RESEARCH ARTICLE

Testing mechanisms of compensatory fitness of dioecy in a cosexual world

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Abstract

Questions: All else being equal, populations of dioecious species with a 50:50 sex ratio have only half the effective reproductive population size of bisexual species of equal abundance. Consequently, there is a need to explain how dioecious and bisexual species coexist. Increased mean individual seed mass, fecundity, and population density have all been proposed as attributes of unisexual individuals or populations that may contribute to the persistence or resilience of dioecious species. To date, no studies have compared sympatric dioecious and cosexual species with respect to all three components of fitness. In this study, we sought evidence for these compensatory advantages (higher seed mass, greater seed production per unit basal area, and higher population density) in dioecious species.

Location: Five 20–25 ha forest dynamic plots spanning a latitudinal gradient in China, including two temperate, two subtropical, and one tropical forest.

Methods: We used a phylogenetically corrected generalized linear modelling approach to assess the phylogenetic dependence and joint evolution of sexual system, seed mass and production, and ecological abundances among 48–333 species and 32,568–136,237 individuals per forest.

Results: Across all five forests, we detected no consistent advantage for dioecious relative to sympatric cosexual species with respect to mean individual seed mass, seed production or the density of stems in any size class.

Conclusions: Our study suggests that seed traits may provide compensatory mechanisms in some forests, but most often the coexistence of sexual systems cannot be explained by advantages of dioecy related to seed quality and demographic parameters. Future investigations of the factors that promote coexistence may increase our understanding by expanding the search to include attributes such as lifespan and tolerance or resistance to herbivores.

KEYWORDS
abundance, bisexual, dioecy, forest dynamics plot, multiple forest type, *per basal area*, seed mass, sexual system

1 | INTRODUCTION

The mechanisms that promote the persistence of dioecious species in sympatry with cosexual species continue to puzzle ecologists and evolutionary biologists (Barrett, 2010; Bawa et al., 1989; Vamosi & Vamosi, 2004). Relative to gender-monomorphic species (i.e., monoecious taxa or those with bisexual flowers) of equal abundance, dioecious species with a 1:1 male:female ratio have only half the effective reproductive population size (Vamosi, Mazer, & Cornejo, 2008). This demographic disadvantage is intensified in the many populations and species that exhibit male-biased sex ratios (Chazdon, Areaga, WebbB, & Argas, 2003; Gao, Queenborough, & Chai, 2012; Queenborough, Burslem, Garwood, & Valencia, 2007). It is not clear, however, whether there are any consistent fitness advantages to dioecy that can compensate for the reduction in the number of seed-bearing individuals and the lower density of available mates (Bruijning et al., 2017; Queenborough et al., 2009; Vamosi et al., 2008). If dioecious taxa share and compete for any limited resource (e.g., light, space, or soil nutrients) with co-occurring bisexual taxa, then the former must outperform the latter with respect to one or more components of fitness in order to maintain similar population growth rates.

In theory, a division of labor in unisexual plants may increase components of both male and female fitness per reproductive individual due to resource allocation towards, and specialization on, gender-specific functions (e.g. Lloyd & Webb, 1977; Sutherland & Delph 1984). Among females, for example, natural selection may result in higher seed quality or quantity, compensating for the loss of male function (e.g. pollen production) (Ashman, 2006; Lloyd, 1975; Mitchell & Diggle, 2005). In addition, if seed production in females is less pollinator-limited than pollen removal in males, then natural selection among females may favour a reduction in traits that promote repeated visitation, such as large flowers, large inflorescences, and long-lived flowers. Similarly, males may evolve to produce more attractive flowers or inflorescences than females because these traits induce a higher visitation rate by pollinators (Stanton, Snow, & Handel, 1986; Vamosi & Otto, 2002).

Previous studies have sought evidence for compensatory increases in fitness-related attributes among the females of dioecious species relative to their cosexual counterparts. Vamosi et al. (2008) found that females produced bigger or higher-quality seeds (i.e., higher rates of seedling emergence and seedling vigour) than cosexual individuals in woody species, shrubs and lianas (and among woody species, trees, and lianas when controlling for phylogenetic effects), but this pattern is not universal (Miyake & Olson, 2009; Queenborough et al., 2009). Given the common trade-off between seed mass/size and seed quantity (Moles & Westoby, 2004; Muller-Landau, 2010), however, the production of bigger seeds or higher seed production alone will not necessarily generate elevated mean individual fitness among the females of dioecious species.

In the absence of compensatory increases in mean individual seed quality or fecundity, if unisexual individuals are physiologically more robust and more likely to survive than cosexual individuals, then higher demographic performance, leading to greater adult abundances (Lebrija-Trejos, Reich, Hernández, & Wright, 2016), may enable dioecious species to persist in some communities. Consistent with this view, Matallana, Wendt, Araujo, and Scarano (2005) and Vamosi (2006) found that dioecious species had higher abundances than non-dioecious species in two Brazilian rain forests. However, support for this mechanism has not been found in all studies (e.g., Queenborough et al., 2009). Further exploration of the relative abundances of dioecious vs cosexual species, especially in diverse tropical vs temperate floras, are likely to provide insights into the costs and benefits of the evolution and maintenance of alternative sexual systems (Heilbuth, Ilve, & Otto, 2001; Vamosi, 2006; Vamosi & Vamosi, 2004).

The current study was designed to address two empirical gaps in the study of dioecious relative to co-occurring cosexual species. First, little is known of the comparative demography and population densities of dioecious vs cosexual species in subtropical and temperate forest communities, potentially due to their low species diversity (relative to tropical forests) as well as to the relatively low proportion of animal-dispersed species with fleshy fruits (a strategy that is associated with dioecy in tropical forests — Chen, Cornwell, Zhang, & Moles, 2016; Howe & Smallwood, 1982; Schlessman, Vary, Munzinger, & Lowry, 2014). Second, this study provides the first test of the proposed increase in mean fecundity among females in dioecious relative to cosexual taxa. Seed production is the foundation of plant population regeneration and persistence. Previous work has tested for an increase in mean individual seed mass among females of dioecious taxa (Queenborough et al., 2009; Vamosi et al., 2008) but has not focused on seed production.

In sum, we tested for three mechanisms of compensatory fitness advantages of dioecious species compared to co-occurring, cosexual hermaphroditic and monoecious species in five fully mapped plots distributed across a latitudinal gradient in China. We aimed to determine whether dioecious species have: (a) higher mean individual seed mass, (b) greater mean seed production per unit basal area, and (c) higher densities of established individuals. Our central goal was to detect, if present, general compensatory mechanisms that contribute to the persistence of dioecious species in temperate, sub- and tropical forests.

