

FLOWERING SEX RATIOS AND SPATIAL DISTRIBUTION OF DIOECIOUS TREES IN A SOUTH-EAST ASIAN SEASONAL TROPICAL FOREST

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GAO J, QUEENBOROUGH SA & CHAI JP. 2012. Flowering sex ratios and spatial distribution of dioecious trees in a South-East Asian seasonal tropical forest. Few studies have investigated multiple dioecious species at the community level. We, therefore, documented flowering sex ratios and analysed the relative spatial distributions of males and females in a diverse suite of tree species in a little-studied tropical forest in Xishuangbanna, south-western China. Male-biased sex ratios were common. Population-level male-biased sex ratios were found in four of the eight species studied and female-biased sex ratios in one. Significant male-biased sex ratios were found in at least one size class in all eight species. Male bias was caused by the onset of flowering at smaller sizes in males than females in four species. Male and female individuals had random to aggregated spatial distributions relative to each other. We concluded that similar selection pressures drove the evolution and ecology of dioecious species in many forest ecosystems.

Keywords: China, permanent plot, reproductive age, Xishuangbanna

GAO J, QUEENBOROUGH SA & CHAI JP. 2012. Nisbah jantina bunga dan taburan ruang pokok diesius di hutan tropika bermusim di Asia Tenggara. Kajian terhadap spesies diesius pada peringkat populasi tidak banyak. Justeru, kami mengkaji nisbah jantina bunga dan menganalisis taburan ruang relatif pokok jantan dan betina di kawasan yang mengandungi pelbagai spesies pokok di sebuah hutan tropika yang kurang diselidiki di Xishuangbanna di barat daya China. Nisbah yang cenderung kepada bunga jantan adalah biasa. Pada peringkat populasi, didapati nisbah jantina cenderung kepada jantan dalam empat daripada lapan spesies yang dikaji manakala satu spesies cenderung kepada betina. Nisbah jantina yang cenderung kepada jantan adalah signifikan dalam sekurang-kurangnya satu kelas saiz dalam kelapan-lapan spesies. Kecenderungan kepada jantan adalah disebabkan oleh pembungaan pada saiz yang lebih kecil dalam jantan berbanding dengan betina dalam empat spesies. Individu jantan dan betina mempunyai taburan ruang yang rawak hingga berkelompok antara satu sama lain. Kesimpulannya ialah tekanan pemilihan yang serupa mempengaruhi evolusi dan ekologi spesies diesius banyak ekosistem hutan.

INTRODUCTION

The evolution of organisms with individuals of the opposite sex (dioecy) and its ecological consequences are fundamental questions in evolutionary ecology (Dellaporta & Calderon-Urrea 1993). Although only 6% of all angiosperms are dioecious (Renner & Ricklefs 1995), dioecy has evolved independently in many different plant families (e.g. Vamossi et al. 2003). Many studies have examined populations of dioecious herbaceous plant species (e.g. Garcia & Antor

1995), but community-level studies are rare, especially in tropical tree communities where up to 30% of species are dioecious (Queenborough et al. 2007). Documenting reproduction of dioecious trees in these diverse systems can help elucidate the selection pressures that act on dioecious species, determine resource availability for pollinators and frugivores, and lead to recommended effective population sizes for conservation management.

Patterns of flowering and fruiting in populations of dioecious species are generally thought to be driven by the typically large disparity in allocation to reproductive structures by males and females (Charnov 1982). Female investment in flowers and fruits in any one reproductive episode often exceeds male investment in flowers and pollen by more than one order of magnitude (Queenborough et al. 2007). This inequality in allocation patterns can lead to striking differences in the flowering, growth and survival of individuals of each sex. Specifically, males have been documented to become reproductive at smaller sizes (Garcia & Antor 1995), flower more frequently (Ataroff & Schwarzkopf 1992), grow faster and survive longer (Wheelwright & Logan 2004), and occupy different microhabitats compared with females (Freeman et al. 1976). Documenting these differences requires enumeration of all potentially-reproductive individuals in a population and careful monitoring of flowering individuals to ensure that sex is assigned correctly and that the populations are truly dioecious.

The spatial structure of a population may be of particular importance for dioecious species, if pollen limitation determines reproductive success (House 1992). Aggregation of males and females reduces the distance between individuals of opposite sex, thus aiding pollen transfer. Alternatively, a population could partition the environment along a resource gradient, leading to spatial segregation of the sexes (Bierzychudek & Eckhart 1988). In species that do spatially segregate, females generally predominate in areas of high resources (Sakai et al. 2006, Marciniuk et al. 2010). Although two thirds of published studies on spatial patterns of dioecious species report evidence of segregation (Bierzychudek & Eckhart 1988), it has not yet been documented in tropical tree or shrub species (Queenborough et al. 2007).

