Review

Survival and reproduction of plant species in the Qinghai–Tibet Plateau

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Abstract The Qinghai–Tibet Plateau (QTP) is the highest and largest plateau in the world. It covers correspondingly wide geological, topographical, and climatic gradients, and thus hosts greater biodiversity than surrounding lowlands and other high elevation regions. Due to its extreme environmental and biological diversity, the QTP is an ideal region for studying adaptations of plant species under harsh environmental conditions at multiple evolutionary levels. Many recent ecological studies have revealed functions of distinctive morphological features of various plants in the region that improve their reproductive success. Examples include large and showy bracts, hairy inflorescences, and drooping flowers. Numerous other investigations have examined QTP plants' sexual systems, patterns of biomass allocations, and biotic interactions. This paper summarizes recent advances in understanding of morphological adaptations, plant–plant interactions, plant–pollinator interactions, floral color patterns, pollination adaptations, and resource allocation patterns of alpine plants of the QTP. The overall aim is to synthesize current knowledge of the general mechanisms of plant survival and reproduction in this fascinating region.
Key words adaptation and evolution, plant species, Qinghai–Tibet Plateau.

The Qinghai–Tibet Plateau (QTP) extends from the southern edge of the Himalayan Range to the northern edge of the Kunlun Mountains, and from the western boundary of the Pamir Mountains to the eastern edge of the Hengduan Mountains ($26°00'12''$–$39°46'50''$N, $73°18'52''$–$104°46'59''$E), covering ca. 2.5×10^6 km^2 (Zhang et al., 2002). As the highest and largest plateau in the world (average elevation more than 4000 m a.s.l.), it is called the "third pole" or "roof of the world", and has extremely complex landscapes (Zhang et al., 2002). The high (and highly varying) altitude massively affects ecosystems on the plateau, because of the strong physical correlations between altitude and major abiotic factors related to evolutionary adaptation of plants, including atmospheric pressure, temperature, and precipitation (Körner, 2012). Furthermore, the complex alpine landscape results in correspondingly complex distributions of

direct solar irradiance and thermal conditions, which over long time periods have fostered the development of highly inhospitable geomorphological landforms, such as scree and rock glaciers, in some areas, interspersed with alpine meadows and grasslands in others (Nagy & Grabherr, 2009). In addition, at altitudes between 5500 and 6000 m a.s.l. the atmospheric pressure is 50% lower than at sea level and UV radiation is correspondingly strong (Körner, 2003). Due to the decline in temperature with altitude, but high diurnal amplitudes at high elevations, there are complex spatial–temporal distributions of cryospheric elements and phenomena, such as ice and glaciers, permafrost, seasonal snow cover and ground frosts, all of which also strongly influence QTP habitats (Nagy & Grabherr, 2009). Wide variations in wind regimes and precipitation add further complexity. All these factors strongly influence plant growth and reproduction in the QTP, and plants inhabiting its harsh environments have evolved highly specialized phenological, morphological, and physiological mechanisms and structures, such as epidermal accumulation of flavonoids as an adaptation to the strong UV radiation (Caldwell, 1968, 1979; Nagy & Grabherr, 2009). Generally, in comparison to plants of lowland areas,

plants on the QTP (and other high-altitude areas) have dwarf morphology and smaller, rounder leaves with more frequent pubescence, and often fold to form crypts or similar structures (Nagy & Grabherr, 2009). They often have high densities of leaves and branches, or persistent leaves (rosette leaves). There are also several types of plants with highly distinctive morphologies, such as "greenhouse" plants (e.g., various species of *Rheum* L., *Saussurea* DC. and *Ajuga* L.) and "woolly plants" (e.g., various species of *Saussurea* and *Cirsium* Mill.). As discussed in more detail below, the former have specialized, enclosing bracts or leaves whereas the latter are covered in long, dense hairs that act as heat collectors, thus accelerating their growth and reproduction. Such adaptations can be highly important in the hostile environments of the QTP, where the growing seasons are short (3–4 months) and vegetation is generally very sparse (Xu et al., 2014b).

Due to the complexity of their environments, alpine sites are ideal "natural laboratories" for probing mechanisms of species adaptation and evolution (Hedberg, 1975). The QTP has also been described as a natural museum of the floristic evolution that has occurred synchronously with its geological evolution (Sun, 2002). It has very rich diversity of vascular plants, hosting approximately 12 000 species of 1500 genera (Wu, 2008), of which more than 3000 are exclusively alpine (Li et al., 2014). A number of genera present in the QTP (*Saussurea*, *Corydalis* DC., *Pedicularis* L., *Primula* L., *Meconopsis* Vig., *Anaphalis* DC., *Cremanthodium* Benth., and many others) have dramatically differentiated and formed modern diversity centers in which plant evolution can be seen at work. The evolutionary processes of many genera (e.g., *Cyananthus*, *Soroseris–Stebbinsia–Syncalathium*, and *Ligularia–Cremanthodium–Parasenecio*) clearly reflect geological events (Liu et al., 2006; Zhang et al., 2011b; Zhou et al., 2013), so the QTP is of great interest to biogeographers and evolutionary biologists. In addition, plants of the QTP have evolved multiple ecological and reproductive strategies for adapting to the harsh environments of the plateau. Substantial advances have been made towards understanding the phylogeny, biogeography, and phylogeography of QTP plants (Qiu et al., 2011; Liu et al., 2012; Wen et al., 2014), and numerous studies have explored their ecological adaptions and reproductive mechanisms (Ohba, 1988; He et al., 2005; Yang & Sun, 2006; Peng et al., 2012b). This paper reviews recent advances in understanding survival and reproduction mechanisms of alpine plants in the QTP, focusing on morphological adaptations, interactions between plants, plant–pollinator interactions, floral color patterns, pollination adaptations, and resource allocation patterns.

1 Specialized morphological adaptations of plants in the QTP

As outlined above, to cope with their hostile alpine environments, QTP plants have evolved various specialized traits (Shao et al., 2007), and several types of plants with highly distinctive morphological features have been distinguished, including glasshouse structures, nodding flowers, downy leaves, and cushion habits. These, and others, are described and discussed below.