2 | MATERIAL AND METHODS

2.1 | Study sites

Five forest tree communities spanning a latitudinal gradient (Table 1, Figure 1) were chosen for this study, including Changbaishan (42°23′ N, 128°05′ E, temperate, abbreviated here as CBS), Donglingshan (39°57′ N, 115°26′ E, temperate, DLS), Tiantongshan (29°49′ N, 121°47′ E, subtropical, TTS), Gutianshan (29°15′ N, 118°07′ E, subtropical, GTS) and Xishuangbanna (21°37′ N, 101°34′ E, tropical, XSBN). Within each forest, a 20–25 hectare plot had been surveyed and censused using the methods of Condit (1998): all free-standing

TABLE 1 Summary of plots included in this study and the proportions of the species and individuals representing different sexual systems in each forest

Plot expositions	Size (ha)	Year of census	No. determined species[a]	Number of trees	Dioecy %		Monoecy %		Hermaphroditism %	
					Prop. spp.	Prop. ind.	Prop. spp.	Prop. ind.	Prop. spp.	Prop. ind.
CBS (42°23′ N, 128°05′ E)	25	2009	48 (51)	32,568	29.2	15.3	18.8	61.7	52.1	23.0
DLS (39°57′ N, 115°26′ E)	20	2010	53 (55)	52,670	18.9	6.4	9.4	17.5	71.6	76.1
TTS (29°49′ N, 121°47′ E)	20	2010	146 (152)	93,640	26.0	43.7	21.9	17.6	52.1	38.7
GTS (29°15′ N, 118°07′ E)	24	2005	145 (159)	136,237	24.8	18.1	14.5	17.9	60.7	64.0
XSBN (21°37′ N, 101°34′ E)	20	2011	333 (389)	86,778	28.2	31.2	16.8	10.6	55.0	58.2

No. species = the number of angiosperm species; Prop.spp. = proportion of all species in each sexual system and Prop.ind. = proportion of all individual trees in each sexual system.

[a]No. determined species = Number of angiosperm species of determined sexual system in each forest dynamics plot; the total number of tree species present is shown in parentheses; Year of census = the year in which each forest was surveyed for the current study.
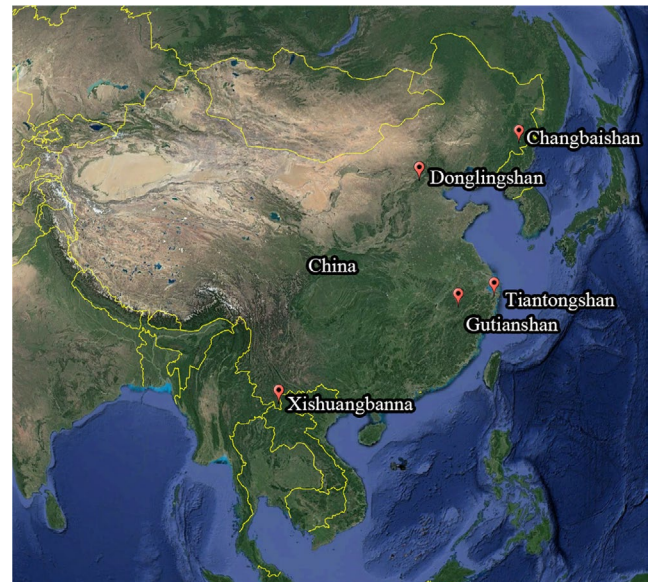
FIGURE 1 Forest dynamic plots spanning a latitudinal gradient in China including Changbaishan (CBS, temperate), Donglingshan (DLS, temperate), Tiantongshan (TTS, subtropical), Gutianshan (GTS, subtropical) and Xishuangbanna (XSBN, tropical) included in this study [Colour figure can be viewed at wileyonlinelibrary.com]

trees ≥1 cm diameter at breast height (dbh = 1.3 m above the ground) were mapped, tagged and identified to species (Table 1). Plot size, the number of angiosperm species with determined sexual system, and the abundance of individual trees per plot are recorded in Table 1. This study was restricted to trees and shrubs because most of the plots surveyed here include only a small proportion of lianas and no herbaceous species [only 3.9% (2 of 51) in CBS, and 2.6% (10 of 390) in XSBN; the other three plots included no lianas].

2.2 | Sexual system

The sexual system of each species was identified using the following sources in descending order of use: *Flora of China* (www.eflora.cn), *Seeds of Woody Plants in China*, *Flora of Liaoning*, *Flora of Zhejiang*, *Flora of Yunnan*, and a series of recent publications (Appendix S4). For species for which the sexual system was provided by multiple sources, we used the latest and/or the most comprehensive treatment. Still, a very small percentage of species (3.6% in DLS; ~14.4% in XSBN) could not be assigned a sexual system with certainty. The proportion of angiosperm species for which a sexual system could be assigned ranged from 87.5% in XSBN to 100% in both temperate forests CBS and DLS (Table 1). We classified these species into three categories following the classification by Gross et al. (2005): dioecious (separate male and female individuals), monoecious, and hermaphrodite (spatial separation of investment in male and female function). The category of dioecy includes all the androdioecious, gynodioecious and polygamodioecious species, while monoecy includes the monoecious, andromonoecious and gynomonoecious species. The bivariate relationships of the proportion of species in each sexual system (and the number of individuals in each sexual

system) vs latitude, mean annual temperature, and mean annual precipitation are shown in Appendix S5.

2.3 | Seed mass and seed production

Seed mass (thousand-seed weight) was obtained from seed collections in the field and from the literature. Seed mass was estimated for 50 species in CBS, 46 species in DLS, 127 species for GTS, 109 species for TTS, and 201 species for XSBN respectively. Seed collection was conducted using seed traps set in forest plots (Appendices S1, S2, and S3). One to several seeds were collected per species and dried in an oven at approximately 105°C for 48 hr, weighed and the mean individual seed mass calculated (additional details can be found in Du & Ma, 2012; Yang, Tang, & Cao, 2010; Zhang et al., 2008). For those species for which traps yielded samples too small to calculate the thousand-seed weight (three replicates × 1000 seeds), we extracted seed mass (thousand-seed weight) information from the published literature, including *Seeds of Woody Plants in China* (Zhou & Chen, 2001); *Flora Reipublicae Popularis Sinicae* (Committee of Flora Reipublicae Popularis Sinicae, 1959–2004; 125 volumes, a result of the work of more than 450 well-qualified Chinese taxonomists over the past 50 years); *Flora of Zhejiang* (He, 1993); *Flora of Yunnan* (Wu, 2006) and a series of articles from the primary literature focusing on individual species. The number of species for which seed mass was obtained from field-collected seeds vs the literature was 41 vs 10 in CBS, 35 vs 11 in DLS, 142 vs 0 in GTS, 101 vs 12 in TTS, and 160 vs 122 in XSBN.

