

# The evolution of plant reproductive ecology in China

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Scientific interest in plant reproduction has a long and venerable history going back to early European naturalists including Carl Linnaeus, Christian Konrad Sprengel, Joseph Kölreuter, Fritz and Hermann Müller, George Henslow and of course, Charles Darwin. Darwin can be considered the founder of modern plant reproductive biology. His three books (Darwin 1862, 1876, 1877) laid the conceptual foundation for the field, and many of the ideas they contain are still topics of active research (reviewed in Barrett 2010). The turn of the 20th century saw the rediscovery of Mendel's Laws and breeding experiments on flowering plants played an important role in establishing many key elements of modern genetics. By the 1940s, Fisher had developed the population genetic principles for theoretical analysis of the evolution of plant mating systems (Fisher 1941), and experimental taxonomists were starting to investigate breeding patterns, recognizing that reproductive mode played an important role in governing the patterns of phenotypic variation on which species delimitation was based (Davis and Heywood 1963). Subsequently, the 'electrophoresis revolution' (Lewontin 1974), birth of plant population biology (Harper 1977) and development of sex allocation theory (Charnov 1982) each broadened the approaches used in studies of plant reproductive biology. The 1980s saw the coming of age of investigations on the ecology of plant reproduction with the publication of 'Plant Reproductive Ecology' (Willson 1983) and 'Plant Reproductive Ecology: Patterns and Strategies' (Lovett Doust and Lovett Doust 1988). Today the field is an integral part of evolutionary ecology with articles routinely appearing in the most influential international scientific journals.

During much of the 20th century, research in China on plant reproduction focused largely on crop breeding and forestry. Most nonapplied work in plant biology involved the basic subdisciplines (e.g. taxonomy, morphology, physiology and genetics) and the limited number of scientists trained in plant evolutionary ecology meant that this area was largely a backwater that few were prepared to explore. However, the turn of the new millennium in China saw an awakening of interest in the ecology and evolution of plant reproduction. Progress in this area over the past 15 years has been remarkable with a growing number of research groups across China playing an important role in

raising the profile of the field, particularly in pollination biology. Useful summaries of Chinese research on pollination are available in Huang and Guo (2000) and Huang (2012). A recent unpublished survey by Ying-Ze Xiong and Shuang-Quan Huang, based on data from Web of Science of global publications in plant reproductive ecology from 2000 to 2014, indicates that articles by Chinese scientists now account for ~6% of the roughly 35 000 that have appeared in this area. Table 1 presents a representative selection of 12 articles published over the past 15 years that in my view have made especially valuable contributions to the diverse areas that comprise modern plant reproductive ecology.

This special issue of the *Journal of Plant Ecology* on plant reproductive ecology, edited by my colleagues Shuang-Quan Huang, Wan-Jin Liao and Da-Yong Zhang, is an impressive testimony to the recent accomplishments of Chinese plant ecologists. I was delighted to be asked to write the editorial to this volume and reflect on past accomplishments and future prospects. Over the past 15 years, I have been fortunate to visit China to give lectures, participate in workshops and collaborate with several research groups; these experiences have been among the most rewarding of my academic career. Not only have I benefited considerably from my interactions with students and faculty, but I have also been impressed on each visit by the rapid progress and increasingly diverse approaches being employed to tackle problems in plant reproductive ecology. I begin this editorial with some personal reflections on some of the potential reasons for the explosive growth of plant reproductive ecology in China and then provide a brief summary of some of the exciting work presented in this volume. I conclude with a glimpse into the future and suggest some areas that could be strengthened so that Chinese contributions can move to the forefront of research in this area.

What accounts for the impressive growth of plant reproductive ecology in China over the past 15 years? Obviously no single person, event or historical precedent is likely to have been pivotal. Rather, a variety of factors probably played a role, including the value that the Chinese government and its people place on scientific research, the growing concerns about environmental issues and the loss of biodiversity, and the increase in research funding available to plant ecologists.

