

Sexual Systems and Ecological Correlates in an Azonal Tropical Forests, SW China

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ABSTRACT

Unlike the seriate lowland rain forests in SE Asia, the tropical vegetation of Xishuangbanna (SW China) has developed in habitats with comparatively lower temperatures and precipitation. Consequently, although most of the families and genera of the flora are components of tropical ecosystems, many have reached their distribution limits in latitude. Selection pressures on sexual systems in these environments may be different from that experienced in lowland tropical regions. Here, we examine the sexual systems of 685 species of flowering plants belonging to 109 families and 356 genera based on 42 plots with a total area of 15.4 ha and compare our results with surveys of sexual systems from other tropical ecosystems. Among these species, 60.6 percent were hermaphroditic, 14.3 percent were monoecious, and 25.1 percent were dioecious. The percentage of dioecious sexual system among tree species (26.1%) was similar or higher than that of other tropical tree floras. Monoecy was significantly associated with the tree growth form and was relatively common in seasonal forest vegetation. Sexual systems involving unisexual flowers (dicliny) are particularly well represented in the tropical forests of Xishuangbanna accounting for 39.4 percent of all species surveyed. This pattern may be associated with the prevalence of relatively small inconspicuous flowers in the tropical forests of SE Asia and their correlation with diclinous sexual systems generally.

Abstract in Chinese is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: dioecy; flower sizes; fruit types; monoecy; montane forest; seasonal forest.

REPRODUCTIVE TRAITS PLAY AN IMPORTANT ROLE IN DETERMINING PLANT FITNESS, stand dynamics, genetic diversity, and species interactions both at the population and community level (Chazdon *et al.* 2003). Since tropical forests are characterized by high species richness and low population densities, understanding the ecology of reproductive success and the dynamics of gene flow is critical for determining the diverse forces maintaining species diversity. Among reproductive traits, sexual systems have been the most important subjects for study in surveys of tropical forests (Ashton 1969, Bawa 1974, Bawa *et al.* 1985, Ibarra-Manríquez & Qyama 1992, Gross 2005, Mataliana *et al.* 2005). This attention is due to the key role played by sexual systems in influencing many components of the ecology and evolution of plant populations.

Most community-level surveys demonstrate a roughly similar general pattern in the frequency distribution of sexual systems; hermaphroditic species are dominant, followed by different proportions of dioecy and monoecy. Although only *ca* 6 percent of flowering plants are dioecious (Renner & Ricklefs 1995), dioecy has received particular attention in studies of the evolution of plant sexual systems (Geber *et al.* 1999). Significant effort has been spent in documenting correlations between dioecy and morphological and ecological traits (reviewed in Renner & Ricklefs 1995, Vamosi *et al.* 2003). The traits most consistently associated with dioecy at the family level are monoecy, wind or water pollination, and the climbing growth form (Renner & Ricklefs 1995).

Dioecy is often considered to be evolutionary derived from monoecy, although relatively little is known about the ecological and genetic mechanisms responsible for this transition in sexual systems (Charlesworth & Charlesworth 1978, Renner & Won 2001, Barrett 2002). The ecology, evolution, and distribution of monoecy

have received relatively little attention in comparison with dioecy. This may be because of the lower frequency of monoecy compared to dioecy in tropical forest trees (see Bawa & Opler 1975), and the general interest that gender dimorphism has attracted among plant evolutionary biologists (reviewed in Geber *et al.* 1999). Correlates of monoecy have rarely been documented, although Flores and Schemske (1984) found that monoecious trees and shrubs commonly exhibit many-seeded dry fruits. Because dioecy is often associated with fleshy fruits and may often evolve from monoecy, this association clearly needs further investigation.