1.1 Glasshouse plants
The upper leaves of "glasshouse" species have developed into large translucent or cream-colored bracts that cover the inflorescences (Ohba, 1988). Glasshouse morphology has been recorded in more than 10 plant families, including the Ranunculaceae, Caryophyllaceae, Lamiaceae, Asteraceae, and Polygonaceae (Yang & Sun, 2006; Xu et al., 2014a). A typical glasshouse plant species that has received substantial attention (Omori & Ohba, 1996, 1999; Omori et al., 2000; Iwashina et al., 2004) is *Rheum nobile* Hook. f. & Thoms. (Polygonaceae), a monocarpic perennial herb endemic to the eastern high Himalayas (SE QTP). Due to high levels of flavonol glycosides in its cells, the highly specialized bracts of *Rh. nobile* can efficiently absorb UV radiation and thus act as a UV screen (Omori et al., 2000; Iwashina et al., 2004; Song et al., 2013). However, these bracts almost completely transmit photosynthetically active and infrared radiation, resulting in thermal modification (Omori et al., 2000; Yang & Sun, 2009), that is, warming interior reproductive organs and protecting them from the low temperatures in their alpine habitats (Omori & Ohba, 1996, 1999; Song et al., 2013). In addition, bracts of *Rh. nobile* reportedly protect pollen grains from damage by UV-B radiation and rain, promote pollen germination by maintaining warmth, enhance pollinator visitation by providing a vivid visual display during flowering, and facilitate the development of fertilized ovules during seed development (Song et al., 2013). Interestingly, the bracts appear to be particularly important for seed development, as Song et al. (2013) found that they increase reproductive success more during fruiting (by 28.2%) than during flowering (15.3%). Studies of its reproductive ecology have shown that *Rh. nobile* is self-compatible, but depend on fungus gnats for pollination. As a reward for pollination, warming by bracts could

also benefit pollinators engaged in activities such as foraging and oviposition during flowering, and larval development in the ripening seeds during fruiting (Song B. et al., 2013, unpublished data). Thus, the multifunctional bracts of *Rh. nobile* have clearly been selected because they both provide adaptive advantages in the plant's harsh abiotic environment and enhance pollination success. Gene expression analyses have indicated that the resistance to abiotic stresses provided by bracts is related to the upregulation of a number of genes. For example, the synthesis and high concentrations of UV-B radiation-absorbing flavonoids in the bracts of *Rh. nobile* are reportedly associated with upregulation of a flavonol synthase-encoding gene (Zhang et al., 2010a). Similar patterns have also been found in another glasshouse plant, *Rh. alexandrae* Batal. (Liu et al., 2013). These findings indicate that the parallel evolution of adaptive functions in glasshouse phenotypes might have similar molecular bases.

1.2   Plants with nodding flowers

Another striking morphological specialization observed in plants inhabiting alpine zones of the QTP is the production of "nodding" or "drooping" flowers (Yoshida, 2002), a common trait among species of *Cremanthodium* (Asteraceae), *Fritillaria* L., *Lloydia* Salisb. ex Rchb., *Allium* L. and *Lilium* L. (Liliaceae), and *Adenophora* Fisch. and *Codonopsis* Wall. (Campanulaceae). This highly specialized morphological feature is assumed to be an adaptation to cold rain and short periods of very intense solar radiation (Yoshida, 2002). Accordingly, in the SE QTP, Chen et al. (2013) found that the nodding capitulum of *Cremanthodium campanulatum* (Franch.) Diels. protects pollen from damage by rain and UV radiation during the cool and wet monsoonal period, resulting in longer pollen presentation to pollinators and reductions in pollen losses from stigmas. In the Andes, the nodding capitulum of *Culcitium canescens* Bonpl. (another member of the Asteraceae) may also provide warmth for the inflorescence by absorbing radiation reflected from the substratum (Sklenár, 1999). However, Chen et al. (2013) detected no such warming effects of the capitulum of *C. campanulatum* in the SE QTP, probably because of the low level of radiation reflected from the substratum due to overcast skies. Unlike flowers of *C. campanulatum*, which always droop throughout the reproductive period, Wang et al. (2010) found that flower stalks of *Anisodus luridus* Link ex Spreng. (Solanaceae), a perennial herb native to the QTP, became erect after anthesis and increased the stability of temperatures inside the persisting calyx by retaining water, thus promoting the development of fertilized ovules. Additionally, in contrast with the proposition that the evolution of floral traits is predominantly driven by interactions between plants and their pollinators (Galen, 1989; Galen & Cuba, 2001; Sun et al., 2008), no pollinator preference has been observed between artificially erected flowers and natural nodding flowers of both *C. campanulatum* and *A. luridus*, suggesting that abiotic factors other than pollinators have played important roles in shaping floral traits of these two plants (Wang et al., 2010; Chen et al., 2013). These observations indicate that selective pressures acting on plants with very similar phenotypes may substantially differ.

1.3   Downy plants

Downy plants (also called "woolly plants", Yang & Sun, 2006) have characteristically dense trichomes on well-developed bracts that are tightly packed around the inflorescences. This kind of unusual specialized morphology is mainly presented by species of *Saussurea* (e.g., *S. medusa* Maxim, *S. laniceps* Hand.-Mazz., *S. leucoma* Diels) and *Cirsium* (*C. eriophoroides* (Hook. f.) Petr.) of the Asteraceae (Tsukaya & Tsuge, 2001; Yoshida, 2002; Yang et al., 2008), *Eriophorum* L. of the Cyperaceae, and *Eriophyton* (*E. wallichii* Benth.) of the Lamiaceae. Studies on *S. medusa* in the QTP have shown that its spectacular pubescence has three main functions: keeping the inflorescence warm, repelling water, and reflecting short peaks of high radiation (Tsukaya et al., 2002; Yang et al., 2008). Another study, on *E. wallichii* (Lamiaceae), also found that dense trichomes on leaves could enhance net photosynthetic rates by increasing both absorption of photosynthetically active radiation and the temperature of leaves (Peng D.-L. et al., 2014, unpublished data).

1.4   Cushion plants

Cushion plants, which have a highly compact growth form and low stature, are commonly found in alpine, subalpine, arctic, and subarctic environments around the world (Körner, 2003). Many studies have explored the adaptive mechanisms of cushion plants to alpine habitats in various regions, especially the Andes and Alps (Körner, 2003). Their specialized morphology has been assumed to be effective for trapping and retaining heat, and enhancing soil moisture (Körner & De Moraes, 1979; Núñez et al., 1999; Cavieres et al., 2008). In the QTP, several systematically distant species of *Androsace* L. (Primulaceae), *Arenaria* L., *Thylacospermum* Fenzl (Caryophyllaceae), *Saxifraga* Juss. (Saxifragaceae), *Rhodiola* L. (Crassulaceae), *Salix* L. (Salicaceae), *Potentilla* L. (Rosaceae), *Solms-*

laubachia Muschl. ex Diels, *Baimashania* Al-Shehbaz, *Draba* L. (Brassicaceae), and *Chionocharis* I. M. Johnst. (Boraginaceae) share similar cushion morphology. However, little attention has been paid to them until recently, and the results have been conflicting. Yang et al. (2010) found no difference in substrate temperatures between ground under *Arenaria polytrichoides* Edgew. (Caryophyllaceae) cushion plants and bare ground, but the cushions maintained higher moisture and soil nutrient contents (N and P) than open areas. Chen et al. (2014) reported differences in the capacity of two species (*Potentilla articulata* Franch. and *Ar. polytrichoides*) with similar cushion morphology to modify soil nutrient (P and K) contents. Furthermore, no apparent modification of thermal or soil nutrient conditions by *Thylacospermum caespitosum* (Cambess.) Schischk. at extremely high elevations in the Trans-Himalayas (W QTP) has been detected (de Bello et al., 2011; Dvorský et al., 2013). This may be because the very dry and cold climate of the Trans-Himalayas retards decomposition of dead tissue (the main contributor to the enhanced nutrient levels in soil below cushions), which thus accumulates within cushions and only releases nutrients very slowly (Dvorský et al., 2013). Thus, broader examination of plants in diverse habitats is needed to fully understand the adaptive strategies of cushion plants in the QTP (Dvorský et al., 2013).