Several studies have investigated sex expression in populations of tropical woody plants (Mack 1997, Nicotra 1998). Fewer studies, however, have documented multiple species in a community (Thomas & LaFrankie 1993, Queenborough et al. 2007) and all but one of these focused on only a single or few closely-related clades (Opler & Bawa 1978). Furthermore, few studies have documented sex expression in the Paleotropics. In order to increase our understanding of the selection pressures operating on dioecious

species, it is important to examine whether patterns of male-biased sex ratios and their proximate causes are consistent in ecosystems and families with different evolutionary histories.

In this paper we describe short-term flowering and sex expression in a diverse suite of tropical forest tree species in south-west China. We used a large-scale plot within which all trees ≥ 1 cm diameter at breast height (dbh) were mapped, marked and identified, thus ensuring a complete census of the entire population. Our census of 2461 individuals (865 of which flowered) in eight species allowed us to examine the following specific questions: (1) do flowering sex ratios deviate from 1:1? (2) do males flower at smaller sizes than females? (3) is there evidence of non-random spatial association of males and females? and (4) are these patterns evident among all dioecious species at one site?

MATERIALS AND METHODS

Study site

Xishuangbanna of south-western Yunnan, south-west China, is located in a biogeographic transitional zone between tropical South-East Asia and subtropical East Asia. Xishuangbanna has typical monsoon climate and is strongly seasonal (Cao et al. 2006). Annual mean temperature is 21.8 °C. Mean annual precipitation is 1490 mm, 84% of which falls between May and October. Dense radiation fog occurs throughout the dry season. Mean relative humidity is 80%. Soils in Xishuangbanna comprise laterite, lateritic red soil and limestone hills (Cao et al. 2006).

The study was conducted in Xishuangbanna National Nature Reserve, an area of tropical dipterocarp seasonal rainforest (21° 36' N, 101° 34' E, Figure 1). The forest canopy is dominated by *Parashorea chinensis* (Dipterocarpaceae), *Pometia tomentosa* (Sapindaceae), *Semecarpus reticulatus* (Anacardiaceae) and *Sloanea tomentosa* (Elaeocarpaceae) (Cao et al. 2006).

20-ha plot establishment and measurements

A 20-ha permanent forest dynamics plot was established at the site in 2007, following standard protocols (Condit 1998, Lan et al. 2008). The plot measures 400 m $\times$ 500 m and covers an elevation gradient from 709 to 869 m asl with the highest elevation located in the north-west.