Most community-level studies of reproductive biology in tropical forests have been conducted in the Neotropics (Flores & Schemske 1984, Bawa *et al.* 1985, Bullock 1985, Ibarra-Maríquez & Oyama 1992, Chazdon *et al.* 2003, Gross 2005, Mataliana *et al.* 2005). Knowledge of reproductive biology of tropical Asian forests is less well known except for work on dipterocarp forests in lowland SE Asia, which have been studied particularly with respect to their patterns of flowering phenology (Appanah 1985, Kato 1996, Momose *et al.* 1998, Sakai *et al.* 1999). Community-level investigations of plant reproductive biology in tropical forests of China have not been examined in any detail and hence little is known about the distribution of sexual systems in this region.

Xishuangbanna (Yunnan Province, SW China) is located at the northern margin of tropical Asia, and is in a geographically intermediate zone between continental Asia and the SE Asian Peninsula. Its climate is transitional between the tropics and subtropics (Zhu 1993b, Cao & Zhang 1997). The flora of Xishuangbanna is thought to have originated from ancient Gondwana and Laurasian elements, but is also strongly affected by the modern tropical Asian flora (Zhu *et al.* 2001). Records of 3336 native seed plant species belonging to 1140 genera and 197 families have been made from Xishuangbanna region (Zhu *et al.* 2001). The flora is largely tropical in nature with most of the tropical families and genera at their

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northern latitudinal limits of distribution (Zhu 1997). The biotic groups, mainly composed of tropical elements, mix together with temperate elements (Cao & Zhang 1997), and differ from lowland rain forests of equatorial areas in having some deciduous trees in the canopy layer (Zhu 1997). Through decades of investigation, there is now a reasonable taxonomic framework for the flora in this area enabling community-level work on plant reproductive biology.

Tropical forests of Xishuangbanna developed under comparatively low temperatures and precipitation in comparison with lowland tropical forests to the south. It is therefore possible that because of less tropical conditions and the somewhat different taxonomic composition of the forests the selective forces on sexual systems may be different to that experienced in other tropical regions. To investigate this possibility, we addressed three principal objectives based on a survey of 685 angiosperm species to: (1) determine the frequency distribution of hermaphroditic, monoecious, and dioecious sexual systems; (2) compare the frequency distribution of sexual systems with that of other tropical floras; and (3) quantify the association between sexual systems and several morphological and ecological traits.

METHODS

PHYSICAL GEOGRAPHY AND VEGETATION TYPES.—Xishuangbanna (21°09'–22°33' N, 99°58'–101°50' E), located in SW China bordering Laos and Myanmar, is a mountainous area at the southern terminal of the Hengduang Mountains. The upper course of the Mekong river flows through this area from north to south (Fig. 1). The climate of Xishuangbanna is dominated by a SW monsoon with high rainfall from May to October and low rainfall from November to April (Zhu 1997). Tropical forests of Xishuangbanna were clas-



FIGURE 1. The geographical location of Xishuangbanna. (A) 1-ha permanent plot of tropical seasonal rain forest, (B) the dipterocarp forest, and (C) the tropical montane rain forest in Mengsong.

sified into seasonal rain forest and montane rain forest according to their habitats and community structures (Zhu 1993a).

The tropical seasonal rain forest is the most luxuriant vegetation in Xishuangbanna and is mainly distributed in wet valleys or on low hills and flats below 1000 m asl (Zhu 1997, Zhu *et al.* 2004a). The annual mean temperature is 21°C, with the hottest month being 24.6°C, and the coldest month being 15.2°C (Zhu *et al.* 1998a); annual precipitation is 1532 mm, with 282 mm falling in the dry season (November–April), and 1250 mm in the wet season (May–October) (Zhu *et al.* 1998a).

Tropical montane rain forest at Xishuangbanna occupies altitudes usually from 700 to 1500 m (Cao & Zhang 1997). The annual temperature is 16.7°C, with the hottest temperature being 28.5°C, and coldest temperature 1.7°C (Zhu *et al.* 2004b); the annual precipitation is 1800–2379 mm, with 80 percent concentrated in May to October (Zhu *et al.* 2004b).