With respect to seed production, a direct measurement of total seed production (in a given year) was used to estimate reproductive success (Sonkoly et al., 2015). Seed production was estimated by the total number of mature seeds falling into all traps for each plot across surveyed years. Seed traps were arranged regularly (in CBS and XSBN) or along a trail (in GTS) (Appendices S2 and S3), with 150 traps placed in the 25-ha CBS plot and in the 20-ha XSBN plot, and 169 traps placed in GTS. To ensure data reliability for seed production, we excluded species with fewer than 20 seeds across surveyed years.

In CBS, for all species that were assigned to a sexual system, a total of 21 species (41.2%) were included in the survey of seed production across eight years. Similarly, seed production was estimated for 41 species (27.0%) in GTS across four years, and for 77 species (19.8%) in XSBN across eight years (Appendix S1). Seed production was recorded in TTS for only a single year and was not recorded for DLS, so we did not include these two plots in the analysis of seed production.

2.4 | Growth form

Growth form (tree or shrub) for the majority of species was assigned based on that of individuals present in the forest dynamics plots themselves. For some species, field records were ambiguous, in which case growth form was assigned according to species descriptions in the literature cited above. Species without explicit growth

forms (two species from CBS, three from DLS, 10 from GTS and 49 from XSBN) were excluded from the relevant analyses.

2.5 | Tree abundance

We counted the number of individuals of all tree and shrub species in each plot for two size classes: 1–10 cm dbh (treelet) and >10 cm dbh (tree) (Queenborough et al., 2009). We used the plot data from the 2009 census for CBS, the 2011 census for DLS, the 2010 census for GTS, the 2010 census for TTS, and the 2007 census for XSBN. The total numbers of individual trees censused in each forest plot are shown in Table 1.

2.6 | Wood specific gravity

Because longevity is strongly associated with wood specific gravity (WSG) (Williamson & Wiemann, 2010), we used WSG as a proxy for longevity in the analyses described below. A total of 44 (91.7%) species were assigned wood density (WSG) in CBS, 123 (80.9%) in TTS, 147 (92.5%) in GTS, and 333 (85.6%) in XSBN. Species lacking WSG values were excluded from the relevant analyses. We did not have WSG information for DLS, so the corresponding analysis with this factor was not conducted for this location.

2.7 | Statistical analyses

We first tested whether there is evolutionary divergence (the presence and strength of phylogenetic signal) between closely related plant species in sexual system (dioecy vs cosexual), and whether there is evolutionary covariation between sexual system and mean seed mass, mean seed production per basal area, and tree abundance. When significant covariation was detected between sexual system and seed attributes, we then tested whether dioecious species produce bigger seeds or more seeds per basal area than non-dioecious species within growth forms (Queenborough et al., 2009; Vamosi et al., 2008). Similarly, we examined whether the evolution of dioecy is associated with higher population density compared to the cosexual species for each of the two age classes.

2.8 | Phylogenetic tree construction

To examine the joint evolution of sexual system and seed mass or seed production, we examined the relationships between these traits while taking account of their evolutionary history (Vamosi et al., 2008). For sites where DNA data were available, we used the online *phylomatic* software to generate the phylogeny with branch lengths provided by one of the available mega trees (R20160415.new version provided by Camwebb; https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20160415.new) for CBS, DLS, and TTS separately. Thus, each phylogeny included the species present and surveyed in the corresponding forest. Phylogenetic analyses were conducted using the R package 'ape' (Paradis, Claud, & Strimmer (2004), R Core Team, 2015). Based on DNA sequences of each species, we constructed the phylogenetic tree of the species at GTS and

XSBN using the MUSCLE software (Edgar, 2004) and the Phylotools package in R (see Du et al., 2017 for more details, Appendix S6).

2.9 | Phylogenetic signal detection

We tested for statistical dependence of trait values among tree species owing to their phylogenetic relationships ('phylogenetic signal') (Blomberg, Garland, & Ives, 2003). First, we examined the strength of the phylogenetic signal for each variable across the co-occurring species in each forest. We quantified the phylogenetic signal for seed mass, seed production, WSG, species abundance (stems 1–10 cm dbh; stems >10 cm dbh), growth form and sexual system using Blomberg's K statistic (Blomberg et al., 2003). We used the 'picante' package (Kembel et al. 2009) for continuous variables and the function 'phylo.D' in the 'caper' package for binary traits (tree/shrub, dioecy/not; Fritz & Purvis, 2010) in the R programming language (R Core Team, 2015).

For each trait, Blomberg's K value was used to evaluate the strength of the phylogenetic signal. K has a value of 1 when trait evolution across a phylogeny follows Brownian motion perfectly; $K > 1$ shows stronger similarities among closely related species than expected under a Brownian trait evolution model, and $K < 1$ indicates a weaker phylogenetic signal than that expected by Brownian motion (Blomberg et al., 2003; Kraft & Ackerly, 2010). Values of K significantly greater than zero but less than 1 indicate that closely related species are more similar than expected by chance, but less similar than expected under the assumption of Brownian motion. We compared the observed value of K to the null distribution of K values (K_{null}) obtained by randomly shuffling the traits across the tips of the phylogeny 999 times. This randomization procedure generates hypothetical trait distributions where there is no phylogenetic signal, thus $K_{null} \ll 1$. Traits were significantly phylogenetically conserved (relative to the random-tip-shuffling model) if the observed K was in the upper 2.5% of the K_{null} values (Kraft & Ackerly, 2010). The Fritz & Purvis D statistic, reflecting phylogenetic signal in a binary trait, estimates significant departure from both random association and the clumping expected under a 'Brownian evolution threshold' model (Fritz & Purvis, 2010). A value of $D > 1$ showed that traits were phylogenetically overdispersed, $D = 1$ indicates a trait following a random trait distribution, while a value of $D = 0$ indicates a trait consistent with a Brownian threshold model.

The influence of phylogenetic non-independence on seed mass, seed production per basal area, and population density was modeled by incorporating the phylogenetic covariance matrix in a generalized least squares regression ('$pgls$', Freckleton, Harvey, & Pagel, 2002; Pagel, 1997) using the 'caper' package in R (R Core Team, 2015). The maximum likelihood value of λ was used to adjust the phylogenetic variance matrix to fit Brownian motion (see below for details).

