during the pollinator density observation for temperature, humidity and diurnal temperature variation.
(mean ± SE values were given; *: represented a significant difference between altitudes across month, capitalized letters: represented the comparison of medium-altitude weather, small letters: represented the comparison of low-altitude weather, same alphabets mean no significant difference).

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