DATA COLLECTION.—The species included in this study occurred in 42 sample plots used for detailed ecological and phytogeographic studies (see *e.g.*, Zhu 1992, 1993c; Cao *et al.* 1996; Zhu *et al.* 1998a, b; Wang *et al.* 2001) with a total area of 15.7 ha. Most plots were 25 × 20 m in area, and all trees in those plots were identified. In each plot, five 5 × 5 m subplots were set for floristic survey of the understory including herbs (Zhu *et al.* 2005). In a few plots, only species with dbh > 5 cm were recorded (Zhu *et al.* 1998a, b). Gymnosperms, ferns, and bamboos were excluded from our study. In addition, we also excluded 15 species because their sexual systems could not be determined. A total of 685 species were involved in our survey.

We determined plant traits from a variety of sources, including published literature (Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita 1958–2003, Institutum Botanicum Kunmingense Academiae Sinicae Edita 1975–2003; Chen *et al.* 2004), herbarium specimens (Herbaria HITBC & KUN), field observations in our plots, and personal communications with taxonomists. We conducted weekly observations at a 1-ha permanent forest plot and monthly surveys at a dipterocarp forest during 2004–2006 (Fig. 1). At each census we recorded floral and fruit traits. Of the 685 species included in our study, we observed first-hand field data for 173 species (25.3%).

LIFE-FORMS.—Species were classified into the following life-forms: trees, shrubs, climbers, and herbs. We considered shrubs as woody, nonclimbing, multiple-stemmed perennials usually < 5 m in height (Opler *et al.* 1980). Vines, lianas, and woody epiphytes with trailing growth were classified as climbers. Herbaceous epiphytes, such as some orchids, and subshrubs were included as herbs.

SEXUAL SYSTEMS.—Each species was classified into one of the three sexual systems: hermaphrodite, dioecy (including androdioecy, gynodioecy, and trioecy), and monoecy (including andromonoecy, gynomonoecey, and polygamonoecy; Gross 2005). Species with mixed sexual systems were classified as dioecious if both monomorphic and dimorphic individuals were present and monoecious if both monoecious and hermaphroditic individuals were detected. We

checked specimens or living collections for species having poorly known sexual systems or where there is disagreement in the literature about the type of sexual system (*e.g.*, some species in Araliaceae and Sapindaceae are difficult to determine because their flowers are polygamous).

FLOWER SIZES.—Flowers were classified as large (> 1 cm), medium (0.5–1 cm), or small (< 0.5 cm) according to the diameter of open flowers. In most cases, the information of flower sizes was available from descriptions in the literature. Otherwise, we measured living collections in the field or specimens in the herbarium.

FRUIT TYPES.—Fruit types were classified as fleshy or dry (Chen *et al.* 2004). Berries, drupes, syncarps, and pomes were considered fleshy fruits; whereas legumes, follicles, capsules, nuts, samaras, utricles, and achenes were considered dry fruits. In some cases, achenes within fleshy receptacles or some nuts and capsules surrounded by fleshy exocarps or calyxes were also considered to be fleshy fruits.

COMPARISON WITH OTHER TROPICAL COMMUNITIES.—Many community studies do not include all growth forms and we could only compare the percentage of each sexual system for trees. We compared the frequencies of hermaphroditic, monoecious, and dioecious tree species in tropical forests of Xishuangbanna with that of three published floras from the Neotropics—Mexico (Ibarra-Manríquez & Oyama 1992), Costa Rica (Bawa *et al.* 1985), Brazil (Mataliana *et al.* 2005), and with that of two Paleotropical floras—Malaysia (Ashton 1969) and Australia (Gross 2005).

DATA ANALYSIS.—Associations between sexual system and life-form, fruit type, and vegetation type were assessed with chi-square tests using SPSS version 12.0.1 for windows (SPSS Inc., Chicago IL, U.S.A.). The null hypothesis for all comparisons was that the frequency distribution of sexual systems in the various traits and ecological categories was not significantly different from the distribution for the entire flora or vegetation. To take into account the phylogenetic effect on these associations, we repeated the analysis at the family and generic levels. Because of the sampling methods, herbs were underrepresented in the plots, so we compared the distribution of sexual systems among life-forms after the exclusion of all herbs.