**Table 1:** selected journal articles on research conducted in China representing diverse topics and approaches in plant reproductive ecology

Author(s), year, journal	Topic	Study system	Significance
Zhang (2000) <i>American Naturalist</i>	Resource allocation and selfing	Theory	Selfing promotes evolution of the annual habit
Li et al. (2001) <i>Nature</i>	Floral biology	<i>Alpinia</i>	Novel floral polymorphism
Wang et al. (2004) <i>Nature</i>	Floral biology	<i>Caulokaempferia</i>	Novel selfing mechanism
Huang et al. (2004) <i>Evolution</i>	Floral sex allocation	<i>Aquilegia</i>	Male allocation decreases with successive flowers in a protogynous species
Zhang et al. (2005) <i>American Journal of Botany</i>	Pollination syndromes and mating	<i>Tacca</i>	Paradox of high selfing in a sapromyophilous species with extravagant display
Bai et al. (2007) <i>New Phytologist</i>	Mating and heterodichogamy	<i>Juglans</i>	Heterodichogamy promotes disassortative mating
Wang and Chen (2009) <i>Ecology</i>	Seed dispersal	<i>Apodemus</i> in pine forest	Seed size affects dispersal by seed caching rodents
Ren et al. (2011) <i>PNAS</i>	Mimicry and pollination	<i>Cypripedium</i>	Floral mimesis of fungus-infected foliage
Shang et al. (2012) <i>Molecular Ecology</i>	Maintenance of sexual polymorphism	<i>Acer</i>	Pollen transfer model and mating patterns predict sex phenotype frequencies
Fang and Huang (2013) <i>Ecology</i>	Pollination networks	Alpine meadow	Generalist flowers receive more heterospecific pollen
Liao and Harder (2014) <i>American Naturalist</i>	Clonality and mating	Artificial flowers and simulations	Clonality has the potential to reduce geitonogamy
Zhou et al. (2015) <i>New Phytologist</i>	Function of heterostyly	<i>Luculia</i>	Distyly promotes disassortative mating

A symposium on plant breeding systems at the International Genetics Congress in Beijing in 1998 can be identified as an early beginning, and gatherings of plant reproductive biologists at Wuhan University in 2001 and 2007, Xishuangbanna Tropical Botanical Garden (XTBG) in 2004, and Beijing Normal University in 2003 and 2006 featuring lectures by invited foreign and Chinese scientists undoubtedly stimulated early interest and collaboration. The meeting in 2006, 'International Workshop on Plant Reproductive Biology', organized by Da-Yong Zhang was especially significant because, in addition to formal lectures by Lawrence Harder, Christopher Eckert, John Pannell and myself, it involved a field component at three different locations spanning diverse ecosystems in China (Dongling Mountain, Xiaolongmen National Forest Park, Jade Dragon Field Station near Lijiang and XTBG) where 20–30 Chinese students conducted short field projects on reproductive ecology, some of which have ultimately led to valuable publications (Fig. 1). The great success of the 2006 workshop led to the organization of five subsequent workshops in 'Plant Reproductive Ecology' held at Beijing Normal University (2009), Wuhan Botanical Garden (2010), XTBG (2011), Xinjiang Agricultural University, Urumqi (2012) and South China Botanical Garden, Guangzhou (2014) organized by Da-Yong Zhang, Ming-Xun Ren, Jiang-Yun Gao, Dun-Yan Tan and Dian-Xiang Zhang and colleagues, respectively. These workshops have grown in popularity, with ~150 attendees at the 2014 meeting in Guangzhou, and solidified plant reproductive biology as one of the most vibrant areas of research in ecology and evolution in China.