2.9.1 | Seed mass models

To test whether dioecious species have an advantage in terms of mean individual seed mass compared with gender-monomorphic species, we compared the full model, including mean individual seed mass (natural-logarithm transformed) (tree, shrub, and all stems pooled)

as a function of sexual system, growth form and woody density (i.e., wood specific gravity, or WSG), to single-variable models using *PGLS* (Table 2). Because of the well-known relationships among species between seed mass and growth form (Moles et al., 2005), and between seed mass (size) and longevity (for which we used WSG as a proxy) (Chave et al., 2006; Queenborough et al., 2009), we included growth form and WSG as covariates in the PGLS analyses when investigating the independent relationship between sexual system and seed mass for each forest plot. Then, for each plot, to detect differences in mean seed mass among sexual systems (without accounting for phylogenetic relationships), we also conducted nonparametric one-way Wilcoxon signed-rank tests for all pairwise comparisons of sexual systems. Nonparametric one-way Wilcoxon signed-rank tests were used because of the left-skewed distributions of natural-logarithm transformed seed mass (Vamosi et al., 2008).

2.9.2 | Models for community-level mean seed production per basal area

To detect possible compensatory increases in the fecundity of dioecious species relative to their cosexual counterparts, we tested whether dioecious species (tree and shrub) have higher seed production per basal area than sympatric monoecious or cosexual hermaphroditic species in CBS, GTS and XSBN. Although our sample size for species with seed production data was relatively small in each plot, these species likely accounted for most of the seed production in each community because they collectively represent most of the individuals in each forest community (96.3% in CBS, 89.1% in GTS and 98.3% in XSBN, Appendix S1).

Owing to the absence of data for individual-level seed production, we used the community-level mean seed production per basal area as a proxy for the seed production of each species (hereafter mean seed production). For gender-monomorphic species, we estimated mean seed production per basal area using total seed production divided by the total basal area of co-occurring individuals per species (stems >1 cm dbh for each species, Appendix S8) within 20-m circles centred around each focal trap (trap area = 0.5 m^2). For dioecious species, we divided total seed abundance by half of the total basal area of all conspecific individuals (assuming a 1:1 sex ratio) (Amorim, Mendes-Rodrigues, Maruyama, & Oliveira, 2011; Dantas, Santos, & Marini, 2009; Thomas & LaFrankie, 1993). The mean seed production per basal area was natural-logarithm-transformed before analysis.

Given the well-documented seed mass–seed abundance trade-off (Moles & Westoby, 2004; Appendix S8), we conducted weighted ANOVAs (species values were weighted by their seed mass) to detect differences among sexual systems with respect to the mean seed production per basal area.

2.9.3 | Tree abundance models

To test for compensatory advantages in demographic performance of dioecious species (including both the juvenile phase [characterizing regeneration] and adult abundances), we constructed the model of

TABLE 2 Summary of the 'pgls' models designed to detect effects of sexual system (SS) on seed mass (thousand-seed weight, SM), seed production per basal area (SP) and population density (PD), with growth form (GF) and wood specific gravity (WSG) as the covariates (see below)

Model	CBS λ	CBS Estimate	DLS λ	DLS Estimate	TTs λ	TTs Estimate
SM ~ SS + GF + WSG	0.1	H(−0.37) + M(−0.39) + Tree(0.11) + WSG(2.87)	−	−	0.827	H(0.21) + M(1.36) + **WSG(−5.10*)** + T(−1.30)
~SS	0	H(−0.39) + M(−0.30)	0.970	H(0.92) + M(−1.58)	0.774	H(−0.51) + M(1.13)
~GF	0	Tree(−0.23)	1.000	Tree(0.69)	0.877	T(−0.72)
~WSG	0	2.765	−		0.790	**−4.83***
SP ~ SS + WSG + SM	0	H(−0.14) + M(2.55) + Tree(0.63) + WSG(−10.17)	−	H(0.85) + M(−2.03) + Tree(0.86)	−	H(−4.16) + M(−18.97) + WSG(20.05) + **SM(−22.61***)**
~SS	0	H(0.34) + M(1.79)	−		−	H(10.09) + M(−48.28)
~SS	0	0.32	−		−	573.58
~WSG	0	−5.45	−		−	**−23.31***
PD						
(a) >1 cm dbh						
~SS + SM	0.192	H(0.63) + M(2.19) + **SM(0.54**)**	0	H(1.28) + M(1.52) + SM(0.06)	0.314	H(−0.17) + M(0.53) + SM(0.06)
~SS	0.464	H(0.80, 0.35) + **M(2.13*)**	0	H(0.80) + **M(2.13*)**	0.313	H(−0.15) + M(0.56)
~SM	0.502	**0.52**	0	0.12	0.293	0.04
(b) >10 cm dbh						
~SS + SM	0	H(0.33) + M(0.80) + SM(0.37)	0	H(1.28) + M(1.52) + SM(0.06)	0	H(0.12) + **M(1.34*)** + SM(−0.03)
~SS	0	H(0.37) + M(0.63)	0	H(1.42) + M(1.60)	0	H(0.13) + **M(1.31*)**
~SM	0	0.35	0	0.12	0	0.007
(c) 1–10 cm dbh						
~SS + SM	0.240	**H(1.59*)** + **M(2.48**)** + **SM(0.73***)**	0	H(1.53) + M(2.00) + SM(−0.003)	0.614	H(−0.47) + M(−0.69) + SM(−0.12)
~SS	0.367	H(1.65) + **M(2.50*)**	0	H(1.52) + M(200)	0.594	H(−0.41) + M(−0.57)
~SM	0.063	**0.75***	0	0.06	0.674	−0.103

Model	GTS λ	GTS Estimate	XSBN λ	XSBN Estimate
SM ~ SS + GF + WSG	0.827	H(0.08) + M(−0.30 ns + WSG(1.59) + T(0.01)	0.857	H(−0.13) + M(0.83) + **WSG(3.24***)** + T(1.15)
~SS	0.774	H(0.07) + M(−0.31)	0.879	H(−0.003) + M(0.94)
~GF	0.877	Tree(0.05)	0.908	Tree(1.25)
~WSG	0.790	1.599	0.893	**3.27***

TABLE 2 (Continued)