RESULTS

TAXONOMIC REPRESENTATION.—This study included 685 species belonging to 109 families and 356 genera (Table S1). Eleven families (Lauraceae, Rubiaceae, Euphorbiaceae, Moraceae, Annonaceae, Meliaceae, Fagaceae, Urticaceae, Apocynaceae, Orchidaceae, and Papilionaceae) accounted for 44.2 percent of all sampled species, in which each family had more than 15 species. The six largest genera sampled were *Ficus* (23 species), *Litsea* (13 species), *Elaeocarpus* (12 species), *Lithocarpus* (12 species), *Piper* (10 species), and *Syzygium*

(10 species) accounting for 11.7 percent of all species, while 213 genera (60% of the genera) had only one species.

SEXUAL SYSTEMS.—Of 109 families recorded in the flora, 61 (56.0%) were represented by exclusively hermaphroditic species, 13 (11.9%) were represented by exclusively dioecious species, and six (5.5%) were represented by exclusively monoecious species (Begoniaceae, Fagaceae, Juglandaceae, Malvaceae, Passifloraceae, and Santalaceae) (Table S1). The remaining 29 (26.6%) were families with species of at least two sexual systems. Of 356 genera recorded in this survey, 229 (64.3%) were hermaphroditic, 75 (21.1%) were dioecious, and 44 (12.4%) were monoecious. A genus was often exclusively of one type of sexual system except in eight genera: *Mitrephora* (Annonaceae), *Microtropis* (Celastraceae), *Terminalia* (Combretaceae), *Cleidion* (Euphorbiaceae), *Garcinia* (Guttiferae), *Ficus* (Moraceae), *Rapanea* (Myrsinaceae), and *Debergeasia* (Urticaceae). Of 685 species in this survey, 415 (60.6%) were hermaphroditic, 172 (25.1%) were dioecious, and 98 (14.3%) were monoecious.

ASSOCIATION OF SEXUAL SYSTEMS WITH LIFE-FORMS.—Of 685 species in the Xishuangbanna tropical forest, sexual systems were strongly associated with life-forms both at the species and generic level ($\chi^2 = 30.2$, $P < 0.001$; $\chi^2 = 26.5$, $P < 0.001$ respectively; Table 1; Fig. 2). Tree species included proportionately fewer hermaphroditic species, while herbs and climbers had proportionately more hermaphroditic species than expected, although this association was not statistically significant ($P > 0.05$; Table 1; Fig. 2). Tree species included proportionately more monoecy, while herbs and climbers had proportionately less monoecy than expected, showing a positive significant association between trees and monoecy (Table 1; Fig. 2). After the exclusion of herbs, sexual systems were still significantly associated with life-forms both at the species and generic level ($\chi^2 = 22.9$, $P < 0.001$; $\chi^2 = 14.2$, $P < 0.05$, respectively), showing a significant association between trees and monoecious sexual system.

COMPARISONS OF SEXUAL SYSTEMS BETWEEN VEGETATION TYPES.—When calculations were conducted separately for two different vegetation types in the Xishuangbanna region (tropical seasonal forest vs. tropical montane forest), the frequencies of sexual systems were different. Among 436 species recorded in tropical seasonal forest, 247 (56.7%) were hermaphroditic, 72 (16.5%) were monoecious, and 117 (26.8%) were dioecious. Of 309 species recorded in tropical montane forest, 201 (65.0%) were hermaphroditic, 30 (9.7%) were monoecious, and 78 (25.2%) were dioecious. Sexual systems were significantly associated with vegetation types both at the species and generic level ($\chi^2 = 8.4$, $P < 0.05$; $\chi^2 = 7.6$, $P < 0.05$ respectively; Table 1; Fig. 3). Tropical seasonal forest had proportionately more monoecious species than expected, whereas tropical montane forest had proportionately less monoecious species than expected (Table 1; Fig. 3). Tropical montane forest had proportionately more hermaphroditic species than expected, and tropical seasonal forest had proportionately less hermaphroditic species than expected, but the association was not statistically significant (Table 1).