This volume contains 16 articles describing recent research findings in plant reproductive ecology. The topics are diverse and include investigations from a wide range of ecosystems in China including the alpine (6 articles), forests and woodlands (6), weedy habitats (3) and the desert (1) and involving diverse taxa from orchids to oaks as well as several introduced weeds. Most studies involve specific focal species but three take a community-level approach. Nine of the articles involve functional questions related to the adaptive significance of particular traits or patterns of sex allocation and phenology. The popularity of pollination biology in China is evident with 10 articles concerned with some aspect of the pollination process and three investigating pollen limitation of maternal reproductive success. Given the importance of field experiments in plant reproductive ecology it is encouraging that the majority of articles (9) employed some form of experimental manipulation. Below I provide a brief review of the articles in this special issue—highlighting the main findings and also considering unresolved issues.

## ALPINE MEADOW POLLINATION BIOLOGY: FROM FLORAL BIOLOGY TO SEX ALLOCATION

Alpine meadows have always been an attractive setting for research in pollination biology because of the high diversity of animal-pollinated species. The extent of pollen transfer between coflowering species and its influence on plant fitness



**Figure 1:** images from the field component of the *International Workshop on Plant Reproductive Biology* (May 2006) organized by Da-Yong Zhang. (A) Spencer Barrett and students investigating the complex sex expression of *Acer pictum* subsp. *mono* at Dongling Mountain (see Shang *et al.* 2012). (B) Lawrence Harder and Christopher Eckert supervising the data analysis of projects at Dongling Mountain with Shi-Xiao Luo and Shu-Rong Zhou, among others, scrutinizing the results. (C) Bi-Ru Zhu, Yuan-ye Zhang, Christopher Eckert, Yan-Fei Zeng and Wan-Jin Liao recording the floral characteristics of *Rhododendron* at the Jade Dragon Field Station near Lijiang.

is an important question in pollination biology (Ashman and Arceo-Gómez 2013; Fang and Huang 2013). Any pollen deposition on stigmas of other species represents a loss of male outcross mating opportunities raising the question of what mechanisms might limit this type of pollen transfer. Huang *et al.* (2015) investigate the influence of pollinator fidelity and pollen segregation on the bodies of bumblebees as potential mechanisms limiting interspecific pollen transfer in coflowering species of *Salvia* (Lamiaceae) and *Delphinium* (Ranunculaceae) in an alpine meadow. They found that the relatively high foraging fidelity and different deposition sites of pollen on the single effective species of *Bombus* visiting the two species they investigated serve to limit interspecific pollen transfer. This may account for the lack of evidence for any reductions in seed set in open- versus cross-pollinated flowers despite hand crosses showing such effects when interspecific pollen was used. The ecological and evolutionary significance of interspecific pollen transfer in plant communities remains an unresolved question in pollination biology and alpine meadows are an ideal ecological context for these types of investigations.

Alpine communities are inevitably composed of species that vary in floral longevity and determining the ecological and evolutionary factors responsible for maintaining variation in flower life spans is an important general question in plant reproductive ecology. Earlier studies established that flower construction and maintenance costs, and the time necessary for fitness accrual through male and female function, play important roles in explaining variation in floral longevity (Schoen and Ashman 1995). In a study of floral longevity in a community of alpine plants, Gao *et al.* (2015) report that floral sexual investment and dichogamy are also associated with floral longevity. Larger flowers produced more pollen and tended to 'live' longer whereas ovule number was not associated with floral longevity. They also found that protandrous species on average exhibited longer floral longevities than adichogamous species, as might be expected because of the temporal requirements for separation of male and female function. Interestingly, in contrast to predictions from sexual selection theory (see Lloyd and Yates 1982) these authors found that the female phase of protandrous species was significantly longer than the male phase, despite the association between the duration of male function, pollen production and floral longevity.