Model	GTS		XSBN	
	λ	Estimate	λ	Estimate
SP ~ SS + WSG + SM	-	**H(-1.67*)**+M(-1.80) + WSG(0.40) + SM(-0.29*)	0	H(0.17) + M(0.59) + **WSG(-2.26**)** + SM(-0.18)
~Sexual system	-	H(-1.40) + **M(-2.53*)**	0	H(0.52) + M(0.95)
~seed mass		**-0.29***	0	**0.25****
~WSG	-	-2.43	0	**-3.38****
PD				
(a) >1 cm dbh				
~SS + SM	0.314	H(0.32) + M(-0.55) + SM(0.05)	0	**H(-0.72*)** + **M(0.69*** + **SM(0.14***)**
~SS	0.313	H(0.32) + M(-0.51)	0	**H(-0.62*)** + M(-0.62)
~SM	0.293	0.04	0	**0.13*****
(b) >10 cm dbh				
~SS + SM	0	H(0.09) + **M(1.56*)** + SM(0.09)	0	H(-0.33) + M(-0.21) + **SM(0.08*)**
~SS	0	H(0.08, 0.88) + **M(1.68*)**	0	H(-0.28) + M(-0.18)
~SM	0	0.137	0	**0.07***
(c) 1–10 cm dbh				
~SS + SM	0.614	H(0.51) + M(-0.83) + SM(0.05)	0	**H(-0.80**)** + **M(-0.90*)** + **SM(0.17***)**
~SS	0.594	H(0.51) + M(-0.81)	0	**H(-0.65*)** + **M(-0.78*)**
~SM	0.674	0.05	0	**SM(0.16*)**

We present here the full model using the maximum likelihood value of λ (a measure that adjusts the phylogenetic variance matrix to fit a Brownian model in a pgls analysis). We included only tree species in the seed-production model because data on seed production for shrub species were scarce in both CBS (only two species) and XSBN (no species). Seed mass, seed abundance and WSG were natural-logarithm transformed prior to analysis. The power of each model is indicated by *p*-value and asterisks (Significance value: *** *p* < , 0.001; **, *p* < 0.01; *, *p* < 0.05). H = Hermaphrodite, M = Monoecy and D = Dioecy.

TABLE 3 Phylogenetic signal among tree and shrub species sampled from five forest dynamics plots distributed across a latitudinal gradient

Trait	K or estimated D and p- value									
	CBS		DLS		TTS		GTS		XSBN	
(a) Quantitative traits examined by Blomberg's K										
	K	p	K	p	K	p	K	p	K	p
Seed mass	0.461	0.012*	0.658	0.11	0.525	0.001**	0.64	0.001**	0.25	0.027*
Wood specific gravity (WSG)	0.473	0.072	-	-	0.298	0.01**	0.306	0.001**	0.361	0.001**
Abundance 1–10 cm dbh	0.548	0.001**	0.321	0.431	0.327	0.082	0.282	0.001**	0.195	0.097
Abundance >10 cm dbh	0.384	0.273	0.438	0.164	0.322	0.659	0.247	0.073	0.238	0.063
(b) Categorical traits evaluated using the D statistic										
	D	p	D	p	D	p	D	p	D	p
Sexual system	−0.053	0***	−1.088	0***	0.254	0***	−0.322	0***	−0.131	0***
Growth form	−0.192	0***	0.026	0.002**	0.197	0***	0.392	0***	0.299	0***

For a detailed description of K statistics, see Blomberg et al. (2003); Growth form just included tree and shrub.
Quantitative traits were assessed using Blomberg's K, and categorical data were evaluated using the D statistic for binary traits (dioecy/non-dioecy, tree/shrub). The continuous variables were natural-logarithm transformed prior to statistical analysis. The significance (p-values) indicates the probability that K or D differ significantly from zero. (p-values: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$).

abundance (using the natural-logarithm-transformed numbers of stems 1–10 cm dbh, stems >10 cm dbh, and all stems combined) as a function of sexual system. Abundance showed a weak phylogenetic signal, so non-parametric one-way Wilcoxon signed-rank tests were also conducted to detect whether sexual systems differ significantly in mean tree abundance. All statistics were conducted in R 3.2.1 (R Core Team 2015).

3 | RESULTS

The proportions of dioecious species in all five plots ranged from 18.9% in DLS to 29.2% in CBS. Hermaphroditism (with bisexual flowers) is the most common sexual system, but there is substantial variation in the proportion of species with bisexual flowers among the forests examined here (Table 1). Sexual system showed significant phylogenetic signal in all five forest plots (Table 3). In most cases, no significant effects of sexual system on mean individual seed mass, seed production per basal area, or population density were detected (Table 2).

3.1 | Seed mass

The observed differences in mean seed mass between sexual systems were not in the direction we predicted. Mean seed mass (thousand-seed weight) of the sampled species representing different sexual systems varied greatly among the five forest plots, ranging from 9.56 g (SD = 12.3 g) for dioecious species in DLS to 1600.7 g (SD = 3577.3 g) for monoecious species in XSBN (Appendix S7). Mean individual seed mass (natural-logarithm-transformed) was phylogenetically conserved in both subtropical and tropical forests

(TTS, GTS and XSBN) but not in temperate forests (CBS and DLS) (Table 3). When controlling for phylogenetic relationships, sexual system showed only a weak or non-significant effect on mean seed mass in all plots (Table 2). In XSBN, monoecious species had a significantly higher mean seed mass than species with bisexual flowers, but the mean individual seed mass of neither group differed significantly from that of dioecious species (Table 2).

In Wilcoxon tests conducted on all tree and shrub species, sexual systems differed with respect to mean seed mass only in GTS, where monoecious species had significantly higher mean seed mass than dioecious and cosexual hermaphroditic species (Figure 2a; Table 2). Similar to the case for both life forms pooled, among tree species, monoecious species had significantly higher mean seed mass than dioecious and cosexual hermaphrodite species in the sub-tropical GTS forest plot (Figure 2b). Among shrub species, sexual systems did not differ significantly in mean individual seed mass in any of the five plots (all $p > 0.05$) (Figure 2c).

3.2 | Seed production *per basal area*

Weighted ANOVA showed no significant differences among sexual systems in mean seed production per basal area in temperate CBS and tropical XSBN (Figure 3). In subtropical GTS, dioecious species produced significantly more seeds per basal area than monoecious species, but did not differ from cosexual hermaphroditic species (Table 2). The '*pgls*' regression showed that, independent of the effects of phylogenetic relatedness ($\lambda = 0$, Table 2), dioecious species had higher mean seed production per basal area than monoecious species in subtropical GTS (Table 2).