TABLE 1. The association of plant sexual systems with reproductive traits and ecological traits both at species and genera level in the tropical forests of Xishuangbanna. * indicates $P < 0.05$, ** indicates $P < 0.001$, ns = not significant at $P > 0.05$.

Parameters	No. of species				No. of genera			
	H ^a	M	D	Total	H	M	D	Total
<i>Life-forms</i>								
Trees	214	77	103	394	112	41	52	205
Shrubs	65	11	23	99	45	9	19	73
Herbs	57	7	13	77	43	2	6	51
Climbers	79	3	33	115	51	2	15	68
Total	415	98	172	685	251	54	92	397
χ^2	6.5 (ns)	20.8**	3.0 (ns)	30.2**	7.5 (ns)	15.3*	3.6 (ns)	26.5**
<i>Fruit types</i>								
Dry fruits	157	51	52	263	112	25	35	172
Fleshy fruits	258	47	116	422	139	29	57	225
Total	415	98	172	685	251	54	92	397
χ^2	0.05 (ns)	7.8*	3.0 (ns)	10.8*	0.18 (ns)	0.23 (ns)	1.06 (ns)	1.41 (ns)
<i>Vegetation types</i>								
TSR	247	72	117	436	158	42	62	262
TMR	201	30	78	309	135	15	48	198
Total	448	102	195	745 ^a	293	57	110	450 ^a
χ^2	2.2 (ns)	6.1*	0.18 (ns)	8.4*	1.10 (ns)	6.5*	0.01 (ns)	7.6*
<i>Flower sizes</i>								
Large	127	11	5	143	85	6	4	95
Medium	67	11	15	93	45	9	9	63
Small	218	58	136	412	116	34	73	223
Total	412	80	156	648	246	49	86	381
χ^2	22.8**	3.6 (ns)	41.2**	67.5**	15.1*	4.2 (ns)	28.3**	45.9**

H = hermaphroditic; M = monoecious; D = dioecious.

TSR = tropical seasonal forest; TMR = tropical montane forest.

^aSome species and genera coexisted in tropical seasonal rain forest and tropical montane rain forest.

ASSOCIATION OF SEXUAL SYSTEMS WITH FLOWER SIZES.—Of the 648 species for which information of flower size was available, 143 (22.1%) produced large flowers, 93 (14.4%) produced medium-sized flowers, and 412 (63.6%) produced small flowers (Fig. 2). The frequency distribution of flower sizes was significantly associated with sexual systems both at the species and generic level ($\chi^2 = 67.5$, $P < 0.001$; $\chi^2 = 45.6$, $P < 0.001$ respectively; Table 1; Fig. 2). Hermaphroditic species produced proportionately more large flowers and less small flowers than expected, while dioecious species produced more small flowers and less large flowers than expected. Monoecious species produced flowers with different size classes randomly ($P > 0.05$).

ASSOCIATION OF SEXUAL SYSTEMS WITH FRUIT TYPES.—Of 685 species, 422 (61.6%) produced fleshy fruits, and 263 (38.4%) produced dry fruits. Sexual systems were significantly associated with fruit types at the species level ($\chi^2 = 10.8$, $P < 0.05$; Table 1). Monoecious species produced proportionately more dry fruits and

less fleshy fruits than expected ($\chi^2 = 7.8$, $P < 0.05$; Table 1). In contrast, dioecious species produced proportionately more fleshy fruits and less dry fruits than expected, but the association was not significant ($\chi^2 = 3.0$, $P = 0.09$; Table 1). However, there was no significant association between sexual systems and fruit types when we made phylogenetic correction by repeating analysis at the generic level ($P > 0.05$; Table 1).

COMPARISON WITH OTHER TROPICAL COMMUNITIES.—Xishuangbanna tropical forest has a lower percentage of hermaphroditic trees compared to other five tropical communities (Table 2). The percentage of the dioecious sexual system for the 394 tree species in Xishuangbanna tropical forest was comparable to that of Malaysia, Mexico, Costa Rica, and Brazil, but higher than that of tropical Australia, which has a higher percentage of monoecious species. The percentage of monoecious tree species in Xishuangbanna tropical forest is slightly lower than tropical Australia, but is higher than the three Neotropical communities (Table 2).