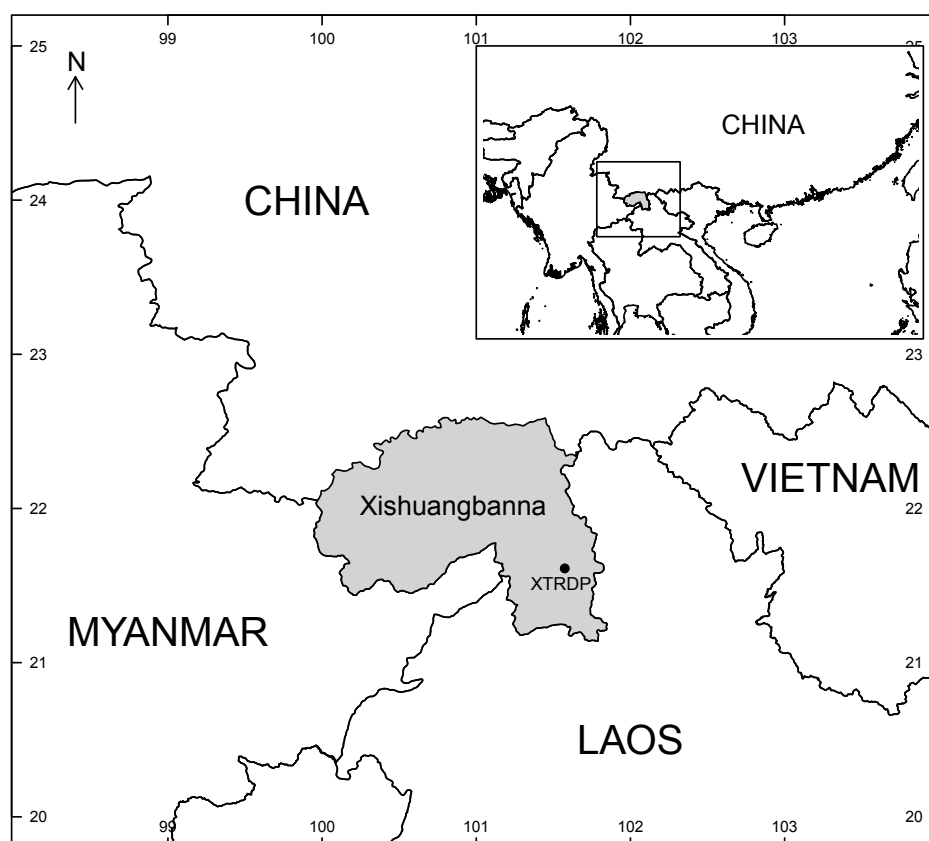


Figure 1 Location of the 20-ha Xishuangbanna forest dynamics plot in southern Yunnan, China; values indicate degrees latitude and longitude

Three perennial streams join south-west of the plot. Free-standing trees of ≥ 1 cm dbh (1.3 m) were tagged, mapped and identified to species. The identifications of plant species were based on the English version of Flora of China (Wu et al. 1994–2011). Voucher specimens were placed in Xishuangbanna Tropical Botanical Garden. The plot is located within the full protection zone of the nature reserve and no human interference has been recorded in the area.

A total of 95,834 individuals with dbh ≥ 1 cm were recorded in the 20-ha plot. Over 99% of these were identified to species (Lan et al. 2008, 2009). The plot includes 468 species in 213 genera and 70 families. *Shorea wantianshuae*, which dominates the forest canopy, ranks second in terms of importance value, although it has the largest basal area. *Pittosporopsis kerrii*, an understorey tree species, is the most abundant species (20,918 individuals).

Flowering census

A total of 32 species known to be dioecious were monitored in the forest plot. For each species,

three trees with the greatest dbh were chosen as signal trees for reproductive behaviour. Every four days between April 2008 and March 2009, the signal trees were observed to monitor the flowering period of each species. When signal trees were seen in flower, all tree stems ≥ 1 cm dbh of that species were visited. Flowers were collected from the canopy of small-statured species or from the ground when tree canopies were too high to reach. The sex of all individuals of *Dendrocnide sinuate*, *Litsea baviensis* and *Mallotus tetracoccus* was determined based on flower morphology and assigned as male or female. Large trees, trees with few flowers or trees that were close to conspecifics where abscised flowers could be confused were checked again for fruit later in the year. Trees with fruit were recorded as female; trees without fruit were recorded as male. Most individuals of *Gironniera subaequalis*, *Gomphandra tetrandra*, *Eurya austroyunnanensis*, *Myristica yunnanensis* and *Mallotus garrettii* were sexed this way. We were aware that in some species, male trees did occasionally produce fruit (e.g. Verdu et al. 2006) or had more complex breeding systems. Careful documentation of

multiple flowering events would be required to fully elucidate these possibilities.

Data analysis

Deviations of sex ratios from 1:1 were tested using the G test for goodness of fit for the whole population and increasing 5-cm dbh size classes (Hurd 2001, Wilson & Hardy 2002). Variation in size distribution of males and females was tested using the Kolmogorov–Smirnov two-sample test. Spatial association between the distributions of male and female trees of each species was tested using the common method of bivariate second-order spatial pattern analysis based on Ripley's K function corrected for edge effects (Ripley 1976). This was done using the 'Kcross' function in the R package spatstat (Baddeley & Turner 2005). All analyses were conducted in the statistical computing software R (2009).

RESULTS

Flowering patterns

We present data on 2461 individuals in eight species that flowered in 2008–09 that are in seven different families from basal and derived orders (Table 1). Of the 2461 trees, 867 trees (35%) flowered in the season 2008–09 (Table 1). Population sizes for the eight species ranged from 101 to 788 trees, with the number of flowering trees ranging from 22 to 375 trees. We recorded a total of 355 female and 512 male trees

over all species. Although Xishuangbanna is a seasonal forest, species were observed to flower throughout the year.

Flowering sex ratios

Flowering sex ratios ranged from 0.45 to 0.82 proportion male in 2008–09 (species mean 0.68; male proportion for all flowering individuals 0.59). These sex ratios significantly deviated from 1:1 in five species (Figure 1). Male-biased sex ratios were observed in four of these species (*G. subaequalis*, *M. yunnanensis*, *G. tetrandra* and *M. garrettii*), and female-biased sex ratio, in one (*Eurya austroyunnanensis*). In the remaining three species, more males than females flowered but the proportions were not significant.