3.3 | Population density

Abundance varied considerably among species in all five forest plots: mean species abundance per hectare ranged from 8.23 (SD = 13.36) to 92.12 (SD = 107.71), both of which occurred in XSBN (Appendix S10). The abundance of small trees (1–10 cm dbh) was random with respect to phylogeny in DLS, TTS and XSBN, and the abundance of trees >10 cm was random with respect to phylogeny in all five forests (Table 3).
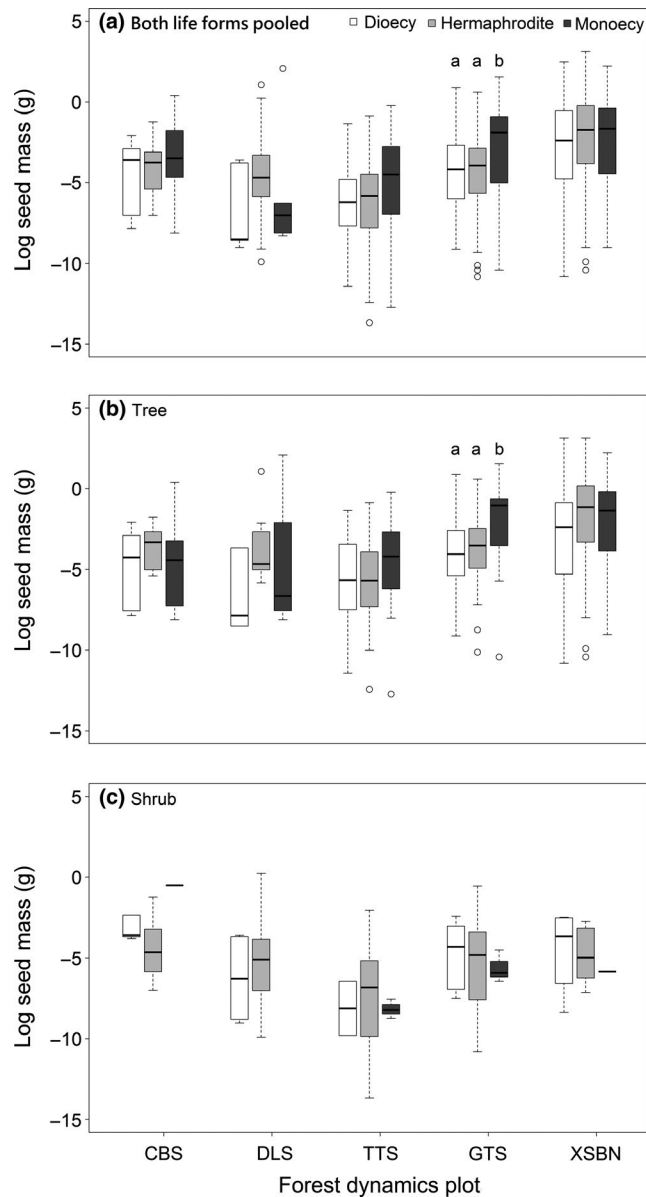

FIGURE 2 The distribution of seed mass (natural-logarithm transformed) (± SE) for tree and shrub species in five forest dynamics plots in China. Within each forest plot, significant differences between breeding systems are indicated by different letters (p < 0.05). A log scale was used for the y-axes due to the wide variation in seed mass across species. Note that there is only one monoecious species in CBS and XSBN, and there are no monoecious shrub species in DLS. The sample size of each group is provided in Appendix S11

Similarly among all stems pooled (stems >1 cm dbh), dioecious species were significantly more abundant than cosexual hermaphroditic species in XSBN, whereas no significant differences among sexual systems were detected in the other four forests (Figure 4a). Among stems >10 cm dbh, dioecious species had lower population density than monoecious species in both temperate DLS and sub-tropical forests (GTS), but sexual system did not affect tree abundance in temperate CBS, sub-tropical TTS and tropical XSBN (Figure 4b). Among stems 1–10 cm dbh, sexual systems did not differ in mean abundance in temperate or subtropical forests, but dioecious species had significantly higher mean abundances than cosexual hermaphroditic species in tropical XSBN (Figure 4c).

4 | DISCUSSION

Across the five forests examined here, we found no consistent fitness advantage of dioecious species over sympatric gender-monomorphic species with bisexual flowers with respect to mean seed mass, seed production, or population abundance. The proportions of dioecious species across all five plots ranged from 18.9% in DLS to 29.2% in CBS, which is comparable to other forest communities (Matallana et al., 2005; Queenborough et al., 2007, 2009; Réjou-Méchain & Cheptou, 2015; Vamosi & Queenborough, 2010).

4.1 | Mean individual seed mass and fecundity

Reproductive advantages including higher mean individual seed mass and seed production could potentially increase the fitness of dioecious species and enhance their viability relative to competitors with bisexual flowers (Moles & Westoby, 2004; Muller-Landau, 2010; Vamosi et al., 2008). However, in the five plots examined here, dioecious species did not consistently produce heavier or more seeds than species with bisexual flowers, a result that is consistent with several other studies (Ibarra-Manriquez & Oyama 1992; Carpenter, Read, & Jaffré, 2003; Queenborough et al., 2009). We observed some compensatory advantages for dioecious species that may be environment-dependent; dioecious species at GTS were characterized by lower seed mass but higher seed production than co-occurring monoecious species (Figures 2 & 3). Although estimates of fecundity based on the number of seeds that fall into seed traps do not provide maximal resolution, this method has been used in numerous studies conducted to estimate seed dispersal and dispersal limitation (Hanya, 2005; Lee, Kim, & You, 2004; Lichstein, Grau, & Aragón, 2004; Nathan & Muller-Landau, 2000; Tsujino & Yumoto, 2007). As long as the estimates from seed traps are not differentially biased among sexual systems, the comparison of sexual systems with respect to this fecundity estimate is valid.

It is important to acknowledge that reproductive compensation among dioecious species may have been expressed by traits not examined here. First, investment in rewards and protective structures associated with individual fruits, including pulp, flesh, and protective husks was not measured because our seed traps were used only
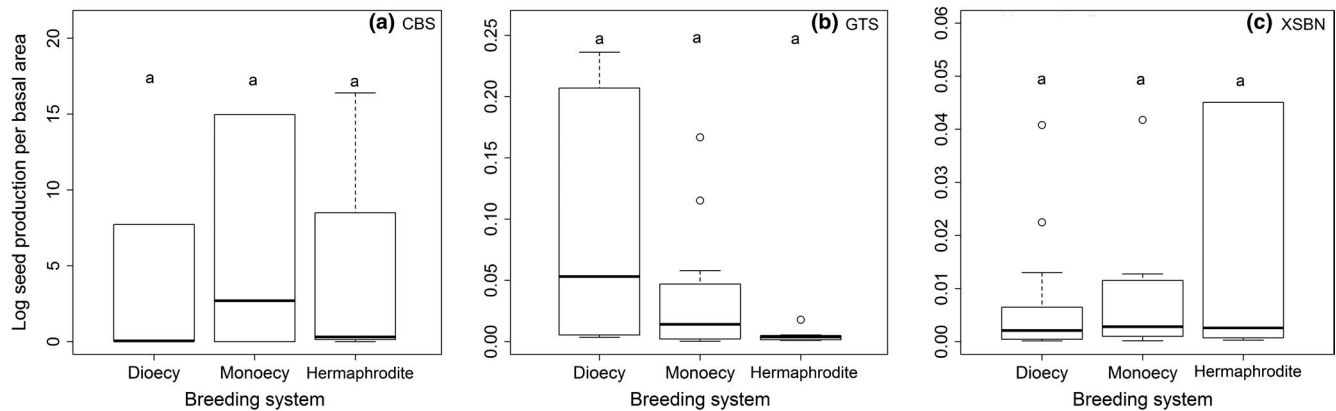
FIGURE 3 Mean seed abundance *per basal area* (LN) of tree species in CBS, GTS and XSBN forest dynamics plots by breeding system. Within all three forest plots, significant differences between breeding systems were tested at $p < 0.05$. Mean values associated with the same letter do not differ significantly in mean seed production per basal area. Note that we included only tree species because of the relatively low number of seeds collected of the shrub species in the CBS (two species) and XSBN (no species) plots. The sample size of each group is provided in Appendix S12