Nectar production is an important trait affecting patterns of pollinator foraging, gene dispersal and mating patterns in plant populations. Studies of nectar amounts indicate wide variation within plants and efforts have been directed toward understanding the adaptive significance of this variation (Biernaskie and Cartar 2004). Lu *et al.* (2015) focus their attention on the correlates of nectar production in protandrous *Aconitum gymnanthum* (Ranunculaceae), an annual bumblebee-pollinated species of alpine meadows. They confirm the common finding that basal flowers within inflorescences produce more nectar than distal flowers; however, in

contrast to most other studies they found no evidence for differences in nectar production between the male and female phases of flowers, or between nectar volume and flower or inflorescence size. In *A. gymnanthrum* attractive traits do not appear to be 'honest' signals of the amount of floral rewards, as has been reported in other species and raising the intriguing question as to why this might be.

A second article in this special issue also investigates position-dependent influences on floral attributes in *A. gymnanthrum*, but from the perspective of the ecology of sex allocation. Plasticity in sex allocation and gender is a common feature of flowering plants probably because of their immobile habit and occupation of heterogeneous environments (Lloyd and Bawa 1984). One of the predictions of sex allocation theory is that low resource conditions should result in male-biased allocation, but how position-dependent effects on floral investment interact with resource supply has not been investigated within an experimental framework. By manipulating opportunities for resource acquisition through leaf removal in *A. gymnanthrum*, Zhao *et al.* (2015) demonstrate that allocation to male function increased in more distal flowers within an inflorescence whereas female allocation was unaffected or declined. As the experiment made use of full-sib families, they were also able to demonstrate additive genetic variation for plasticity in floral sex allocation. This is significant as it indicates the potential for selection on sex allocation plasticity if environmental conditions require such a response.

## FACTORS INFLUENCING POLLEN LIMITATION

The proximate causes and evolutionary consequences of pollen limitation in flowering plants are central problems in reproductive ecology. Over the past decade, considerable progress has been made in our understanding of the prevalence of pollen limitation and the recognition of pollen quantity and quality limitation of fruit and seed production (Aizen and Harder 2007; Knight *et al.* 2005). Orchids have notoriously low fruit set and are commonly pollen limited (Ren *et al.* 2011). However, relatively few long-term studies have combined pollinator observations with measurements of pollinia removal and open-pollinated fruit set. Xiong *et al.* (2015) conducted an 8-year study of this type in *Habenaria glaucifolia* (Orchidaceae) in an alpine meadow in SW China. In most years, no pollinators were recorded and the transfer of pollinia between plants was very low. However, in three consecutive years numerous hawkmoths were observed and pollinia removal and fruit set were correspondingly high, although fruit set was still pollinator limited based on evidence from supplemental pollination. The authors suggest that the irregular 'mast fruiting behavior' of *H. glaucifolia* may be a 'sit-and-wait' adaptive strategy that results from unreliable pollinator service. Why the authors observed an abundance of pollinators in three consecutive years and not at other times during

the 8 years of observation is an intriguing question that remains unresolved.

An important question in studies of plant sex allocation is to explain the common observation of gradients of investment to pollen, ovules and seeds from basal to distal flowers within inflorescences of hermaphroditic plants (Brunet and Charlesworth 1995; Huang *et al.* 2004). To address this problem, Cao *et al.* (2015) investigated the roles of pollen and resource limitation in governing patterns of fruit and seed set within inflorescences of *Hosta ventricosa* (Asparagaceae) using controlled pollinations and flower removal experiments. As this species is a pseudogamous apomict, seed set is a satisfactory estimate of fitness, and the complicating influences of inbreeding depression in affecting seed production is therefore avoided. The authors predicted different patterns of sex allocation than are usually expected in sexual hermaphrodites. They found a significant decline in pollen-ovule ratios from basal to distal flowers and suggest that this pattern reflects the absence of fitness gain through male function in their asexual species. There are few comparative studies of sex allocation in related sexual and apomictic species and future investigations on this topic could provide novel insights into the forces shaping reproductive investment in plants.

