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Patterns of flower morphology and sexual systems in the subnival belt of the Hengduan Mountains, SW China

De-Li Peng · Zhi-Qiang Zhang · Bo Xu · Zhi-Min Li · Hang Sun

Abstract The adaptations of alpine plants that enable them to survive in extreme environments are hotly debated. Floral traits are likely important since they are usually considered as evolutionary adaptations to pollinators, and thus to play a key role in the reproductive success of plants. In the subnival belt of the Hengduan Mountains (a globally important biodiversity hotspot with extreme environmental conditions in southwest China) plants show diverse floral morphologies. However, information on the flower diversity of this unique alpine ecosystem is scarce, especially at the regional scale. Therefore, using published information, herbarium collections and field observations, we have studied the sexual system and floral morphology of plants in the subnival belt of the Hengduan Mountains. Of the 823 species recorded in the region, 88.5 % are hermaphroditic (a particularly high proportion compared to floras of other regions). The flower morphology patterns indicate that showy flowers (attracting pollinators) and generalized floral traits (suited to a wide range of pollinators) are common in our study region. Some floral traits were clearly associated with each other among specialized flowers as well as among generalized ones. Our results identify key reproductive features of plants in the subnival belt of the Hengduan Mountains, and show how these plants might optimize their probability of pollination and thus maintain reproductive success. The study provides a foundation for further research on floral adaptation and plant–pollinator relationships in the study region.

Keywords Alpine · Floral traits · Hengduan Mountains · Sexual systems · Subnival belt

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Introduction

Floral traits, including color, shape, display size and symmetry, are thought to reflect plant adaptations to pollinators (e.g., Waser 1983; Stanton et al. 1986; Nilsson 1988; Dafni and Kevan 1997; Neal et al. 1998). In addition, flower or floral morphology can affect pollinator behavior and pollen transfer efficiency, and thus influence the reproductive success of plants (Harder and Barrett 1995). However, in addition to pollinators, various other factors seem to have influenced the evolution of floral morphology, including the abiotic environment and floral herbivory (Faegri and van der Pijl 1979; Fenster et al. 2004; Mao and Huang 2009). Alpine climates are generally harsh: characterized by low air temperatures, high solar radiation, strong winds and overcast conditions or high precipitation (at least relative to lower areas nearby). Several recent studies have demonstrated that such abiotic factors have played important roles in the evolution of floral morphology in alpine habitats (e.g., Bynum and Smith 2001; Wang et al. 2010). For example, the development of pendulous flowers and erect fruits in *Anisodus luridus* appears to have been an important

adaptation to several abiotic aspects of its hostile alpine environments (Wang et al. 2010). The harshness and variability of alpine environments also make them less-suited for insect-pollination. Hence, a number of studies from around the world have found that insect pollinator diversity, abundance, and activity often progressively decline with increasing elevation above the timberline (Arroyo et al. 1982, 1983). In addition, pollinator assemblages tend to shift from specialized species to more generalized species with increasing altitude (reviewed in Arroyo et al. 2006; Makrodimos et al. 2008). A generalized plant pollination strategy would be expected to evolve when pollinators are rare or variable (Waser et al. 1996), thus small, open or actinomorphic flowers might be favored by alpine plants, for example, zygomorphic flowers are often visited by only one type of pollinator, while the simpler structure of actinomorphic flowers allows them to be generally visited, and pollinated, by diverse groups of pollinators (Richards 1997). Accordingly, several previous studies have reported that alpine plants have predominantly open flowers (Warren et al. 1988; Totland 1993), allowing them to be visited by generalist pollinators rather than specialists. This has been interpreted as an adaptation to unpredictable pollination conditions in alpine environments (Rathcke 1988). Actually, there is limited empirical data to support that.

Breeding systems are among the most important plant floral traits, and there is a general hypothesis that selfing rates of alpine plants should increase with increasing altitude (García-Camacho and Totland 2009; Körner and Paulsen 2009). Under this hypothesis, hermaphroditic species (the precondition for self-pollination), could be favored in alpine vegetation. As most unisexual flowers are obligate outcrossers and many rely on insect visitors, unisexual flower occurrence should decrease with increases in elevation because of associated reductions in insect diversity, abundance and activity. Accordingly, Vamosi and Queenborough (2010) found that relative proportions of monoecious species decline with altitude in the forests of Costa Rica. However, Arroyo and Squeo (1990) showed that the proportion of dioecious species increases with elevation in Chilean Patagonia.