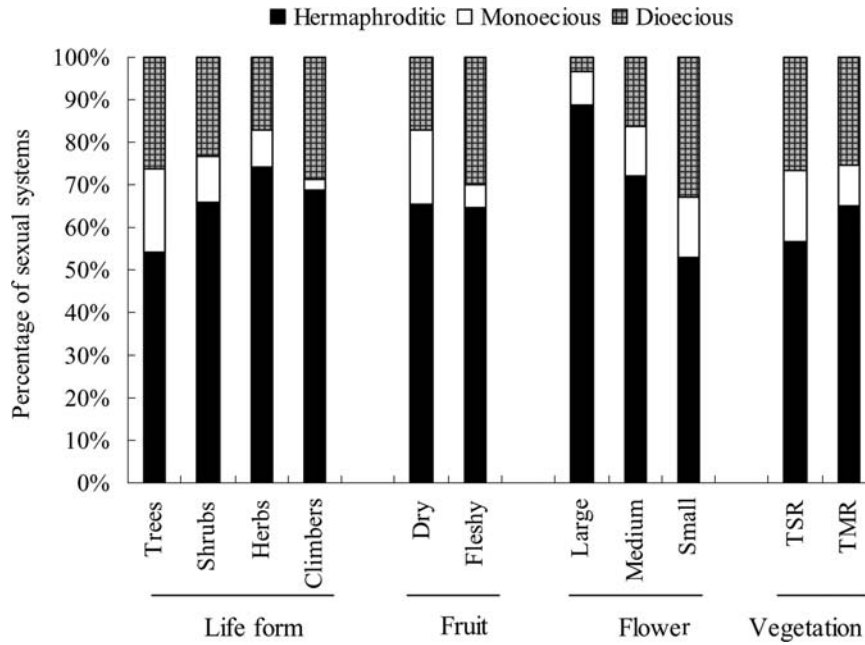


FIGURE 2. The percentage of species in each of three sexual systems associated with life-forms, fruit types, flower sizes, and vegetation types (TSR = tropical seasonal rain forest, TMR = tropical montane rain forest).

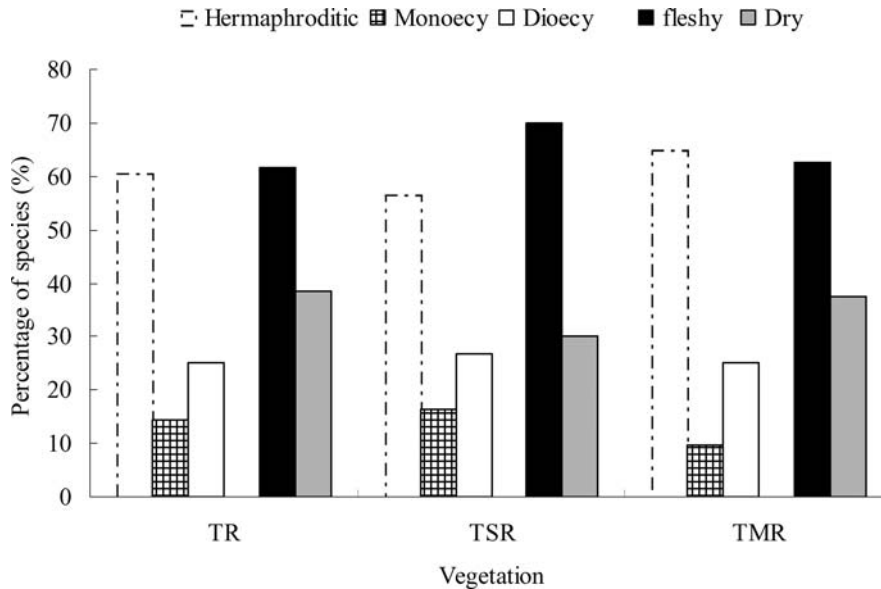


FIGURE 3. The percentage of species in each of sexual systems and fruit types associated with particular vegetation types (TR = tropical rain forest, TSR = tropical seasonal rain forest, TMR = tropical montane rain forest).