A wide range of environmental and demographic factors can influence pollen limitation of maternal reproductive success. In animal-pollinated plants, population size is of particular importance because small populations may attract few pollinators (Ågren 1996), but conversely in larger populations there may not be enough pollinators to service flowers (Larson and Barrett 1999). Thus, determining the specific relations between population size and the intensity of pollen limitation is of interest, especially in invasive plants because of the wide range of population sizes commonly associated with colonization of new territory. Zhang and Lou (2015) report a significant relation between pollen limitation and population size in invasive populations of bee-pollinated *Solanum rostratum* (Solanaceae). A high degree of pollen limitation was evident in two small populations with much less in four larger populations. It is unclear in this system whether variation in the intensity of pollen limitation has demographic consequences for population growth rates (Morgan *et al.* 2005). Future studies would be worthwhile to determine if insufficient pollinator service influences colonization dynamics in this introduced species.

## THE FUNCTION AND ADAPTIVE SIGNIFICANCE OF TRAITS

Studies of adaptation are fundamental to the discipline of evolutionary ecology. Because of their immobile habit and experimental tractability, plants offer outstanding opportunities for investigating the function and adaptive significance of morphological, reproductive, and life-history traits. Alpine environments commonly experience stressful abiotic

conditions requiring the evolution of diverse adaptations to enable survival and reproduction. Peng *et al.* (2015) investigate the function of the woolly, overlapping leaves that characterize *Eriophyton wallichii* (Lamiaceae), a diminutive mint that occurs on alpine screes in the Himalaya-Hengduan Mountains. The environments in which the species occurs experience frequent rain, brief periods of intense solar radiation and fluctuations in temperature. Through a series of manipulative laboratory and field experiments, the authors provide evidence that the woolly trichomes on leaves repel water and absorb solar radiation, thus serving to limit fungal infections and maintain leaf heat, respectively. The overlapping habit of the leaves was further shown to buffer pollen and seed development against wide temperature fluctuations. Convergent evolution of vegetative structures among unrelated lineages is commonplace in alpine environments in response to stressful conditions (Körner 2003). The mountainous regions of China therefore offer outstanding opportunities for additional functional work of this type.

Color polymorphisms are ubiquitous in plants and animals. A central question that has been the focus of considerable research concerns the origin and maintenance of this form of variation. Flower color polymorphisms most commonly involve the occurrence of several morphs within populations that differ in flower color (e.g. the white and blue color morphs of *Linanthus parryae*—Schemske and Bierzychudek 2001). Less common are polymorphisms involving the reproductive organs themselves and this is particularly the case for female sex organs. Yang *et al.* (2015) report for the first time a stigma color polymorphism in the woodland tree *Acer pictum* subsp. *mono* (Sapindaceae) and investigate the possible functional significance of this variation, which involves individuals with either red or green-yellow stigmas. They provide evidence that stigma color differences affect various fitness components associated with pollen germination and seed maturation and propose that temperature could be a factor in maintaining the observed variation. They hypothesize that red stigmas may function more effectively during flowering at cooler temperatures. Future surveys of populations occurring across temperature gradients in China would be valuable to determine if stigma color morph ratios change in a predictable way, with cooler environments favoring the morph with red stigmas.

Many angiosperm taxa with relatively small flowers, including *Cornus*, *Davidia*, *Hydrangea*, *Mussaenda* and *Viburnum*, possess showy petaloid bracts. Their role in pollinator attraction or other potential functions is a topic of considerable interest to reproductive ecologists (Jin *et al.* 2010; Sun *et al.* 2008). Song *et al.* (2015) extend previous studies of this problem by considering the relative importance of olfactory as well as visual cues in pollinator attraction in *Cornus capitata* (Cornaceae), a small tree pollinated primarily by *Anthophora*. Using behavioral bioassays and experiments involving inflorescence and bract manipulation they provide evidence that the showy white bracts of *C. capitata* mainly function as a visual flag in

long distance signaling of bees, whereas olfactory cues assist landing at short distance. A major future challenge in studies of this sort will be to determine the relative importance of showy bracts to fitness gain through female versus male function. Manipulative experiments and the use of highly polymorphic genetic markers would be required to address this problem.