to assess seed production. Second, seed trap data may underestimate seed production for some taxa owing to the complex nature of dispersal, the spatial distribution of adults, various types of species rarity among reproductive trees, and temporal variation in fruit and seed production (Lavabre, Daniel, Stouffer, Sanz, & Bascompte, 2014; Schupp, Milleron, & Russo, 2002), together with the specific behaviors of animal dispersers and predators. Thus, our estimates of seed production may not be highly accurate, although extensive data for the 50-ha tropical rainforest plot on Barro Colorado Island, Panama, indicate that in many species, fruit parts are not moved by animals (Joseph Wright, pers. comm.). In community-level studies of seed rain, labour and time may constrain sampling effort (Clark et al., 1999); obtaining accurate measures of seed production is highly labour-intensive due to the difficulty of species identification, seed trap maintenance, and harsh environmental conditions.

4.2 | Population density

Dioecious species did not differ from cosexual species with respect to the mean abundances of any size class in any of the five plots examined (Figure 4). A lack of empirical support for the prediction that greater population abundances compensate for dioecious species' demographic disadvantage is not uncommon. For example, Queenborough et al. (2009) found that there was no difference in population density between dioecious and cosexual species in a high-diversity tropical forest. Comparison of young vs mature forests revealed that the occurrence and abundances of dioecious species are higher in early-successional forests (Réjou-Méchain & Cheptou, 2015). This suggests that the abundances of species with different sexual systems can be highly context-dependent; consistent with this hypothesis, Réjou-Méchain et al. (2014) found that soil type has a strong influence on the abundances and functional composition of co-occurring species in tropical forests in south-western Central Africa. Given that the composition and dynamics of plant communities are driven by plant growth and mortality (Pacala et al. 1996; Rees

et al. 2001), dioecious taxa may outperform cosexual species with respect to their demographic performance at life history stages other than the ones reported here. Ongoing efforts to monitor growth and mortality regularly at CTFS-ForestGEO (http://www.forestgeo.si.edu/) may provide further insight.

It is also important to recognize that dioecious taxa may persist in communities as a consequence of mechanisms other than demographic advantage when in competition with cosexual taxa. For example, if for some reason dioecious taxa exhibit a greater ability to disperse to and to colonize new locations than their cosexual counterparts, then their persistence might be explained by their greater dispersability rather than due to an intrinsic demographic advantage when in competition with taxa with other sexual systems. In this case, a given subpopulation or deme of a dioecious taxon might be short-lived, but regional persistence might be maintained due to high dispersability and a high rate of colonization.

4.3 | Phylogenetic patterns

Similar to the findings of Queenborough et al. (2009), our analyses detected strong phylogenetic signal in the distributions of sexual system, seed mass and wood density in all five forests examined here. The latter two traits were phylogenetically conserved in the two local temperate forests (CBS and DLS in Table 3), where species richness was much lower than in the sub-tropical and tropical forests surveyed here. This indicates that species' values for these traits (seed mass and wood density) are influenced by phylogenetic affiliation.

Phylogenetic patterns of functional traits reflect their responses to ecological conditions. Each species is not only a discrete evolutionary unit, they diverge with respect to functional traits as they adapt to their temporal-spatial circumstances, approaching a balance between the costs and benefits associated with reproduction and growth (Berdanier & Clark, 2016; Rios, Salgado-Luarte, & Gianoli, 2014; Roff, 2000). For example, species may shift their mating system between inbreeding and outcrossing in response to local
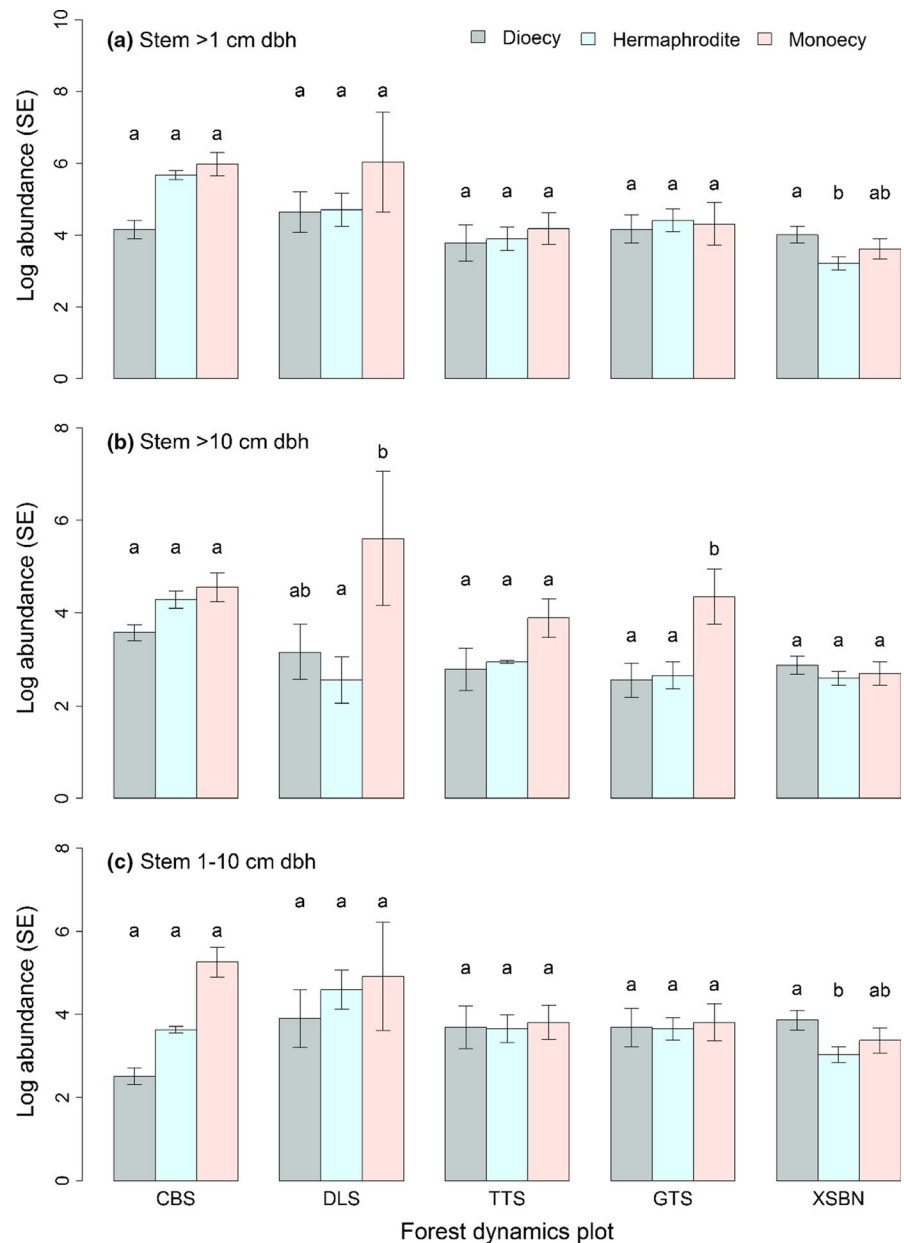
FIGURE 4 Mean abundance (natural-logarithm transformed) (± SE) of species in the five forest dynamics plot by breeding system and size class. Within each forest plot, significant differences between breeding systems with respect to their mean abundances are indicated by different letters (ANOVA with quasi-Poisson error distribution, $p < 0.01$). The sample size of each group is provided in Appendix S13 [Colour figure can be viewed at wileyonlinelibrary.com]