A second, contrasting hypothesis, the increased pollination probability hypothesis, postulates that increases in flower showiness or flower longevity may compensate for the scarcity of pollinators in high alpine regions (reviewed in Fabbro and Körner 2004; Arroyo et al. 2006). More effective pollination may also offset the decreased pollinator availability in alpine ecosystems (Bingham and Orthner 1998). If so, selection may favor specialized and showy flowers. In accordance with these predictions, many alpine plants have large and colorful flowers. Further, Fabbro and Körner (2004) found that high altitude species allocated three times higher proportions of their above-ground biomass to floral

structures than lowland species. As illustrated by these contrasting hypotheses, the origins of floral morphology patterns in alpine vegetation are still strongly debated.

The Hengduan Mountains have all the altitudinal belts that are common to the southeast part of Qinghai-Tibet Plateau, which is widely regarded as a global biodiversity hotspot due to its high endemism and species diversity (Myers et al. 2000). The subnival belt is the highest vertical zone of vegetation, and it is characterized by extreme environmental conditions including a short growing season, frequent frosts during the vegetative period, and low pollinator activity (Körner 2003). Analyses of relationships between reproductive traits and selection agents should ideally be conducted at the community level or at relatively large scales (reviewed in Hegland and Totland 2005). However, most previous community- or large-scale studies on plant reproductive traits have focused on tropical regions (reviewed in Chen and Li 2008a). In contrast, very few such studies have been conducted in alpine communities (Arroyo et al. 1982, 1983; McCall and Primack 1992), especially in the mountainous regions of China (but see Gong and Huang 2009, 2011).

In this study, we examined the floral morphology, sexual systems and life-forms of plants in the subnival belt of the Hengduan Mountains, based on a survey of 823 angiosperm species. We had two main objectives: (1) to characterize patterns of flower morphology and presumed pollination systems; (2) to determine the frequency distributions of hermaphroditic, monoecious and dioecious sexual systems and quantify the association of sexual systems with life-forms.

Materials and methods

Study region

The Hengduan Mountains cover ca. 364,000 km^2, from 24°84′ to 34°80′N, 96°82′ to 104°83′E, in northwestern Yunnan, western Sichuan, southeastern Tibet, southeastern Qinghai and southwestern Gansu, SW China (Li 1987; Fig. 1). Six mountain chains and major rivers cross the region from north to south, in sharp contrast to other major Chinese mountains and rivers, which run from west to east. The average elevation within the region decreases from west to east and from north to south. The climate of the Hengduan Mountains is affected by the high altitude zephyr circulation and the Indian and Pacific Ocean monsoon circumfluence, which result in distinctly dry and wet seasons. The wet season extends from mid-May to October, with peak precipitation occurring in June–August and, correspondingly, the dry season extends from October to mid-May. The subnival belt is the transition zone between alpine meadows

Fig. 1 The geographical location of the Hengduan Mountains, SW China

and the nival belt, and its average altitude is usually above 4,300 m. Snowfields, moraines, dry scree slopes, rocky outcrops, and rock fissures are common borders of the subnival belt. Usually, snow cover persists from late October to mid-May, and the flowering season lasts from mid–late May to early–mid September. Climatic data for the subnival belt of the Hengduan Mountains are scarce, although some data are available from a meteorological station situated at 28°23′N, 99°01′E, 4,290 m a.s.l. in the Baima Mountains, part of the Hengduan Mountain chain. Annual precipitation recorded here from 1982 to 1984 amounted to 680–790 mm, with means of 30 mm in May, 130 mm in June and 500 mm between July and September (Zhang 1998). In addition, Yang et al. (2010) recorded an annual average air temperature of −1.0 °C, and a mean difference in temperature between the coldest and the warmest months of ca. 15 °C at Lakaka Pass in the Baima Mountains. Due to the diversity of showy flowers, such as *Primula*, *Rhododendron*, *Meconopsis*, *Paraquilegia*, *Gentiana*, *Saxifraga*, *Cremanthodium*, *Saussurea*, and *Delphinium*, the subnival belt of the Hengduan Mountains has been described as an 'Alpine garden'.