1.5   Others
Airbag plants provide further examples of highly specialized morphology. These plants (represented by *Astragalus* L., *Colutea* L., and *Oxytropis* DC. of the Fabaceae and *Przewalskia* Maxim. of the Solanaceae) have airbag-like structures formed by the calyx or carpels covering fruits/seeds during fruiting. However, there have been few explorations of the adaptive significance of these airbag-like structures. In addition, several other survival strategies have been observed in plants of the QTP's alpine zones, such as flower closure by petal movements in *Gentiana straminea* Maxim. (Gentianaceae, He et al., 2005) and *Cyananthus delavayi* Franch. (Campanulaceae, Niu et al., 2011), and flower heliotropism in *Anemone rivularis* Buch.-Ham. ex DC. (Ranunculaceae, Zhang et al., 2010b). For instance, He et al. (2005) found that flowers of *G. straminea* close when the air temperature falls sufficiently, thereby protecting pollen grains from rainfall and increasing both male and female fitness.

However, despite great progress towards understanding the ecology of these plants, greater knowledge of the largely unknown molecular bases of their

adaptations is required to elucidate the role of natural selection in shaping current biodiversity.

2   Plant–plant interactions in the QTP

In recent decades, large numbers of empirical and theoretical studies have shown that plant–plant interactions, both positive (facilitation) and negative (competition), strongly influence the composition and dynamics of plant communities, thus affecting ecosystem structures and functions (Bertness & Callaway, 1994). However, interactions among plant species and their effects on QTP plant communities have only recently received attention. The main findings are summarized below.

2.1   Positive interactions (facilitation)
Positive plant interactions have been described as links between plants that improve the performance of other plants or the diversity and/or productivity of plant communities (reviewed by Callaway, 2007). However, facilitation has been defined at a smaller scale, as any interaction in which the presence of a species alters the environment in a way that enhances the growth, survival, or reproduction of a second, neighboring species (reviewed by Bronstein, 2009). Many studies have recently shown that both positive and negative interactions may act simultaneously, but positive interaction becomes increasingly important with increases in abiotic harshness and reductions in productivity (e.g., Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Brooker et al., 2008).

As discussed in the introduction, high-elevation habitats have characteristically stressful conditions (Körner, 2003). In addition, several key abiotic factors, such as temperature and substrate stability, change with altitude and can be easily quantified. Thus, high elevation habitats are particular useful for evaluating the importance of positive interactions along environmental stress gradients (Callaway et al., 2002). Interactions among plants have been found to be predominately positive in many high elevation communities in various locations, as the distribution, abundance, and biomass production of many species are apparently enhanced by the presence of other plant species in them (Choler et al., 2001; Callaway et al., 2002). However, several studies indicate that the relationships may be more complex, at least in the QTP. For example, a comparison of interactions between roots and shoots of alpine meadow plants in the NE QTP showed that interactions among neighboring species can be facilitative, competitive, or neutral,

depending on the traits of the species involved (Song et al., 2006). Wang et al. (2008b) found that facilitation was the dominant type of interaction in an alpine meadow in the QTP, but biomass growth responses to facilitative effects were species-specific. In addition, empirical observations and modeling of interactions in an alpine meadow in the NE QTP showed that facilitation can affect biomass–density relationships and the size structure of plant populations in stressful environments (Chu et al., 2008, 2009). All the cited findings suggest that explicit consideration of positive interactions is crucial for understanding population dynamics at high elevation sites of the QTP.

Prominent examples of positive interactions among plant species involve organisms defined as "engineering species" that change distributions of material and energy in the abiotic environment through non-trophic interactions, thus creating and maintaining new habitat patches in the landscape (Jones et al., 1994, 1997). In high alpine regions, cushion species often act as "engineers" by ameliorating thermal, water, and soil nutrition conditions in the surrounding environment (reviewed by He et al., 2010). Such "engineers" often act as foundation species in a given ecosystem and play important roles in structuring the community and maintaining ecosystem functions at high elevations (e.g., Badano & Cavieres, 2006; Badano & Marquet, 2008; Cavieres & Badano, 2009). In a global assessment of 70 alpine plant communities in mountain areas in South and North America, Europe, New Zealand, and Asia, Butterfield et al. (2013) found that cushion species significantly increase community-level phylogenetic diversity in abiotically stressful environments. Both general and idiosyncratic positive effects of cushion species on species richness, diversity, and evenness have also been recorded in assessments of 8 and 11 communities dominated by cushion species in the high Andes by Badano & Cavieres (2006) and Cavieres & Badano (2009), respectively.

The QTP has the richest resources of plants with cushion morphology in the world, hosting more than 70 species belonging to 17 genera and 13 families (Huang, 1994). As in other high elevation regions, positive interactions have been found among cushion plants and other, non-cushion species in several recent studies. For instance, in a plant community of alpine areas in the Himalaya–Hengduan Mountains (SE QTP), Yang et al. (2010) detected more pronounced positive effects of *Arenaria polytrichoides* cushions on other plant species at 4700 m than at 4500 m a.s.l., which they attributed to lower soil nutrient availability at the higher elevation. In the same area, two alpine species (*Potentilla articulata* and *Ar. polytrichoides*) with similar cushion morphol-

ogy were found to have variable (but consistently positive) effects on species richness and diversity in an alpine plant community due to differences in the extent to which they modified soil nutrient availabilities (Chen et al., 2014).

At a larger (regional) scale, comparisons of species richness, community structure, and biomass productivity between cushion habitats and cushion-free areas in 11 communities located in different alpine areas of the SE QTP have shown that they generally have positive effects on diversity and ecosystem functions at high elevation sites (Chen J.-G. et al., 2014, unpublished data). In contrast, two recent studies found that another cushion plant, *Thylacospermum caespitosum*, did not act as a facilitator at extremely high, cold, and dry locations in the NW Himalayas (W QTP) and Trans-Himalayas (W QTP) (de Bello et al., 2011; Dvorský et al., 2013). The site examined by de Bello et al. (2011) was located in a cold and dry area, at 5900 m elevation with annual precipitation of 100 mm/year, ca. 600–700 mm less than at sites examined by Yang et al. (2010). This is consistent with a suggestion by Michalet et al. (2006) that at both extremes of a stress gradient, where the species present must be highly stress tolerant and do not necessarily profit from facilitation, the importance of positive interactions could be diminished. In southeastern parts of the QTP, phylogenetic structure analysis along an elevation gradient (3000–5500 m a.s.l.) detected phylogenetic "overdispersion" at lower elevations, implying that distributions of plants at these elevations were mainly determined by interspecific competition (Li et al., 2014). However, phylogenetic structure became rather random above 5500 m, suggesting a weak interspecific relationship, attributed to the solitary and independent distribution patterns of plants at such extremely high elevations. These seemingly conflicting observations relating to interactions among cushion plants and other non-cushion species in the QTP probably reflect differences in temperature and water conditions in different regions. Clearly, further study is required to elucidate cushion plants' interactions fully and determine the major influential factors. Tests of relationships between interactions and environmental gradients in situations where benefactors are limited, such as at the extreme ends of severity gradients, may be particularly illuminating (Brooker et al., 2008). Experimental evaluations of key performance variables (e.g., survival, growth, reproduction, and fitness parameters) are also required to elucidate when and where facilitation acts as a filtering process in plant communities (Brooker et al., 2008). Robust modeling will also be important for exploring the complex interactions between both the

biotic and abiotic components of cushion plants' habitats, but despite the availability of various relevant software suites, they have not yet been widely used. Thus, the unique topographical and climatic characteristics of the QTP offer major opportunities for developing ecological theory to integrate facilitation in the framework of evolutionary adaptations of plant species, both in this area and more generally.