DISCUSSION

The percentage of dioecious sexual systems among tree species (26.1%) in Xishuangbanna tropical flora was similar or higher than that reported previously in other tropical regions. Monoecy was significantly associated with the tree growth form, and montane rain forest vegetation. Monoecy was significantly associated with dry

fruit type among species, but not so after phylogenetic correction. Small flowers were also commonly represented in the flora and as has been previously demonstrated were strongly associated with the dioecy (Bawa 1980, Vamosi *et al.* 2003). We now consider several hypotheses that might explain these associations between life history traits and sexual systems among the species occurring in the vegetation of Xishuangbanna.

TABLE 2. The percentage occurrence of sexual systems of tree species in the tropical Xishuangbanna compared to other tropical communities.

Tropical tree communities	No. species	Sexual system (%)		
		Hermaphroditic	Dioecious	Monoecious
Tropical rain forest in Xishuangbanna, China	394	54.3	26.1	19.5
Central Sarawak, Malaysia (Ashton 1969)	711	60	26	14
Los Tuxtlas, Mexico (Ibarra-Manríquez & Oyama 1992)	139	63	27	9
La Selva, Costa Rica (Bawa <i>et al.</i> 1985)	333	65.5	23.1	11.4
Restinga de Jurubatiba National Park, Brazil (Matallana <i>et al.</i> 2005)	107 ^a	58.9	26.2	15.0
Tropical northern Australia (Gross 2005)	1100 ^b	59.93	16.80	22.10

^aWe selected only the tree species in the study and calculated the percentage of each sexual system.

^bThirteen species with unresolved sex systems were removed from the tabulation.

THE INFLUENCE OF ENVIRONMENT ON PLANT SEXUAL SYSTEMS.—Among the environmental factors influencing plant sexual systems at Xishuangbanna, rainfall in tropical seasonal forest is more infrequent than in tropical montane forests and hence it is possible that stressful conditions are more often experienced. Although tropical montane forests exhibit similar species richness to the seasonal forests (Zhu *et al.* 2004b), the frequency distribution of sexual systems was significantly different with proportionately more unisexuality (dicliny) than is reported for montane forests, especially monoecious systems (16.5% vs. 9.7%). Several recent studies have proposed that the evolution of gender dimorphism (dioecy, gynodioecy) may be promoted by xeric or other stressful environmental conditions (Barrett 1992, Ashman 1999). However, stressful conditions have not been linked to the evolution of monoecy and, moreover, the association between gender dimorphism and stressful environment is certainly not universal as many aquatic plants are dioecious. Stressful environments often result in low population densities and scarce pollinators making it difficult for female individuals to invade hermaphroditic populations due to pollen limitation (Zhang 2004). In addition, environmental factors can interact in a complicated manner, so it is usually difficult to determine which factors play crucial role in the evolution of plant sexual systems.

PHYLOGENETIC CONSTRAINTS ON THE DISTRIBUTION OF SEXUAL SYSTEMS AND OBSERVED ECOLOGICAL ASSOCIATIONS.—At the species level, we detected a significant association between a monoecious sexual system and dry fruit type. However, the association is not significant after a phylogenetic correction was made by analyzing the data at the generic level. For example, at Xishuangbanna, about half of the monoecious species belong to the Fagaceae (20 species), Euphorbiaceae (15 species), and Moraceae (15 species). Three genera in Fagaceae (*Castanopsis*, *Cyclobalanopsis*, *Lithocarpus*) account for *ca* 20 percent (20 of 98) of monoecious species and all produce dry fruits (see Table S1), which most likely contributed to the species-level association between monoecious sexual system and dry fruit type. Other studies have also shown that reproductive traits are highly phylogenetically structured in tropical forests (Chazdon *et al.* 2003, Gross 2005). Some of the species-level traits considered