Data collection

The data set used for this study was mainly based on a checklist of the seed plants from the subnival belt of the Hengduan Mountains (Xu 2010). The checklist covered species that have been found in the subnival belt, based on herbarium specimens, published floras and field photographs. In total, 823 flowering plant species were included in our survey. Information on the plants' reproductive

characteristics was mainly based on published information (Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita 1958–2002; Institutum Botanicum Kunmingense Academiae Sinicae Edita 1975–2002), observations of specimens in the Herbarium collection at the Kunming Institute of Botany, Chinese Academy of Sciences (KUN), field observations, and personal communications with other taxonomists.

Floral morphology and specialization level

Across all species, we recorded 16 floral morphological features in seven categories (floral size, floral color, flower shape, floral symmetry, floral clustering, floral orientation and showiness), as follows. (1) Following the scheme described by Chen and Li (2008a, b), the floral diameter of each species was classified as large (>1 cm), medium (0.5–1 cm) or small (<0.5 cm). In most cases, the information on floral size was obtained from the literature, but we also measured the floral diameter of living specimens in the field, or specimens in the herbaria. Each capitulum of the Asteraceae was treated as a flower. It should be noted that the flower size of a few species may be larger than we measured because flowers of some specimens may have shrunk as a result of dehydration. (2) We distinguished four color types of the most attractive parts of the flowers as observed with the human eye: blue-purple, pink-red, yellow, or white. If floral color information was not consistent on labels of examined specimens we recorded colors of wild flowers in pictures; possible discrepancies of such kinds may have affected data for species with numerous polymorphs, but should have had no effect on the findings for monomorphic

species. (3) The flower shape of each species was classified as open (including open inflorescences) or tubular (including semi-tubular flowers, and pendular flowers, e.g., those of the Labiatae and *Campanula* spp., respectively). Massed groups of tubular flowers that insects could exploit without entering the corolla tube (e.g., those of the Asteraceae) were classified as open flowers. (4) In terms of floral symmetry, we classified species as having zygomorphic or actinomorphic flowers. Asteraceae were included as actinomorphic species following the classification scheme described by Hegland and Totland (2005). (5) Individual florets that were grouped together (e.g., those of the Asteraceae and Umbelliferae), forming a single floral display that could be easily observed in the field were regarded as an inflorescence; others were considered as solitary flowers. (6) We distinguished three categories of floral orientation, based on the flowers' orientation relative to the horizontal axis: upward, horizontal, or downward. The orientation of the majority of florets among each inflorescence was considered the floral orientation of the inflorescence. (7) Finally, species with brightly colored (blue-purple or pink-red) inflorescences, or brightly colored large (or medium-sized) solitary flowers were considered as having large, showy flowers.

The presence of specific or complex flowers has been suggested to reflect the behavioral constraints associated with narrow pollinator groups. Following methods of Gong and Huang (2011), we used their data and defined solitary flowers, large floral size (large and medium), bright color (blue-purple and pink-red), zygomorphic, and tubular morphologies as specialized floral traits. The type of sexual system was not used to assess the level of flower specialization. A measure of flower specialization (FS, hereafter) was calculated from: $FS = N_s/N_i$, where N_s and N_i are the numbers of specialized and investigated floral traits, respectively. If the FS of a species was more than 0.5, we defined the species as having specialized floral morphology, if FS was less than 0.5 it was classified as having generalized flower morphology, and FS values of 1 and 0 indicate absolute specialization and generalization of plant floral morphology, respectively.

Sexual systems

All species were classified into one of three sexual systems: (1) hermaphrodite, when all flowers found on plants of the species were bisexual; (2) dioecy (including androdioecy, gynodioecy and trioecy), when female and male flowers were found on separate individuals, and (3) monoecy (including andromonoecy, gynomonoecy and polygamonoecy), when separate male and female flowers (unisexual) were found on the same individual (Bawa 1980; Endress 1994; Gross 2005). Characterization of floral

sexuality was largely based on a meticulous literature search of published floras. When the sexual system of a species could not be determined from the literature we examined specimens in the herbaria or observed plants in the field.