2.2 Negative interactions (competition)

Plants growing in high elevation regions or plateaus usually have relatively large proportions of below-ground biomass, thus providing ideal systems for studying relationships between above- and below-ground plant parts. By experimentally manipulating root and shoot competition among four grass species (*Kobresia humilis* (C. A. Mey. ex Trautv.) Serg., *Saussurea superba* J. Anthony, *Stipa aliena* Keng, and *Elymus nutans* Griseb.) in an alpine meadow ecosystem in the QTP, Song et al. (2006) showed that competition had different effects on different species and that interactions between roots and shoots varied from negative to positive and additive. More specifically, they found that *K. humilis* and *St. aliena* grew more rapidly with competition, *S. superba* grew more rapidly with shoot competition and *E. nutans* grew more rapidly with root competition. Soil nutrient availabilities are generally lower in high-elevation ecosystems than in lowland areas (Körner, 2003). Therefore, shifts in biotic interactions following fertilization in mountain areas have interested ecologists. In an alpine meadow located in the NE QTP, Qiu & Du (2004) found that light competition reduced diversity with increases in fertilization and productivity, due to dramatic increases in shading by fast-growing species, such as *Poa alpina* L.

3 Plant–pollinator interactions in the QTP

Plant–pollinator interactions are among the most important and ubiquitous interactions between organisms (Waser, 2006). In addition, as discussed below, pollination mechanisms in the QTP have aroused substantial interest in recent years because of the enormous diversity of plant species and intriguing floral phenotypes.

3.1 Pollination at the community level

It has been speculated that zoophilous flowers may be particularly prone to pollen limitation due to the lack of pollinators in the harsh conditions typical of high elevations (Arroyo et al., 2006). However, at least in subalpine regions, which may be far richer in plant species than those just above the treeline, there may not be a shortage of pollinators. Fang & Huang (2012) found that a meadow (approx. 3250 m a.s.l.) in the Himalaya–Hengduan Mountains (SE QTP) harbored strikingly diverse pollinators that visited flowers frequently, bumblebees and hoverflies being especially abundant. With numerous plant and pollinator species packed together, such subalpine meadows provide ideal opportunities to test hypotheses regarding community-level interactions between plants and pollinators. The cited authors found that some links between specific flowers and pollinators varied across years, but the primary structure of the pollination network and key links were stable in the meadow they examined. A theoretical model predicted that pollination links should be numerous in species-rich communities, but this was rejected following analysis based on observations in the meadow. A subsequent analysis of pollination interference showed that generalized flowers received more heterospecific pollen, but did not export more pollen than specialized flowers, and heterospecific pollen transfer was largely unidirectional among species sharing pollinators (Fang & Huang, 2013). In addition, Gong & Huang (2009) found that bilateral flowers in the meadow had less variance in floral size and more specialized pollination systems than radial flowers, supporting the hypothesis that bilateral flowers are under more stable selection pressure because they are visited by fewer pollinators. Moreover, most pollinators consistently prefer specific floral traits, so they may have driven the evolution of specialized and generalized floral traits, but their role may be weakened by variation in community structure (Gong & Huang, 2011).

3.2 Pollination and diversification of plant species: Examples from *Pedicularis*, *Gentiana*, *Primula*, and *Rhododendron*

Further questions of great concern in biodiversity hotspots regard the associations between diversification of plant species and pollinators, and the partitioning of pollination niches among these species (Johnson, 2010). *Pedicularis* (Scrophulariaceae) has intensely diversified, resulting in the presence of numerous sympatric species in a community in the Himalaya–Hengduan Mountains (SE QTP), offering opportunities to address these questions (Eaton et al., 2012). The corolla tubes are remarkably elongated in many *Pedicularis* species, inferring that long-tongued moths are their pollinators. However, empirical evidence collected by Huang & Fenster (2007) conflicts with this inference. They bagged a group of the long-tubed flowers by day and another group by night, demonstrating that nocturnal animals (i.e., long-tongued

moths) contributed nothing to their pollination. Almost all *Pedicularis* species in Asia are pollinated by bumblebees (Wang & Li, 2005; Armbruster et al., 2014) and the reasons why the corolla tubes of many *Pedicularis* are so long remains unclear. However, *Pedicularis* has long been considered a classic example of sympatric species using different parts of a pollinator's body to transfer pollen (a form of mechanical isolation) (Grant, 1994; Kay & Sargent, 2009). This hypothesis is supported by results of experiments in which pollen was stained with safranin to track the pollen taken away by bumblebees (Huang & Shi, 2013), showing that pollen from different *Pedicularis* species was deposited on different parts of the bumblebee body. However, contrary to the hypothesis, such mechanical isolation is far from sufficient to eliminate heterospecific pollination and provide complete reproductive isolation, whereas post-pollination isolation mechanisms are usually strong enough to prohibit sympatric species from merging (Armbruster et al., 2014). This supports the alternative hypotheses that mechanical isolation does not directly contribute to angiosperm speciation and phenotypic diversification is simply a result rather than the cause of diversity (Armbruster & Muchhala, 2009).