Although petals serve as the primary organ of attraction in most animal-pollinated flowers, a variety of other organs can function to increase the attractiveness of floral displays, such as the showy bracts discussed above in *Cornus* and other genera. However, in *Limonium* (Plumbaginaceae) persistent calyces also have the potential to serve this function owing to the very small flowers of most species in this genus. Zhang *et al.* (2015) investigate this possibility by manipulating the presence and absence of calyces in inflorescences of *Limonium leptolobum*, a perennial desert herb from northern Xinjiang Province. Although field observations indicated that diverse pollinators visit plants, there was no evidence that they preferred intact over manipulated inflorescences. Therefore, the pollinator attraction hypothesis for the function of calyces in this species was not supported. As both treatments were applied to inflorescences on each plant in the study, it would be worthwhile in future work to conduct whole plant manipulations to determine if plants without calyces are still as attractive to pollinators as those that possess them.

## REPRODUCTIVE PHENOLOGY: FROM THE HERBARIUM TO THE MOLECULAR LABORATORY

Flowering phenology is a key trait in the reproductive ecology of plants. There is evidence for abundant quantitative genetic variation for flowering time and adaptive differentiation among populations of many species in relation to climatic gradients (Colautti and Barrett 2013). However, less is known about the factors governing flowering phenology in large multispecies assemblages, particularly in tropical and subtropical communities. Using information from herbarium specimens collected from 2059 species between 1920 and 2007 in a subtropical forest in Guangdong Province, Pei *et al.* (2015) investigate differences in flowering phenology among trees, shrubs, herbs and vines, and consider the role of environmental and historical factors in shaping the patterns revealed by their analyses. Correlations between abiotic factors (temperature, rainfall and sunshine) and patterns of flowering indicate that climatic factors are probably most important in governing flowering time; however, their analyses suggest that phylogenetic constraints also play a role. This study highlights the immense store of valuable biological information in the herbaria of China that awaits future investigations.

Range margins can provide novel insights into ecological and evolutionary processes because biotic and abiotic factors affecting mating and dispersal commonly differ from the

center of the range (Hargreaves and Eckert 2014). For species involved in co-evolved mutualisms, changed environmental conditions along geographical gradients may be particularly important because old partnerships may break down resulting in the emergence of new interactions. This appears to have happened in *Ficus squamosa* (Moraceae), a dioecious fig in which a host shift involving its wasp pollinator is evident at the range limit of the species in southern Yunnan. Liu *et al.* (2015) provide evidence that a new species of pollinating wasp, recruited from the co-occurring but unrelated *F. heterostyla*, has replaced its usual partner and examine why this may have occurred. The findings of this study are of particular interest because they suggest ways in which fig species may establish novel fig-wasp partnerships and demonstrate that, at least in some species, pollinator sharing can occur.

One of the main goals of the new field of ecological genomics is to determine the molecular basis of adaptation by finding the specific genes involved and documenting their patterns of variation and expression (Barrett and Hoekstra 2011; Stinchcombe and Hoekstra 2008). Plant reproductive characters provide a rich source of biological diversity for this type of study. Flowering time is a key life-history trait and considerable progress has been made in recent years in understanding the selective forces governing selection on flowering time as well as the genes and their interactions that are responsible (*Arabidopsis thaliana*—Caicedo *et al.* 2004; Stinchcombe *et al.* 2004). Li *et al.* (2015a) report a preliminary study of two geographically separated populations of invasive *Ambrosia artemisiifolia* (Asteraceae), previously shown to differ in flowering time consistent with climatic adaptation. They compare gene expression in eight genes known to influence flowering in other species and find significant differences in expression between the populations. Although preliminary, this study provides a valuable starting point for more detailed future investigations. *Ambrosia artemisiifolia* was introduced to China in the 1930s and therefore research on the molecular basis of contemporary climatic adaptation is of particular interest.