Size distributions of male and female trees

The cumulative size distributions of flowering trees varied between species. All species had more trees in small size classes, but in *Gironniera*, *Gomphandra*, *Litsea* and *Myristica* no tree < 5 cm dbh was observed with flowers (Figure 2). The overall cumulative size distributions of male and female trees significantly differed in three species (*Eurya*, *Litsea* and *Myristica*; Figure 2, top right of each panel). For dbh classes within species, in all eight species, at least one dbh class showed significant male-biased deviation from 1:1 sex ratio (Figure 2). For example, in the 5–10 cm dbh class of *Myristica*, 15 males flowered but no female flowered. Most of the male-biased sex ratios

Table 1 The eight study species and their abundances in the Xishuangbanna forest plot

Species	Family	Order ^a	N _m	N _f	N _{total}	Dbh _{max}	Flowering period
<i>Dendrocnide sinuate</i>	Urticaceae	Rosales	40	27	227	14.06	Oct–Nov
<i>Eurya austroyunnanensis</i>	Theaceae	Ericales	167	208	788	26.04	Nov–Dec
<i>Gironniera subaequalis</i>	Ulmaceae	Rosales	27	6	134	28.35	Feb–Apr
<i>Gomphandra tetrandra</i>	Icacinaceae	Celastrales	15	7	222	26.59	Nov–Jan
<i>Litsea baviensis</i>	Lauraceae	Laurales	23	7	153	28.59	May–Jun
<i>Mallotus garrettii</i>	Euphorbiaceae	Malpighiales	177	80	683	24.92	May–Jul
<i>Mallotus tetracoccus</i>	Euphorbiaceae	Malpighiales	19	11	101	31.61	Jun–Jul
<i>Myristica yunnanensis</i>	Myristicaceae	Magnoliales	44	9	153	43.68	Sept–Dec
Total			512	355	2461		

N_m = number of male trees; N_f = number of female trees; N_{total} = total population > 1 cm dbh; dbh_{max} = mean dbh of the largest three stems

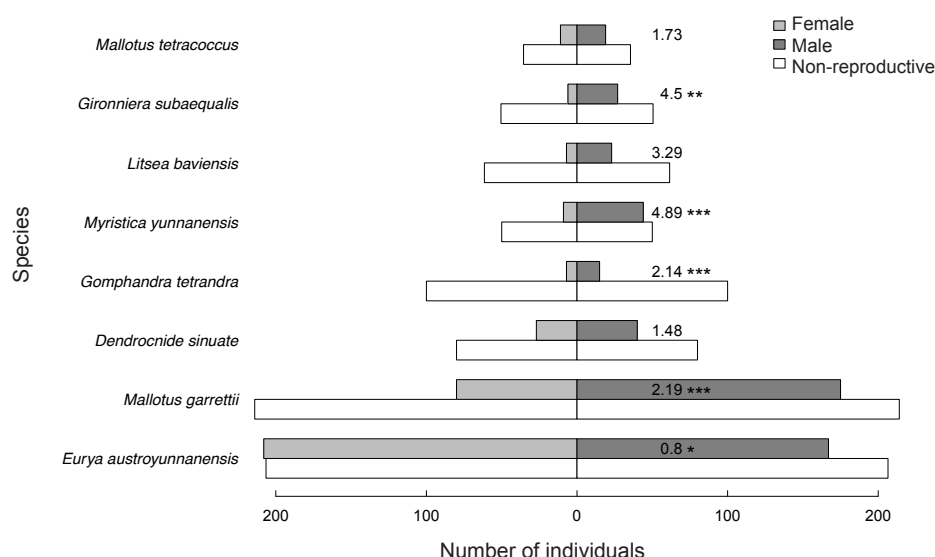


Figure 1 Flowering sex ratios of eight dioecious tree species in the Xishuangbanna forest dynamics plot over one reproductive episode (2008–09); the horizontal bar plot shows the number of individuals in each species, ordered by abundance; white bars indicate the number of non-reproductive individuals, shaded bars indicate reproductive individuals; values indicate the proportion of male individuals; significant deviations from 1:1 sex ratio are indicated by asterisks (G test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

tended to be in the smaller dbh classes. *Eurya* was an exception: more males than females flowered in the 1–5 cm dbh class, but more females than males flowered in the 10–15 and 15–20 cm dbh size classes.

Bivariate spatial distribution

The eight species showed considerable variation in their spatial distribution throughout the plot (Figure 3). *Mallotus garrettii* and *Litsea* were highly clumped, whereas *Eurya* and *Myristica* were much more widely distributed. The relative distribution of the two sexes was much more consistent, however, with every species showing a random pattern of association at small spatial scales, moving to signs of aggregation of males and females at larger spatial scales (Figure 4). This pattern was most obvious in *Eurya* and *Mallotus garrettii*, and least apparent in *Myristica*, where males and females were randomly distributed at most scales. No species showed any indication of over-dispersion of the sexes. The species have differing habitat associations (Lan et al. 2009): *G. subaequalis*, *G. tetrandra* and *L. baviensis* are mainly associated with slope habitats; *M. garrettii* and *D. sinuate* are associated with valley habitats; and *E. austroyunnanensis*, *M. yunnanensis* and

M. tetracoccus are associated with both low slope and valley habitats. Species ranged from small understorey species such as *Dendrocnide* to canopy trees (e.g. *Myristica*).