Three genera that show great diversity like *Pedicularis* in the QTP are *Gentiana* L. (Gentianaceae), *Primula* (Primulaceae), and *Rhododendron* L. (Ericaceae), but there are only a few reports on their pollination and floral diversification in the region. The main findings of these studies are briefly discussed below. First, studies of pollination patterns in two *Gentiana straminea* populations located at different altitudes found little evidence that prolonged floral longevity and exploitation of relatively effective bumblebees as pollinators are adaptations to reductions in pollination service with increasing altitude (Duan et al., 2007b). Second, *Primula beesiana* Forrest and *P. bulleyana* Forrest are sympatric in some regions of the Himalaya–Hengduan Mountains (SE QTP). They are pollinated by bumblebees and butterflies, but Wu & Zhang (2010) found that pollinator species showed different preferences for the two species, potentially contributing to pre-pollination isolation. However, gene exchanges were found in the shared population and the pattern of speciation and hybridization should be further pursued in this system. Third, nectar robbers are not usually considered to contribute to pollination (Inouye, 1983; Maloof & Inouye, 2000). However, Zhu et al. (2010) found that nectar robbers could effectively pollinate the short-styled morph with pollen from the long-styled morph, but not vice versa. They concluded that the asymmetrical pollen flow mediated by nectar robbers may play an important role in shaping flower fitness and evolution in distylous plants. Fourth, to our knowledge, there are no reports on the pollination ecology of *Rhododendron* species in the QTP, despite their renowned floral diversity and horticultural status. However, there is evidence that hybridization occurs in *Rhododendron* and some species may be of hybrid origin in and around the QTP (e.g., Ma et al., 2010b; Zha et al., 2010; Yan et al., 2013), suggesting that pollinators promote diversification of the genus. *Rhododendron* may therefore represent an ideal study system for pursuing patterns of speciation and diversification of angiosperms. Given their floral designs, *Rhododendron*, *Primula*, and *Gentiana* do not have sophisticated morphologies that reduce interspecific pollen transfer like *Pedicularis* if the sympatric congeners share pollinators. This raises questions about the mechanisms that allow congeners to coexist and whether low pollen interference is vital for coexistence.

3.3 Other examples

Non-rewarding plants may benefit from the presence of rewarding plants, while the reproductive success of rewarding plants might be impaired, at least until pollinators learn to avoid the non-rewarders (Internicola et al., 2007; Peter & Johnson, 2008). Rewarding *Galearis diantha* (Schltr.) P. F. Hunt and non-rewarding *Ponerorchis chusua* (D. Don) Soó share some habitats, but partition other habitats in the Himalaya–Hengduan Mountains (SE QTP). Contrary to initial expectations, Sun et al. (2011) found that the non-rewarding species neither benefited from nor affected the rewarding species when they grow together, and the fruit set of the rewarding species growing in plots mixed with non-rewarding species was not different from that in monospecific plots. They tentatively ascribed these findings to limited overlap of flowering time and pollinator spectra between the two species.

Further potentially important features of plants in this context are their "pollination syndromes", that is, suites of floral traits that are presumed to enhance the attraction and exploitation of specific pollinators (Fenster et al., 2004). The validity of pollination syndromes has been disputed in recent decades (Waser et al., 1996; Fenster et al., 2004; Ollerton et al., 2009) and one of the most important arguments against them is that the assemblage of a plant species' pollinators is likely to vary with time and place (Waser et al., 1996). Liu & Huang (2013) found support for both of these views in a 3-year assessment of contributions to seed production by different visitors in populations of three *Adenophora* species in Shangri-La (SE QTP) and distant sites in

Yunnan province, SW China. These species have distinct floral syndromes, implying that one is pollinated by bumblebees and another by moths, while the third has intermediate floral morphology. The cited authors found that the species with bumblebee- and moth-pollination syndromes were pollinated by bumblebees and moths, respectively, at all examined sites, while pollinators of the phenotypically intermediate species differed between sites. These findings suggest that the pollination system may be predictable and stable if the floral syndrome is definite and classic, although pollination systems may vary substantially across sites and years in other cases, as proposed by Waser et al. (1996). Observations of *Stellera chamaejasme* L., which produces fragrant tubular flowers and is distributed in the QTP and northern China, also suggest that other factors, in addition to pollination-associated factors, may influence the evolution of floral color. The color of its flowers varies widely among populations, although the species is pollinated by various Lepidoptera in all of the populations examined by Zhang et al. (2011d), and is not apparently associated with the pollinator species.

Generally, compared with other biodiversity hotspots, for example, the Mediterranean region (Petanidou & Potts, 2006) and South Africa (Johnson, 2010), pollination biology has been poorly studied in the southeastern parts of the QTP and other parts. Some aspects, such as associations between floral trait evolution and pollinator senses, have not been explored in the region at all. Autonomous selfing occurs in various taxonomically distant species in the region (e.g., Sun et al., 2005; Zhang & Li, 2008; Duan et al., 2010; Zhang et al., 2011a; Xiong et al., 2013). This is consistent with the hypothesis that selfing may be more prevalent in high-altitude communities than at lower altitudes (Arroyo et al., 2006). However, proportions of self-pollinated species within QTP communities have not been calculated to test the hypothesis. In addition, we know little about the ecology of pollinators in the region, although such knowledge is important for devising robust plant conservation strategies due to the key role pollinators play in plant reproduction. For example, over-grazing may lead to a sharp decline in the diversity of bumblebees because it can substantially reduce their food resources (Xie et al., 2008).

4 Floral color patterns of plant species in the QTP

The huge diversity of floral colors in angiosperms is widely considered to be a result of selection by pollinators, through their effects on plant reproductive success (Fenster et al., 2004; Streisfeld & Kohn, 2007; Hopkins & Rausher, 2012). Alpine plants from the QTP and nearby regions may provide some of the best examples of floral color diversity, lending opportunities to explore the factors responsible for its evolution. It has also been hypothesized that plants of high-elevation sites may have substantially different coloration from those of lower communities. This hypothesis has been tested to some degree (see below), but further rigorous tests are required.

4.1 Is floral color spatially specific?

Limited data indicate that distributions of floral colors vary geographically among different flora. For example, in Australia and New Zealand, 53.5% and 70% of alpine flowers are white, respectively (Wardle, 1978; Pickering & Stock, 2003), whereas in the subnival zone of the Himalaya–Hengduan Mountain areas (SE QTP) 42.5% are blue–purple (Peng et al., 2012b). Species with blue coloration include members of well-known genera that are strongly represented in alpine genera of the QTP, for example, *Gentiana* (Gentianaceae), *Meconopsis* (Papaveraceae), and *Campanula* and *Cyananthus* (Campanulaceae). The geographical variation in color diversity has postulated associations with traits of the local pollinator fauna. The most abundant flower visitors in the alpine zone in New Zealand are generally flies and solitary bees (Primack, 1983), which reportedly have little color preference (Godley, 1979). Therefore, the absence of social bees (e.g., *Apis* and *Bombus*) may explain why flowers in New Zealand alpine habitats are less colorful than in other alpine areas. In contrast, the dominant blue–purple floral color in alpine regions of the Himalaya–Hengduan Mountains has suggested associations with the preferences of bumblebees, the most abundant and efficient pollinators in this area (Peng et al., 2012b). Based on results of a community study in the same area, Gong & Huang (2011) proposed that blue–purple flowers may evolve under selection by bumblebees. However, the hypothesis of adaptation to local pollinator fauna may not explain seasonal changes in floral color patterns observed in specific locations (see below), unless there are corresponding seasonal changes in pollinators and their preferences.