## GENETIC MARKERS AND THE MATING BIOLOGY OF POPULATIONS

Important advances in plant reproductive ecology have come from the use of genetic markers to investigate the mating biology of populations. It is now possible to directly measure outcrossing and selfing rates, levels of disassortative and assortative mating, multiple paternity, gene flow and hybridization, all of which provide important insights linking mating systems to the ecology and evolution of populations (Barrett and Harder 1996). Genetic markers also enable tests of functional hypotheses concerning the floral biology and sexual systems of populations (Bai *et al.* 2007; Shang *et al.* 2012; Zhou *et al.* 2015). Li *et al.* (2015b) employ this second approach in their investigation of the function of heteranthery in *Commelina communis* (Commelinaceae), an annual

weed of temperate northeast Asia with nectarless flowers and stamen trimorphism. In the majority of nectarless flowers pollen is the main reward for pollinators, but this is also the vehicle for male fitness gain. This evolutionary dilemma has been solved in heterantherous plants in which a ‘division of labor’ in anther function occurs, with conspicuous ‘feeding anthers’ serving to attract pollen-collecting bees and cryptic ‘pollinating anthers’ promoting cross-pollination (Luo *et al.* 2008; Vallejo-Marín *et al.* 2009). Li and colleagues demonstrate that the function of heteranthery in promoting cross-pollination is compromised in *C. communis* because small bees act as pollen thieves causing high selfing rates in several populations. Their study illustrates that we should not expect floral adaptations to always function ‘optimally’ (and see Zhang *et al.* 2005), and raises the question of whether the high selfing rates they document are a general feature of the species throughout its range.

In contrast to many animal groups, hybridization is a widespread phenomenon among many lineages of flowering plants, resulting in complex patterns of variation and the origin of new species. It is now widely appreciated that both morphological and molecular analyses of putative hybrid zones are necessary for in-depth analyses of the causes and consequences of hybridization for plant evolution (Arnold 1997). Wei *et al.* (2015) examine morphological and microsatellite variation in a hybrid zone of two oak species, *Quercus liaotungensis* and *Q. mongolica*, in north China. Because the area of contact between the two species is relatively recent compared with other parts of the range, the authors predicted that reproductive isolation arising from reinforcement might have had insufficient time to develop. This prediction was confirmed because 74% of all the trees sampled were hybrids. Despite the high frequency of hybrids, most resembled *Q. liaotungensis* raising questions about the degree of dominance affecting the morphological traits distinguishing the two species, and whether there are asymmetries in the parentage of crosses.

This collection of articles provides a timely overview of the current status of plant reproductive ecology in China. It highlights particular strengths including pollination biology, sex allocation studies and experimental investigations of the function of reproductive traits, but also suggests opportunities for further growth. Although most articles addressed specific hypotheses, few involved explicit tests of models and the absence of theory development suggests a need to strengthen the conceptual foundations of research. Only two studies explicitly investigated mating patterns using genetic markers and future efforts to investigate functional links between pollination processes and mating outcomes will require the adoption of marker-based technologies in more laboratories. An increased use of genetic markers and genomic approaches would also help to infuse ecological studies of plant reproduction with stronger population genomic content and lead to greater integration between ecology and evolutionary genetics. Phylogenetic methods

are revolutionizing many areas, including reproductive ecology, and future collaborations in comparative biology between systematists and ecologists will undoubtedly provide valuable insights into the origin and adaptive significance of reproductive diversity.

Several other specific topics in reproductive ecology that I believe would benefit from increased attention in the years ahead include: (i) influences of clonality on sexual reproduction; (ii) dynamics of resource allocation in relation to mating and seed production in perennial plants; (iii) correlated evolution of mating and seed dispersal systems; (iv) coevolution between plant reproduction and defense against herbivores; (v) community phylogenetics of plant reproductive traits. These are just a few of the exciting new avenues for research and the forthcoming 19th International Botanical Congress in Shenzhen, China in 2017 will provide an outstanding opportunity for Chinese scientists to showcase recent accomplishments in plant reproductive ecology to the world's plant biologists.

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