Life-forms

The plant species were predominately perennial herbs and low shrubs, therefore the species were classified as herbs (including annual and biennial species) or shrubs.

Data analysis

The distribution of sexual systems according to life-forms were compared by Chi-square test. The null hypothesis for all comparisons was that the frequency distribution of sexual systems in a life-form was not significantly different from the distribution of the entire flora studied here. We tested the degree to which taxonomic level contributed to differences in floral colors and sizes. Floral traits that we tested included floral size, floral shape, floral symmetry, floral clustering and floral orientation.

Results

Taxonomic representation

The survey included 823 species belonging to 41 families and 133 genera. Based on Xu (2010), the 10 largest families were Asteraceae, Saxifragaceae, Brassicaceae, Papaveraceae, Caryophyllaceae, Ranunculaceae, Orobanchaceae Gentianaceae, Primulaceae, and Ericaceae, which accounted for 48.1 % of all surveyed species (116, 74, 71, 58, 44, 41, 40, 39, 31, and 31 species, respectively). Endemic species of the Hengduan Mountains accounted for 65.7 % of the 10 families. The ten biggest genera were *Saxifraga*, *Corydalis*, *Saussurea*, *Pedicularis*, *Arenaria*, *Salix*, *Gentiana*, *Rhododendron*, *Primula* and *Cremanthodium*, which accounted for 43.4 % of all species (73, 45, 45, 40, 32, 28, 28, 27, 21 and 19 species, respectively). Moreover, the following genera endemic to the Hengduan Mountains accounted for 2.3 % of all species: *Sinolimprichtia*, *Sinoleontopodium*, *Syncalathium*, *Baimashania*, *Coelonema*, *Dipoma*, *Hemilophia*, *Shangrilaia* and *Przewalskia*. Moreover, 44 genera (33.1 %) were each represented by a single species.
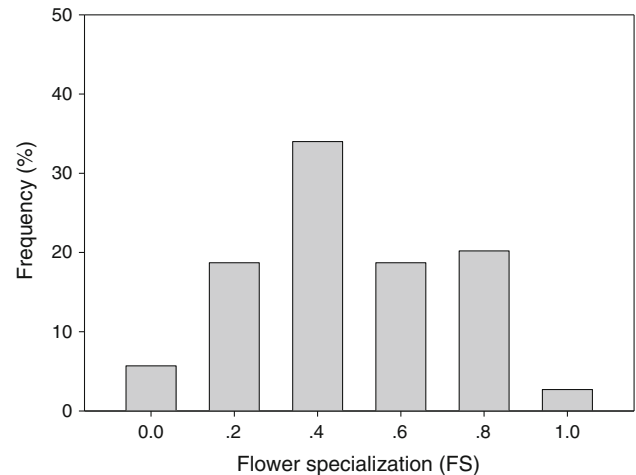
Floral morphology and specialization level

The floral traits of the species of the Salicaceae, Cyperaceae, Juncaceae and Poaceae, except of floral clustering, were not identified because these plants have no obvious showy petals

Table 1 Frequency of different floral traits in seven floral categories among the subnival species of the Hengduan Mountains, SW China

Group of traits	Trait	Percentage (%)
Sexual systems	Hermaphrodite	88.5
	Monoecy	5.5
	Dioecy	6.0
Floral orientation	Upward	78.7
	Horizontal	9.2
	Downward	12.1
Floral clustering	Inflorescence	65.0
	Solitary	35.0
Flower shape	Open	58.7
	Tubular	41.2
Four color	Blue-purple	42.7
	Pink-red	9.4
	Yellow	29.6
	White	18.1
Floral symmetry	Actinomorphic	77.5
	Zygomorphic	22.5
Floral size	Large	59.5
	Medium	24.7
	Small	15.8

Fig. 2 Frequency distribution (%) of species in each of six categories of flower specialization (FS) in the subnival belt of the Hengduan Mountains, SW China

Association of floral traits with each other

In the species with blue-purple or pink-red flower, the proportion of large flower was particularly high, and most of them had a tube. The species with yellow flowers had large flowers, but most of them were open. The species with white flowers had high proportion of small flower, and most of them were open (Table 2). Actinomorphic, open, inflorescence and upward flowers occurred much more frequently in all floral size classes (Table 3). The proportion of upward flowers was particularly high and most of them were actinomorphic, especially, the proportional of upward and actinomorphic flower were particularly frequent in the species with white flowers (93 and 97 %, respectively). Actinomorphic and zygomorphic flowers were more evenly distributed among tubular flowers, while an open flower shape was often associated with actinomorphic flowers.