DISCUSSION

About half of the species studied showed biased sex ratios and most of these were biased towards males. Four species had significant male-biased population-level flowering sex ratios while one had significant female-biased sex ratio. Within populations, all the species studied showed significant male-biased flowering sex ratio in at least one dbh size class, typically in one of the smaller dbh classes. These results indicated that male individuals tended to flower earlier in life or at smaller sizes than females. Biased sex ratios in our populations were not caused by localised spatial segregation of the sexes because we found that males and females had random or aggregated distributions relative to each other. It is, therefore, likely that populations of dioecious species, even those with highly divergent evolutionary histories and in different locales, are subject to comparable selection pressures resulting in similar flowering strategies and male-biased sex ratios.

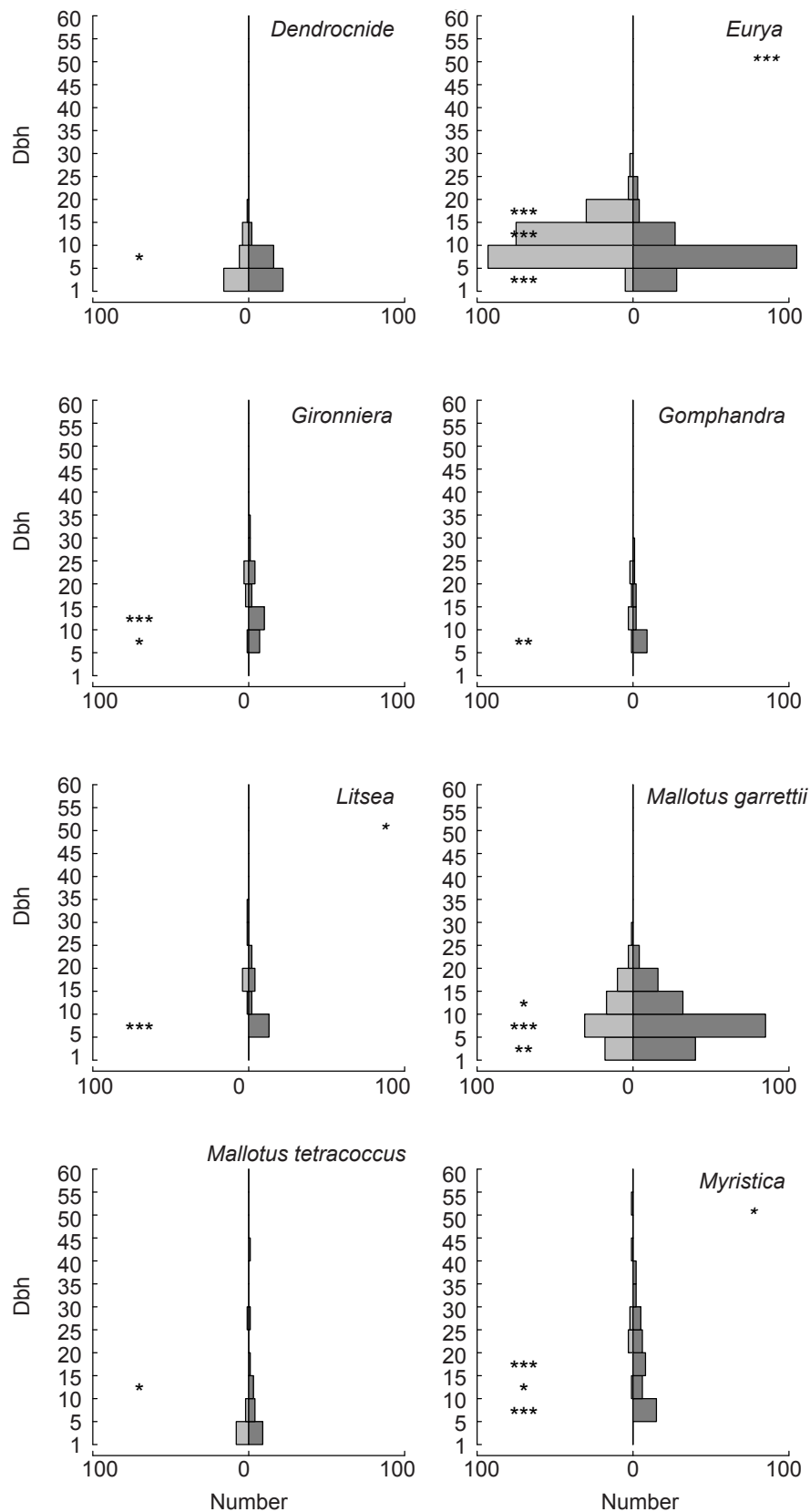


Figure 2 Size distribution by sex for eight dioecious tree species in the Xishuangbanna forest dynamics plot over one reproductive episode (2008–09); each panel shows the number of individuals of each sex in each dbh class (female: light grey, male: dark grey); significant differences of cumulative size distributions are indicated by asterisks under each species name (Kolmogorov–Smirnov test, * $p < 0.05$, *** $p < 0.001$); significant deviations from 1:1 sex ratio within each dbh class are indicated by asterisks (G test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$); Dbh = diameter at breast height