It should be noted that most empirical studies on floral color have been based on human color categories, despite knowledge that the flowers may be perceived very differently by pollinators' eyes. After analyzing spectra of alpine flowers from New Zealand, Bischoff et al. (2013) found that most inflection points (where the curves change most rapidly) of spectral curves fell in the area close to 400 and 500 nm, the area that

hymenopteran pollinators can discriminate most acutely. Their results suggest that flowers that were all pale white to human eyes were actually very attractive to native hymenopteran visitors and quite different from each other, thus facilitating interspecific discrimination (Bischoff et al., 2013). Furthermore, based on another spectral analysis, Arnold et al. (2009) found no significant altitude-related variation in overall coloration among alpine flowers at altitudes ranging from 700 to 1600 m a.s.l. in Norway. The most frequent colors had loci in the blue–green region of bee color space. Recently, data for 107 species from the Himalayan region (S QTP, 900–4000 m elevation) showed that floral colors were significantly more diverse in the subalpine zone than in the subtropical zone (Shrestha et al., 2014), which seems consistent with our experience. However, the chromatic cues for pollinators (based on reflectance spectra) between the two zones were consistent with the hue discriminability of the hymenopteran color visual system (Shrestha et al., 2014).

4.2   Is floral color temporally specific?

Floral color in communities also reportedly varies seasonally (Robertson, 1924; Warren & Billington, 2005), supposedly due to adaptive responses that optimize the attraction of pollinators, which may also vary seasonally. For example, Warren & Billington (2005) concluded that there is a significant interaction between flower color and month in Britain: yellow, white, and pink/purple flowers are most abundant in early summer, while the abundance of blue flowers is more or less constant throughout the flowering season. We have also observed remarkable seasonal changes in floral displays of the alpine flora community in the SE QTP (Peng et al., 2012b). For example, yellow flowers of several genera of Ranunculaceae seem to dominate early in the plant reproductive season, pink–purple flowers of *Primula* in mid-season, and blue–violet flowers of Gentianaceae are abundant in late periods. However, very few studies have tested the veracity and relevance of this apparent pattern. Arnold et al. (2009) found that an association between time and floral color is indeed present in Norway, but only for human color categories, and that the pattern is largely due to phylogenic effects (i.e., plants of the same family are more likely to flower at the same time and have similar colors). The more important finding was that this time–color pattern was absent in bee color categories (Arnold et al., 2009). All the above results imply that any experience or conclusion based on human color categories should be treated with caution, and tested more objectively. To our knowledge, the patterns in the

QTP and nearby regions have been explored in very few studies, although the remarkable diversity of QTP flora provides opportunities to test floral color hypotheses very rigorously and thoroughly. For the first step, species-rich genera that show remarkable floral color diversity in this area may be ideal material to investigate the influence of both biotic factors (related to phylogeny and interactions with pollinators or herbivores) and abiotic factors (physicochemical environmental conditions) on the evolution of floral color.

5   Breeding systems of plant species in the QTP

5.1   Sexual systems

Peng et al. (2014) found much higher proportions of hermaphroditic species (85.2%) and lower proportions of dioecious (6.4%) and monoecious species (8.4%) in the subnival belt of the Himalaya–Hengduan Mountains (SE QTP) than in other, lowland, floras. This pattern of sexual systems may reflect the reproductive strategies of plants that have evolved in response to the alpine environments. When insect pollination fails, hermaphroditism would be very advantageous for alpine plants, for several reasons. First, hermaphroditic species have showy floral displays (Duan et al., 2009; Peng et al., 2014), which can effectively attract more pollinators than less visible flowers and increase pollination probabilities. Second, hermaphroditic species have the prerequisites for self-pollination. Moreover, 97.1% of hermaphroditic alpine plant species of SW China that have been studied are self-compatible, according to published information, herbarium collections, and field observations surveyed by Peng et al. (2014), and most of these species can achieve reproductive assurance by autonomous or facilitated selfing (Sun et al., 2005; Duan et al., 2007a, 2010; Zhang & Li, 2008; Zhang et al., 2011a). However, this may be an over-estimate due to sampling bias, as 88.2% of these plants are autonomous or facilitated selfing species (Peng et al., 2014), which must be self-compatible, and species with distinctive selfing mechanisms may attract disproportionately high research interest. Therefore, objective sampling is required in future studies to gain more robust understanding of the breeding system patterns. Nevertheless, selfing hermaphroditic plants are favored during colonization (Stebbins, 1957), and thus are more likely than others to establish new populations in alpine areas. In contrast, diclinous species (especially dioecious species) depend on vectors for cross-pollination, and thus have high risks of pollination

failure. However, unisexual species (e.g., Poaceae, Cyperaceae, and Saliaceae species) can achieve optimal reproductive fitness through anemophily, generalized floral traits, and adjustments of both the sex ratio and the resource allocation of different sexes (Totland & Sottocornola, 2001; Zhao & Yang, 2008; Peng et al., 2012a, 2012b). For example, most diclinous species have anemophilous or generalized floral traits, and hence can be pollinated by diverse groups of pollinators, thus potentially mitigating the negative effects of the low mate availability and low abundance of biotic pollinators expected at high elevations. In addition, grass or shrub life habits can enable long-term persistence through clonal reproduction and long life-spans in alpine environments (Peng et al., 2014).

5.2   Self-pollination mechanisms

It has often been reported that the diversity, abundance, and activity of insect pollinators decrease with increases in elevation (Arroyo et al., 1982; Bingham & Orthner, 1998; Medan et al., 2002). Therefore, alpine plants are believed to be more prone to pollinator limitations than lowland taxa. Autonomous self-pollination mechanisms, which do not require the participation of an external vector, are selectively advantageous as they can greatly increase chances of successful reproduction when pollinator service is extremely unpredictable or low. To date, four selfing mechanisms have been observed in the QTP. The first mechanism involves the anther contacting the stigma through filament elongation. This occurs, for example, in *Gentianopsis barbata* (Froel.) Ma (Duan et al., 2007a) and *Gen. paludosa* (Munro ex Hook. f.) Ma (Duan et al., 2010). In the second mechanism, the anther contacts the stigma through corolla facilitation, for example, via the corolla wilting in *Pedicularis dunniana* Bonati (Sun et al., 2005), and abscising in *Incarvillea sinensis* var. *sinensis* Lam. (Bignoniaceae) (Qu et al., 2007). In the third, contact between the anther and stigma is facilitated by the petals closing and the stamens moving simultaneously, as observed in *Sinopodophyllum hexandrum* (Royle) T. S. Ying (Berberidaceae) (Xiong et al., 2013). The above three types are considered to be delayed selfing mechanisms, in which self-pollination is delayed until opportunities for outcrossing have passed. In the fourth mechanism, autonomous selfing occurs through the style curling down to contact the anther. For example, in *Roscoea schneideriana* (Loes.) Cowley the stigmas curl towards the anthers early in flowering, so this can also be considered a competing selfing rather than delayed selfing mechanism (Zhang & Li, 2008). Delayed selfing can ensure seed production (or at least greatly increase

its chances) when pollinators are scarce, but allows cross-pollination to predominate when they are abundant (as reviewed by Sun et al., 2005). Therefore, delayed selfing is also a prevalent selfing system in the QTP alpine region.