Sexual systems

Of the 41 families recorded in our study, 32 (78.0 %) were represented by exclusively hermaphroditic species, 2 (4.9 %) by exclusively dioecious species (Salicaceae, Grossulariaceae), and another 2 (4.9 %) exclusively by monoecious species (Euphorbiaceae, Urticaceae). The remaining 5 families (12.2 %) were those with hermaphroditic and dioecious species (Gentianaceae, Crassulaceae and Polygonaceae), monoecious and dioecious species (Cyperaceae), or a combination of all three sexual systems (Asteraceae). Of the 133 genera recorded, 117 (88.0 %) were hermaphroditic, 4 (3.0 %) were dioecious, and 9 (6.8%) were monoecious. Three genera had two types of sexual systems; *Leontopodium* (Asteraceae), *Rhodiola* (Crassulaceae), and *Kobresia* (Cyperaceae). Of the 823 species examined, 729 (88.5 %)

and were therefore not considered to be reliant on insect-pollination. Among the remaining species, we found the following patterns (Table 1). (1) Large flowers were most common, followed by medium-sized and small flowers. (2) The most common flower colors were blue-purple, followed by yellow and white flowers. Pink-red flowers were relatively rare. (3) A total of 575 species produced actinomorphic flowers and 167 produced zygomorphic flowers. (4) Three-hundred and six species produced tubular flowers, and 436 species produced open flowers. (5) Upward flowers were most common, downward and horizontal flowers were substantially less frequent. (6) Two-hundred and eighty-six species produced solitary flowers and 537 species produced inflorescences. (7) Showy and large flowers were common.

We calculated five categories of flower specialization (FS, Fig. 2). The average FS for showy petal species was 0.47 ± 0.009 (mean $\pm$ SE, $n = 742$ species). Absolute specialization and generalization of floral morphology are indicated by FS values of 1 and 0, respectively, and the proportions of both of these extremes were low (2.7 and 5.7 %, respectively). Interestingly, 433 (58.4 %) of the FS values for the species were substantially lower than 0.5. Of the 10 biggest genera, the species of *Saxifraga*, *Saussurea*, *Arenaria*, *Cremanthodium* had small FS values (<0.5), and the species of *Corydalis*, *Pedicularis*, *Gentiana*, *Rhododendron*, *Primula* had larger FS values (>0.5).

Table 2 Association between flower color with floral shape, floral symmetry, floral size and floral orientation in subnival species of the Hengduan Mountains, SW China

Other floral traits	Floral color			
	Blue-purple	Yellow	White	Pink-red
Floral shape ($\chi^2 = 103.32$, $P < 0.001$, $n = 742$)				
Tubular	58.0	25.0	17.8	61.4
Open	42.0	75.0	82.2	38.6
Floral symmetry ($\chi^2 = 52.82$, $P < 0.001$, $n = 742$)				
Actinomorphic	67.5	82.2	97.0	70.0
Zygomorphic	32.5	17.8	3.0	30.0
Floral size ($\chi^2 = 66.04$, $P < 0.001$, $n = 742$)				
Small	9.8	11.8	34.0	20.0
Medium	19.6	26.8	30.4	30.0
Large	70.6	61.4	35.6	50.0
Floral orientation ($\chi^2 = 28.49$, $P < 0.001$, $n = 742$)				
Upward	73.2	76.4	93.3	82.9
Horizontal	13.2	8.6	3.0	4.3
Downward	13.6	15.0	3.7	12.8

Table 3 Association between flower size and floral shape, floral symmetry, floral size, floral clustering, and floral orientation in subnival species of the Hengduan Mountains, SW China