species composition, abundance and environmental conditions over their evolutionary history (Cannon & Lerdau 2015).

4.4 | Coexistence of alternative sexual systems among co-occurring species

Generally, natural selection (acting within phylogenetic, physiological and ecological constraints) shapes patterns of resource allocation, balancing the costs and benefits associated with reproduction vs growth, and resulting in the evolution of alternative life-history strategies (Tognetti, 2012; Visser et al. 2016). Among species, plant functional traits may covary with reproduction, growth, and survival, reflecting trade-offs that define species' ecological strategies, and contribute to their coexistence in a heterogeneous environment (Lebrija-Trejos et al., 2016; Reich, 2014). Thus, to explain the coexistence of woody species with diverse sexual systems, the costs and benefits associated

with functional traits across all life stages and under environment-specific conditions merit further study. Accordingly, recent theoretical models concerning forest dynamics have begun to focus on the combined effects of all demographic processes across the entire life cycle of plants (Bruijning et al., 2017; Visser et al., 2016). For example, Bruijning et al. (2017) used a modeling approach that combined reproduction, growth and survival across the entire life cycle, and found that dioecious females exhibited higher seed production than cosexual hermaphrodite individuals when controlling for seed mass in a tropical forest on Barro Colorado Island (Panama). We encourage future investigations of the factors that promote the coexistence of alternative sexual systems to include comparisons of sympatric species' populations with respect to multiple components of fitness and attributes that affect population growth and persistence, including survivorship, resilience to perturbation, tolerance of climatic variation or extreme weather events, and reproduction.

5 | CONCLUSIONS

Understanding the factors promoting the maintenance of sexual diversity in flowering plants has been a long-term goal in plant evolutionary biology (Barrett, 2002). However, we know relatively little about how variation in these sexual systems persists across forest communities. Based on species surveyed in five forests along a latitudinal gradient, our results suggest that neither seed traits nor population density account for the persistence of dioecy. The dioecious species observed here exhibit no consistent advantages with respect to mean individual seed mass, mean seed production, or abundance that compensate for their unisexuality in the forests examined here. This study also provided the first measures of the relative abundances of species representing the sexual systems studied here among temperate forest angiosperms, which are much less diverse than their tropical counterparts. Our study detected some significant correlations among seed traits, population density and other life-history traits, highlighting the importance of examining multiple traits when searching for those that contribute to the persistence of dioecious species and the maintenance of sexual diversity among sympatric species. We also found that monoecious species sometimes differed from hermaphroditic taxa with bisexual flowers with respect to several of the focal traits examined here, and these therefore merit additional attention in studies of coexistence among sexual systems. Our findings underscore the continued need for studies that evaluate the combined importance of ecological traits expressed across all life stages as determinants of species persistence and community assembly across forests.

AUTHOR CONTRIBUTIONS

WYY and HZQ conceived and designed the experiments. WYY, YZQ, WXG, DYJ, LLX, WXH, SWG, and LXJ performed the experiments. WYY analyzed the data, RPF was consulted on data analyses. WYY and SJM wrote the manuscript, RPF revised the manuscript; other authors provided editorial advice.

DATA ACCESSIBILITY

The data supporting the results in the paper are made available in Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. The number and proportion of tree species and tree total basal area for species with seed production data in three forest dynamics plots, including Changbaishan (CBS), Gutianshan (GTS), and Xishuangbanna (XSBN).

Appendix S2. Arrangement of seed traps in (a) CBS and XSBN plots and (b) GTS plots. Seed traps were arranged regularly (in CBS and XSBN) and along a trail (in GTS), with 150 traps placed in the 25-ha CBS plot, 150 traps placed in the 20-ha XSBN plot, and 169 traps placed along the GTS trail (Table S5).

Appendix S3. Basic attributes of the five plots where seed traps were deployed in this study.

Appendix S4. The list of 16 papers included to identify the sexual systems of angiosperm plants.

Appendix S5. The relationship between the proportions of species and individuals representing each sexual system vs latitude, annual mean temperature, and mean annual precipitation.

Appendix S6. Phylogenetic tree construction methods in GTS and XSBN.

Appendix S7. Seed mass (thousand seed weight) range, mean (± SD), and median values among species representing each breeding system in each of the five forest dynamics plots.

Appendix S8. The relationships among species between seed abundance and basal area within 20-m circles centered around each focal trap (trap area = 0.5 m^2), and between seed abundance per basal area and seed mass. r = Pearson correlation coefficient. Pearson correlation coefficient and significance levels are shown. Significance levels: *$p < 0.05$, **$p < 0.001$. There was no significant correlation at CBS (a & b).

Appendix S9. Summary of the '*pgls*' models designed to detect effects of sexual system on seed mass (thousand-seed weight), seed production per basal area and population density, with growth form and wood specific gravity as the covariates.

Appendix S10. Tree abundance distribution among species representing each sexual system in each of the five forest dynamics plots.

Appendix S11. Sample size for each mean value showed in Figure 2.

Appendix S12. Sample size for each mean value showed in Figure 3.

Appendix S13. Sample size for each mean value showed in Figure 4.