5.3   Ambophily

Self-pollination represents an evolutionary solution to pollen limitation of reproduction in alpine regions. However, dichogamy or herkogamy may reduce the likelihood of self-pollination (reviewed by Barrett, 2002). Winds are frequently strong in alpine environments, so wind pollination might be viewed as a potential alternative mechanism providing reproductive assurance for alpine plants. Moreover, in comparison to insect-pollinated plants, wind-pollinated plants have several advantages in the alpine region, including facilitation of pollen dispersal and low reproductive allocation (reviewed by Totland & Sottocornola, 2001; Peng et al., 2012a). However, the low density and small size of alpine plants may reduce the success of wind pollination. In such cases, ambophily (a mixture of insect and wind pollination) may be highly advantageous, by providing benefits of both strategies and boosting chances of reproductive success when animal pollinator service is extremely unpredictable or low. For example, *Aconitum gymnandrum* Maxim. (Ranunculaceae) has a mixed pollination syndrome of anemophily (degenerate sepals, exposed anthers and stigmas) and entomogamy (showy corolla and nectar). Experiments have also shown that wind pollination contributes to seed production of netted flowers after emasculation, so such a combination of insect and wind pollination in *Ac. gymnandrum* plays an important role in maintaining its sexual reproduction, allowing it to persist in arid habitats of the QTP (Zhang et al., 2006; Duan et al., 2009). The pollination pattern of *I. sinensis* var. *sinensis* suggests that it also has an ambophilous mechanism, which combines actions by bees with indirect participation by wind (Qu et al., 2007). However, when pollinator service is reliable, ambophilous taxa may also transit to exclusive animal pollination. For example, Huang et al. (2013) investigated wind and animal pollination in the alpine rush *Juncus allioides* Franch. (Juncaceae) and found that wind appeared to play a minor role in its pollen dispersal and that its seed set largely resulted from a mixture of insect and self-pollination, although most other members of Juncaceae are exclusively cross-pollinated by wind. Therefore, further exploration of the significance of ambophily for alpine plants is required. More generally, there is evidence that self-pollination and/or ambophily provide reproductive assurance for plants in the QTP and other

alpine areas, but further quantitative studies on their breeding systems and pollination modes, especially at a molecular level, are required.

6   Resource allocation patterns of plants in the QTP

Different selection pressures and environmental constraints will result in different patterns of resource allocation reflecting evolved strategies of plants (Bonser & Aarssen, 2001; Weiner, 2004). Thus, understanding allocation patterns is fundamentally important for understanding both plant ecology and plant evolution. Resource allocation theory predicts that plants should invest most internal resources (biomass, nutrients, and water) in organs that acquire external resources from compartments where those resources are most strongly limited (Bloom et al., 1985), and their investments will depend on both their size and plasticity (Weiner, 2004). Like many other mountain areas (e.g., Charlesworth & Charlesworth, 1981; Poorter & Nagel, 2000; Poorter et al., 2012), the QTP offers an excellent system for studying resource allocation patterns in plant species due to its extreme climatic and geomorphological diversity.

6.1   Reproductive allocation patterns

The relationship between reproductive and vegetative organs is a fundamental aspect of a plant's reproductive strategy. Thus, many studies have focused on the allometric relationship between these two compartments (Sugiyama & Bazzaz, 1998; Weiner et al., 2009; Guo et al., 2012). As one of the most important components of plant reproduction, the evolution of seed mass has received much attention. Several studies have found indications that two sets of factors, extrinsic environmental conditions and intrinsic reproductive factors including life-history constraints, drive evolutionary changes in seed mass (Venable, 1992; Westoby et al., 1996; Moles et al., 2005). In the eastern QTP, Guo et al. (2010a) found that the mean seed mass of *Pedicularis* species decreases with increasing elevation, mainly due to effects of an intrinsic factor (seed number per fruit) rather than the extrinsic factor (elevation). They also produce more, but smaller, seeds at higher altitudes, indicating a trade-off between quantity and quality of progenies (Guo et al., 2010a). This is consistent with indications from other studies that low temperature and short growing seasons can constrain the development of plant seeds in alpine regions (Baker, 1972; Totland & Birks, 1996). However, conflicting patterns have been found for

Anemone rivularis and *Trollius ranunculoides* Hemsl., in that increases in mean seed mass correspond with increases in elevation (Zhao et al., 2006). These patterns may reflect contrasting strategies. The negative relationship may be due to the low temperatures and short growing seasons at high altitude, reducing photosynthetic rates and hence production rates of the carbohydrates required for seed maturation, and time available for seed development and provisioning (Totland & Birks, 1996; Guo et al., 2010a). In stark contrast, the positive relationship may be due to evolutionary pressures on plants to produce large seeds with high levels of nutrients, thereby maximizing germination and seedling survival rates (Pluess et al., 2005). However, the evolutionary drivers of these patterns clearly require further elucidation.

Like many other biological processes, resource allocation in plant species is also associated with biotic factors (e.g., competition among plant species, plant size, and the sexual system) and abiotic factors (e.g., moisture, nutrient availability, and light). Effects of these factors, both generally and specifically in the QTP, are discussed below.

6.1.1   Biotic factors   A major biotic factor, plant size, is a determinant of the amount of energy available for reproduction and seed development. Therefore, large plants generally have large reproductive outputs (seeds and/or flowers) (Bazzaz et al., 2000; Moles & Westoby, 2004; Rees & Venable, 2007; Venable & Rees, 2009). This has been confirmed in the QTP (Zhao et al., 2006; He et al., 2008; Meng et al., 2011; Guo et al., 2012). For example, Meng et al. (2011) found that the biomass of reproductive organs and allocation of resources to reproduction in *Polygonum macrophyllum* D. Don increases with increases in plant size. Similar positive relationships between reproductive allocation and plant size have also been found in three *Oxytropis* species in the QTP (He et al., 2008). Guo et al. (2012) also found that larger *Pedicularis* plants produced more reproductive biomass than smaller ones, and attributed this to their modular architecture, as relatively large individuals within a population have more vegetative and reproductive modules than smaller individuals (Weiner, 1988; Niklas, 1993). However, as usual, conflicting patterns have also been reported (He et al., 2008; Liang et al., 2008; Wang et al., 2012). This can be simply explained by the fact that resources allocated to one function or organ are not available for other functions or organs. Other factors, such as life-history stage, can also influence plants' resource allocations to some extent (Xu et al., 2013).