Other floral traits	Floral size		
	Large	Medium	Small
Floral shape ($\chi^2 = 5.38$, $P > 0.05$, $n = 742$)			
Tubular	41.6	45.9	32.5
Open	58.4	54.1	67.5
Floral symmetry ($\chi^2 = 24.42$, $P < 0.001$, $n = 742$)			
Actinomorphic	74.9	72.7	95.0
Zygomorphic	25.1	27.3	5.0
Floral clustering ($\chi^2 = 13.40$, $P < 0.05$, $n = 742$)			
Inflorescence	62.4	51.9	72.6
Solitary	37.6	48.1	27.4
Floral orientation ($\chi^2 = 68.00$, $P < 0.001$, $n = 742$)			
Upward	79.0	67.8	95.0
Horizontal	5.4	22.4	2.5
Downward	15.6	9.8	2.5

were hermaphroditic, 45 (5.5 %) were dioecious, and 49 (6.0 %) were monoecious.

Association of sexual systems with life-forms

There were 74 shrub species (9.0 %) and 749 herb species (91.0 %). The herbaceous species included proportionately more hermaphrodite species (91.3 %; 684), and shrubs had proportionately fewer hermaphrodite species than expected

from a random distribution (60.8 %; 45), resulting in a strongly significant association between hermaphroditism and herbaceous life-form ($\chi^2 = 7.05$, $P < 0.001$). Similarly, dioecious shrubs were proportionately more frequent and dioecious herbs less frequent than expected, indicating a positive association between shrubs and dioecy ($\chi^2 = 171.49$, $P < 0.001$).

Discussion

Floral traits and presumed pollination systems

It was documented that pollinator diversity, abundance, and activity suffer progressive reductions above the timberline (Arroyo et al. 1982, 1983, 2006). Consequently, alpine plants have great challenges in attracting pollinators, which are believed to have a strong evolutionary influence on floral morphology and function. Our findings indicate that generalized flower morphology was most common in the subnival belt of the Hengduan Mountains (Fig. 2). The average FS value calculated for the 742 studied species was <0.5, and a large number of species had very small FS values, especially members of the families Asteraceae, Saxifragaceae and Brassicaceae. Hence, generalized flower morphologies seem to be favored in alpine pollination conditions. For example, some floral morphologies, such as bowl-shaped flowers (upward, open and actinomorphic), have been considered to be characteristic for generalists and proposed as adaptations to unpredictable pollination conditions (Rathcke 1988). Our results are consistent with the pattern that generalized pollination systems are most common in nature (reviewed in Olesen and Jordano 2002; Herrera 2005) and supports the hypothesis that generalization in pollination ecology should evolve when pollinators are rare or variable (Waser et al. 1996). Furthermore, since many alpine species are selfing, the strength of selection of floral traits that could be driven by pollinator availability may actually be weaker in alpine species compared to species occurring in other habitats. However, it is unclear whether flower morphology is more generalized in the alpine habitats compared to other plant communities because comparable data for other vegetation types is missing. Although generalized flower morphology was common, species with particularly specialized or generalized floral morphologies were rare, and most of the species had elements of both systems (Table 1; Fig. 2). It is possible that some specialized taxa, such as *Delphinium*, *Primula*, *Corydalis*, *Pedicularis*, and *Gentiana*, attract pollinators additionally with a showy floral display. Probably this results from the lower pollination efficiency of generalized flowers and the lack of specialized pollinators in alpine habitats.