here, therefore, are not independent of their phylogenetic history. However, even when analyzed at the generic level, the association between sexual system and other ecological traits (life-form, vegetation type, and flower size) is not strongly influenced by phylogenetic history, which suggests a selective basis for the associations. For example, the Euphorbiaceae and Moraceae have exclusively unisexual flowers and nearly equal numbers of dioecious and monoecious species, providing valuable opportunities for studies of the evolution and maintenance of polymorphic sexual systems. Up to this point, investigations of the reproductive ecology of these taxa have largely been neglected and more work is needed to fully understand the evolution of sexuality in these taxa.

MONOECY ASSOCIATED WITH TREE GROWTH FORM IN THE TROPICAL RAIN FOREST.—Monoecy is a common sexual system, especially in large-sized plants with wind pollination, and it is often considered as an evolutionary starting point for the evolution of dioecy via the monoecy pathway (Renner & Won 2001, Barrett 2002). In most tropical floras, dioecy is the dominant unisexual system (Ashton 1969, Bawa *et al.* 1985, Bullock 1985, Ibarra-Manríquez & Oyama 1992, Chazdon *et al.* 2003, Mataliana *et al.* 2005). However, in the tree flora of tropical northern Australia, monoecy is more prevalent than dioecy (Gross 2005). At Xishuangbanna, although monoecy was not the dominant unisexual system, trees included proportionately more monoecious species than might have been expected (Table 1). It has been proposed that monoecy can provide some reproductive assurance from geitonogamous pollination under low population densities when mates are scarce and the pollinator pool is unreliable and/or inefficient (Gross 2005). Another proposed benefit of monoecy is that this sexual system may reduce inbreeding through spatial segregation of pistillate and staminate flowers (Freeman *et al.* 1981). Furthermore, through size-dependent modification of sex allocation, monoecious species can alter their opportunities for pollen dispersal and pollen capture (Lloyd & Bawa 1984). Although strict dioecy completely prevents self-fertilization and avoids male–female interference, the evolution of dioecy is only possible with reliable pollinators (Zhang 2004). Stressful environmental conditions in tropical rain forest of Xishuangbanna may limit the mobility of potential pollinators, so pollination might

be unpredictable. Under such environmental conditions (low temperature and precipitation, foggy weather in dry season etc.), the monoecious strategy may be advantageous. Further studies should investigate the extent to which isolated monoecious individuals at low density gain reproductive assurance through geitonogamy.

FLORAL TRAITS AND POLLINATION SYSTEMS.—Small flowers dominated the tropical flora of Xishuangbanna, and they were often inconspicuous and bowl-dish shaped with pale-colored perianths (X. S. Chen, pers. obs.). These features suggested generalized pollination systems may be common in tropical vegetation at Xishuangbanna. However, pollination ecology at the community level has not been investigated in any detail. In a lowland dipterocarp forest in Sarawak, Malaysia, plants pollinated by social bees included the largest number of species, followed by beetle-pollinated species (Momose *et al.* 1998). For understory species, the majority (71%) of the plant species were pollinated by bees, followed by birds (Kato 1996). Corlett (2004) reviewed the current knowledge of flower visitors and pollination in the Oriental Region and suggested that most plant–pollinator relationships in the region appear to be relatively generalized. However, in a midelevation wet evergreen forest in Western Ghats, India, approximately 75 percent of the species were specialized to a single pollinator group such as bees, beetles, or moths (Devy & Davidar 2003), and therefore more specialized pollination systems were common in the region. The degree of generalization versus specialization in pollination systems and its significance for the evolution of sexual systems cannot be identified unless community-level surveys are conducted. Current work on species in Xishuangbanna tropical forests is aimed at identifying the extent to which pollination biology plays a significant role in the evolution of plant sexual systems.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp. Table S1. *The number of genera, species, climbers, herbs, shrubs, trees, percentage of species with hermaphroditic, dioecious, monoecious systems, and dry or fleshy fruits in each family.*

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