6.1.2   Abiotic factors   As a factor that integrates effects of several environmental variables (e.g.,

temperature, precipitation, radiation, and soil nutrient availability), elevation has a significant relationship with plants' resource allocation patterns. A low rate of cell division due to low temperatures and cool, short growing seasons, and paucity of nutrients may lead to small plant sizes at high elevations (Ellenberg, 1988; Friend & Woodward, 1990; Suzuki, 1998; Zhao et al., 2006; Guo et al., 2010a). For example, both bulb biomass and the total biomass of *Fritillaria unibracteata* P. K. Hsiao & K. C. Hsia individuals reportedly decrease with increasing elevation, whereas the sexual reproductive (flower) allocation increases with increasing elevation (Xu et al., 2013). Similar patterns have also been observed in *Polygonum viviparum* L. (Fan & Yang, 2009a, 2009b). In contrast, plant size, reproductive biomass, and vegetative biomass of *Saussurea stella* Maxim. are all negatively correlated with elevation, and its allocation of resources to reproductive organs increases as elevation increases, an adaptive response that improves sexual reproductive success in harsh alpine environments (Fabbro & Körner, 2004; Wang et al., 2012). Guo et al. (2012) obtained similar results, but also detected a size-dependent effect, that is, at low altitudes large plants of the species allocate higher proportions of resources to reproduction than small plants, whereas at high altitudes the pattern is reversed. They attributed this size-dependent reproductive allocation pattern to an adaptive response to limits imposed on plant growth and survival by high elevation.

At a large scale, above- and below-ground biomass allocation in populations and/or ecosystems is a central concern for ecologists. In a study of two grassland types (alpine meadow and alpine steppe), Yang et al. (2009) found an isometric relationship between above- and below-ground biomass, which was independent of soil nutrient and moisture content. However, Ma et al. (2010a) found that with increases in elevation, plant species invest more biomass in belowground parts, especially storage organs, while the proportions allocated to leaves remain stable. In contrast, they found it was beneficial for plant species growing at high elevations to compensate for low carbon gain and nutrient uptake rates under low temperature and limited nutrient conditions by stabilizing biomass investment in photosynthetic structures and increasing the absorption surface area of fine roots (Ma et al., 2010a). Many other studies have focused on plant reproduction and vegetation allocation strategies in QTP regions (Liu et al., 2002; Liang et al., 2008; Wang et al., 2008a, 2009; Sonamtso et al., 2013), but most of these studies have been carried out in eastern parts of the QTP.

Thus, as the QTP is so large and covers such varied geographic and climatic types, as well as high plant diversity, further studies are required.

6.2   Sexual allocation patterns

Sex allocation theory predicts that male-biased allocation should be advantageous under environmental stress (Charlesworth & Charlesworth, 1981), because female functionality will be limited under severe environments, such as those of high elevation habitats (Dudley & Galen, 2007). This prediction has been confirmed by studies on *Pedicularis* and *An. rivularis* in eastern parts of the QTP (Zhao et al., 2006; Guo et al., 2010b). However, like resource allocation patterns, sexual allocation patterns may be affected by both biotic and abiotic factors (Kliber & Eckert, 2004; Buide, 2008; Zhao et al., 2008; Brookes et al., 2010; Guo et al., 2010b; Liu & Huang, 2012; Zhang et al., 2012). For example, Zhang et al. (2011c) showed that rewarding type (nectarless, nectar and pollen rewarding) can affect sexual allocation in *Pedicularis* species in the NE QTP. They attributed this floral allocation pattern to activities and foraging behavior of pollinators in the region. In addition, Liu & Huang (2012) studied resource allocation to sexes in the same inflorescences of *Adenophora jasionifolia* Franch. (Campanulaceae) using a flower thinning method and found that floral sex allocation (i.e., pollen and ovule production) was determined long before flowering. Moreover, early flower thinning (but not late thinning) increased the seed output of the remaining flowers, indicating that the flexibility of this species' allocation pattern varies with time and developmental stage (Liu & Huang, 2012). In summary, resource allocation patterns have been studied in many QTP plants, but many aspects of their evolution and associated adaptive strategies require further elucidation.

7   Perspectives

Findings obtained from numerous ecological studies at various evolutionary levels in recent decades have improved understanding of the survival and reproduction of plant species inhabiting high elevation sites in the QTP. However, due to the richness of the alpine flora, extreme spatial gradients in many environmental variables (e.g., elevation), pronounced temporal changes in some factors (e.g., seasonal temperature changes), and extremely diverse types of habitats, the QTP is an ideal system for more detailed explorations of plant species' adaptations at wider and deeper scales. Aspects of the focal phenomena in this

review that warrant further attention include the following.

1. Morphological adaptations: Deeper understanding of the molecular basis of these adaptations is required (Zhang et al., 2010a; Liu et al., 2013). Evidence is accumulating that distinctive morphological features of many QTP plants, such as the translucent bracts of *Rheum nobile* and *Rh. alexandrae*, arise from changes in gene expression (Zhang et al., 2010a; Liu et al., 2013). However, further studies are needed to explore the molecular basis of various other adaptive features.

2. Plant–plant interactions: Further exploration of the effects of interactions among plants on different scales (e.g., below-ground parts of plants) and communities (e.g., microbes and/or fauna) is needed. Nearly all studies on either facilitation or competition we have reviewed focused on the influences of plant–plant interactions on above-ground parts of individual plants and species assemblages in plant communities (but see Song et al., 2006). However, it is well known that most plants inhabiting high elevation sites with perennial life forms have huge below-ground parts that store energy and provide protection from the unpredictable abiotic conditions in their habitats. In the future, more studies should address the impact of interactions among plant species on their below-ground parts. At the community level, future work should include examinations of the effects of plant–plant interactions on the composition and structure of communities of other organisms, such as microbial and fauna communities.

3. Plant–pollinator interactions: The vast plant diversity in the QTP should be exploited to address fundamental problems of floral ecology and evolution. Although the hypothesis that pollinators mediate floral diversity and subsequent speciation in *Pedicularis* has been rejected, the mechanisms that have driven the evolution of so many *Pedicularis* species in the SE QTP are still unclear. Research on genera such as *Rhododendron* and *Primula* is also urgently required. They differ greatly from *Pedicularis* in floral morphology, so different patterns of diversification will probably be uncovered. Many genera have open flowers with rewards available to diverse pollinators and potentially suffer great pollen interference when they are sympatric, casting doubt on the importance of selection for floral diversification in angiosperm speciation and coexistence. However, very little is known about the pollination ecology of those genera.

4. Color patterns of flowers: The color of most flowers is due to the display of pigments (e.g., anthocyanins and carotenoids). Both physiological and biological factors may influence the synthesis of these compounds. It has been suggested that environmental stresses, such as high UV radiation, extreme temperature, and drought, may be directly responsible for the brightly colored flowers in alpine habitats with functions other than pollinator attractiveness or phylogeny constraints (e.g., photoprotection, Hatier & Gould, 2009). However, identifying the factors that are primarily responsible for shaping the floral color is difficult, as plants in alpine habitats are often subject to stresses related to both sets of factors (especially high UV radiation and low pollinator abundance). More studies are needed to examine the relative importance of abiotic and biotic factors in the evolution of floral color.

5. Pollination and resource allocation patterns: The general patterns should be extended in relation to spatial and/or temporal gradients. The patterns of sexual systems and allocation of resources may vary with altitudinal gradient and habitat type, and reflect the divergent adaptive strategies of plant species under different abiotic conditions. Further investigations should include analyses of associations between patterns of sexual systems and allocation in taxa such as *Cyananthus*, *Primula*, and *Delphinium* that have diverse sexual systems and/or are widely distributed in diverse habitats of the QTP.

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