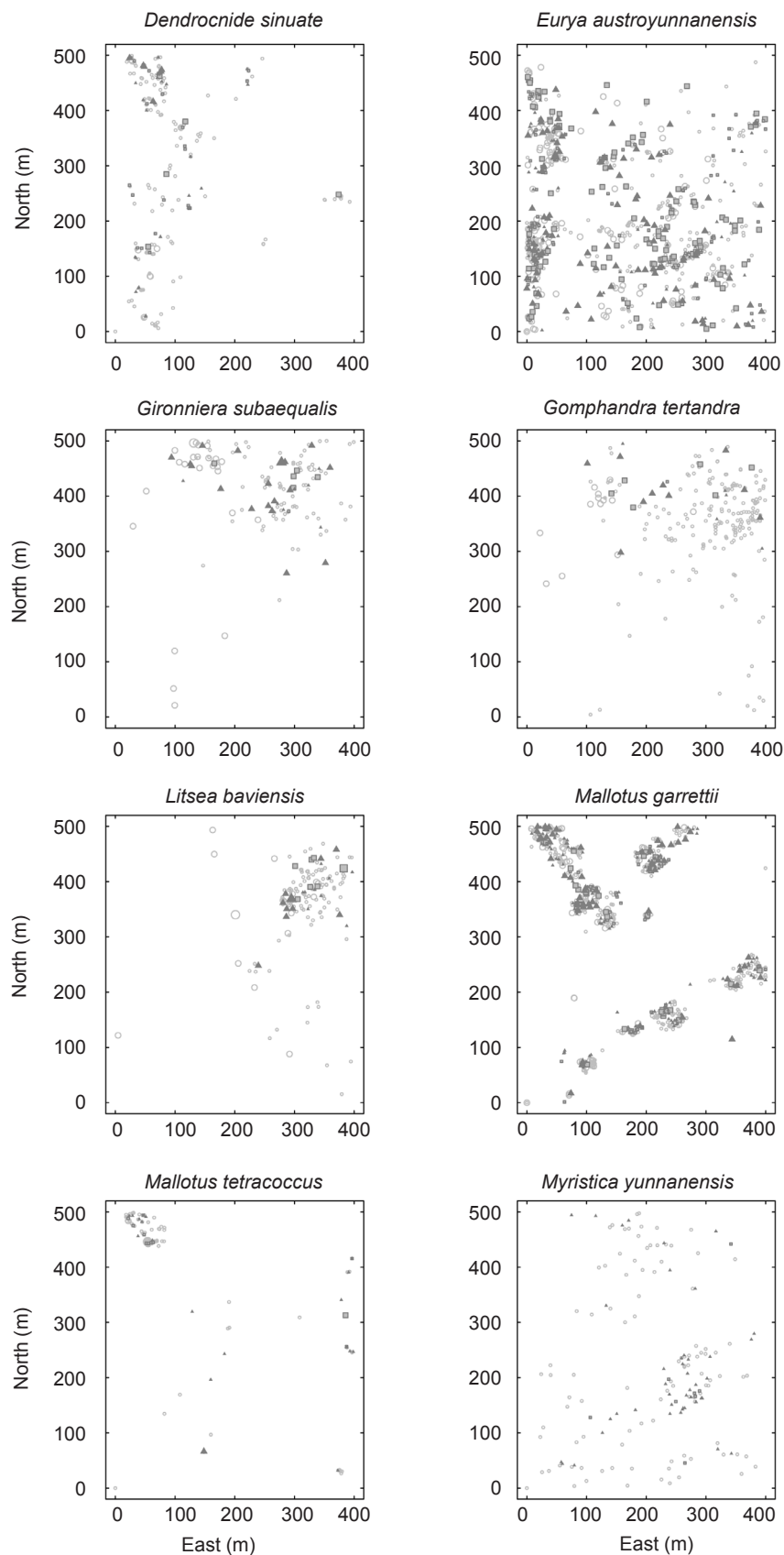


Figure 3 The location of all individuals of eight dioecious tree species within the Xishuangbanna forest dynamics plot; each box shows the locations of all stems ≥ 1 cm dbh for one species; males that flowered in 2008–09 are shown in light grey squares with a dark border, females in dark grey triangles; non-flowering individuals are grey open circles; the size of symbol corresponds to the dbh class of each stem (1–10, 10–30, > 30 cm dbh)

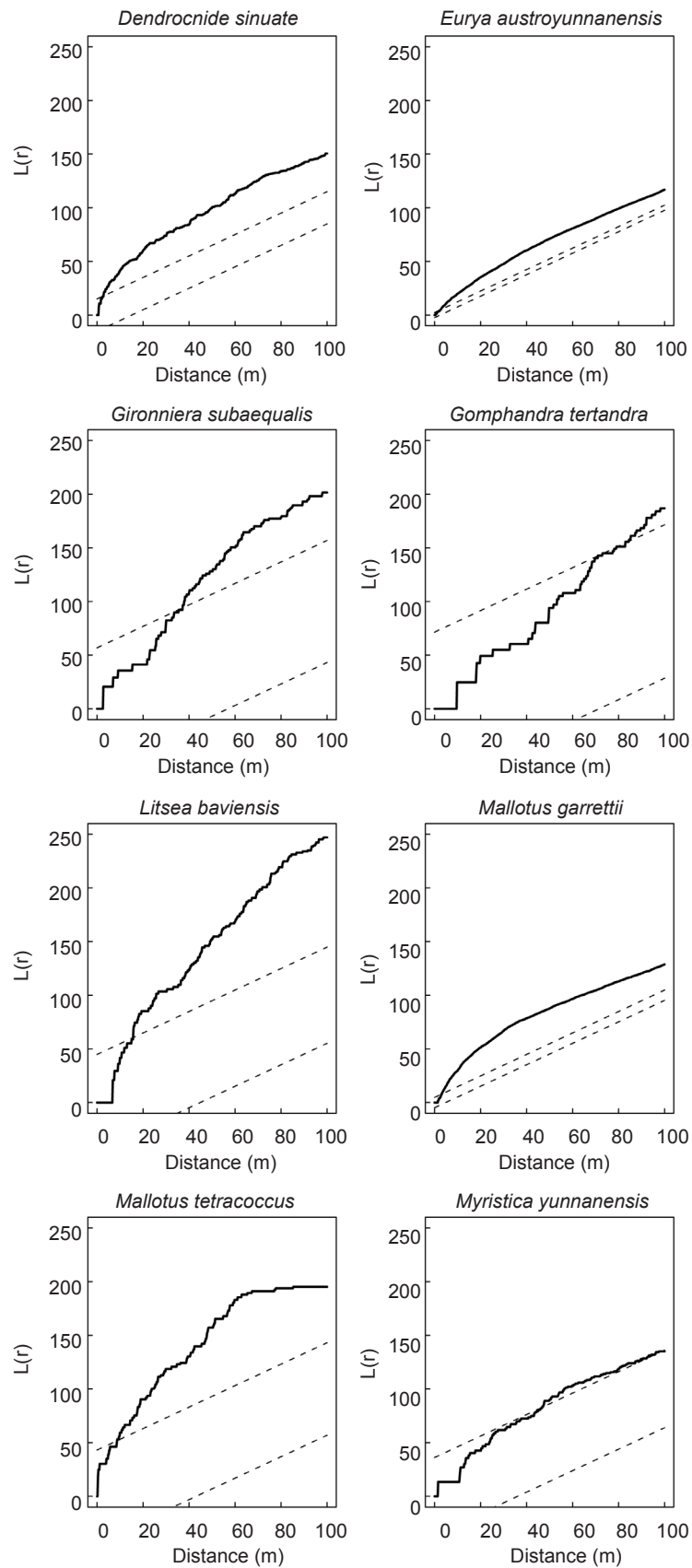


Figure 4 The spatial distribution of flowering males relative to females for eight dioecious tree species in the Xishuangbanna forest dynamics plot over one reproductive episode (2008–09); each panel shows the observed distribution (solid line) with associated confidence intervals (dashed lines); if the observed line lies outside the confidence intervals, this indicates significant aggregation (above), or overdispersion (below), from 0 to 100 m; $L(r)$ = cumulative count using Ripley's R function