Brightly colored flowers with large floral displays were very common in our study area (Table 1). The observed distribution of floral colors differed from those found in other alpine studies. For example, Pickering and Stock (2004) found that 127 of 204 alpine species examined on Mt Kosciuszko, Australia, had large showy flowers, and the most common flower colors among these taxa were white (53.5 %), then yellow (21.3 %), followed by pink-red (11.0 %) and blue-purple (4.0 %). Moreover, they found that Diptera were the most common flower visitors, hence the results of the cited study support the hypothesis that the 'white' flora of alpine areas may be associated with the color preference of flies. However, Nakano and Washitani (2003) suggested that bumblebees consistently prefer blue-purple flowers, and Bingham and Orthner (1998) suggested that bumblebees were efficient pollinators at high elevation. Thus, Gong and Huang (2011) proposed that blue-purple flowers would evolve under selection for bumblebee pollinators, and hence represent specialized flowers in alpine meadow communities. Accordingly, species richness data for the pollinating fauna visiting flowers of the subnival belt community in the Hengduan Mountains indicate that bumblebees are the dominant pollinators in this alpine region (He et al. 2005; our observations). The attractive flowers may compensate for the low density and small size of the plants, due to their unfavorable location, by increasing the number of pollinator visits (Shmida and Dafni 1989).Our results suggested that some specialized floral traits were associated to each other (Tables 2, 3). Therefore, species with showy and specialized flowers could increase pollination probability and reproductive success in the subnival belt, and the observed pattern of flower morphology supports the increased pollination probability hypothesis. Since generalized floral traits were more common and associated to each other, on the other hand, some alpine plants might reach successful pollination by a generalized pollination system or selfing.

Plant sexual systems in the subnival belt of the Hengduan Mountains

Most previous surveys have found the general pattern in the frequency distribution of sexual systems with hermaphroditic species dominating, and a much lower proportion of dioecious and monoecious species (reviewed in Vamosi and Queenborough 2010). While our results are consistent with this general pattern, the proportion of hermaphroditic species is particularly high in the subnival belt of the Hengduan Mountains. Vamosi and Queenborough (2010) found that the distribution of sexual systems is correlated with elevation and suggested that the distribution of different sexual systems along altitudinal gradients may reflect the selective nature of the pollination environment. Subnival belt vegetation, which is restricted to the top of high mountains, is one of the most stressful habitats for plants, and pollinators are rare because of the harsh weather conditions. Nevertheless, insect pollination is still far more important than the wind pollination in alpine ecosystems (Bingham and Ranker 2000). However, when insect pollination fails, due to the scarcity of pollinators in alpine ecosystems, hermaphrodite flowers have a major advantage, because they can achieve reproductive success by self-pollination (e.g., Molau 1993; Duan et al. 2007; Zhang and Li 2008). Furthermore, self-compatible species, particularly those that do not need the services of pollinators, are generally good colonizers (Stebbins 1957). Thus, selfing hermaphroditic plants are expected to be favored during colonization, and are most likely to establish new populations in subnival areas. In contrast, dioecious and monoecious species depend on vectors for cross-pollination and are therefore less abundant in harsh, high-altitude subnival environments.

We found that the species were predominantly herbaceous (91.0 %) hermaphrodite (91.3 %) in the subnival belt, with the proportion of hermaphrodites in herbs much higher than in the tropical rain forests in Xishuangbanna (S Yunnan) (91.3 vs. 74.0 %; Chen and Li 2008a). These findings may be explained by the barren soil and stochastic weather in the subnival belt favoring herbs and hermaphroditic species. Moreover, increased longevity may compensate for the low mate assurance, thereby potentially mitigating the negative effects of the reduced abundance of biotic pollen vectors expected at higher elevations (Arroyo and Squeo 1990). In contrast, we found that dioecy is strongly associated with shrubs and generalist entomophily (floral traits: open, actinomorphic and inflorescence). Mataliana et al. (2005) also found that dioecy was strongly associated with woodiness and generalist entomophily, and the most frequent pollination syndrome for hermaphrodites was specialized entomophily. Bawa (1982) suggested that generalist pollinators allowed dioecious plants to establish more readily than hermaphrodites that require specialist pollinators. The association between dioecy and shrubs is also thought to reflect strong selection for outcrossing in plants with a long life span.

In conclusion, we found that species with generalized flowers dominate in the harsh environments of the subnival belt of the Hengduan Mountains, and that hermaphrodite is strongly associated with herbs, and dioecy is strongly associated with shrubs. However, in our study, we did not record pollinator visits or quantify pollinator preferences for different flower morphologies, therefore it is possible that the generalized flower morphology that we defined may not actually be a generalized flower morphology with respect to pollinators; this was a limitation of our study. In the future it will be important to consider the choice of pollinators for particular floral traits in subnival belt habitats.

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