Proximate and ultimate causes of male-biased sex ratios

Consistent with our results, male-biased sex ratios have been shown to be more common than female-biased sex ratios in dioecious tropical plants (Queenborough et al. 2007). This may be for a number of proximate reasons such as precocial male flowering, more frequent male flowering, higher female mortality or spatial segregation of the sexes (Thomas & LaFrankie 1993). We were able to explicitly test two of these proximate causes. We found that males flowered at smaller sizes than females in all eight species, and that male and female individuals were aggregated and therefore not occupying separate habitats. Males and females might, however, occupy different microhabitats (such as localised high-nutrient patches) at spatial scales smaller than we were able to measure. This deserves further investigation. However, we think such small-scale partitioning is unlikely because the limiting resource in many tropical forests is light, which varies inconsistently across the landscape and through time. We can get a hint at whether females suffer higher mortality than males in our study species by examining the sex ratios of larger dbh size classes (Figure 2). There were no male-biased sex ratios in the larger size classes of any species, suggesting that it was unlikely that females were dying at smaller sizes than male trees. In order to test whether males flower more frequently or females have higher mortality, long-term data on flowering behaviour and demography are needed (e.g. Queenborough et al. 2007). Of course, the ultimate cause of these patterns is likely the inequality in reproductive investment in any one season. We did not quantify the investment in flowers and fruits by each species. However, given that males do not produce seed or fruit, female investment is often substantially greater than male investment (Charnov 1982). This increased cost drives differences in patterns of reproduction and phenology that can have profound implications on the life history and demography of individuals.

Although it is thought that differences in demography between the sexes are generally caused by costs of reproduction, variation in demography itself can also give rise to skewed sex ratios (Shelton 2010). Stable populations with disproportionately high male mortality may be the

cause of the few species documented to exhibit female-biased sex ratios in dioecious tropical trees (Opler & Bawa 1978) and may explain the female-biased sex ratio that we observed in *Eurya*. Alternatively, asexual reproduction has been observed to give rise to female-biased sex ratios in the genus *Garcinia* (Thomas 1997). Furthermore, natural variation in flowering sex ratios in any one year can lead to apparently female-biased sex ratios being recorded if populations are not followed over several reproductive episodes. Further investigation of populations recorded with female-biased sex ratios would be beneficial.

While differences in the costs of reproduction and/or demography can certainly give rise to dimorphism in dioecious species, there are other alternative explanations that have been put forward. In particular, sex-specific selection due to floral visitation and seed dispersal are also potential selective agents that influence sexual dimorphism in plants (Vamosi et al. 2007).

Where would you expect the most biased sex ratios?

Thomas and LaFrankie (1993) raised the question of whether sex ratios were likely to be more biased in resource-poor environments, such as the tropical forest understorey. The data are not yet available to answer this question, even if we combine all known data on sex ratios. We provide a note of statistical caution, in that biased sex ratios are more likely to be detected in understorey species because they are generally more abundant than canopy species. Therefore, the test of deviation is more powerful and requires less of a difference to be statistically significant. Moreover, understorey species are often easier to sex than canopy species because their canopies and flowers are more accessible from the ground. Sexing trees from abscised flowers may lead to erroneous determination of sex and/or apparent sex changing over multiple censuses if flowers from different individuals are assigned to a single tree. Sexing trees from fruit may underestimate the number of males in the population because some male trees in dioecious populations do occasionally produce female flowers and fruits (Rowland et al. 2002). In extreme cases, sexing trees this way could even lead to misdiagnosing the breeding system of the species. Development of sex-specific genetic markers is the only sure-

fire method of sexing trees, including juveniles (Dellaporta & Calderon-Urrea 1993) but is time consuming and expensive. Sexing trees from abscised flowers or the presence of fruit is far from ideal but, as in this study, may be the only option available.

Caveats

Two potential sources of error can be identified in our results. Firstly, we relied mainly on the presence of fruit, rather than floral morphology, to determine the sex of many of the trees. Any female trees that flowered but then failed to set fruit would thus be misclassified as male, which will overestimate males in the population. Secondly, some of the species (specifically *Eurya* and both *Mallotus* species) flowered prolifically in the smallest size class examined, suggesting that these species might be reproductive at sizes < 1 cm dbh. If males reproduce at smaller sizes than females, this will overestimate the number of reproductive females in the population. The reported case of female bias in *Eurya* could possibly result from this bias.

In a further note of caution, we emphasise the short length of our study. Sex ratios can vary markedly among years (Queenborough et al. 2007) and drawing definitive conclusions about these species from one year of data may be hasty.

Future directions

Our paper discusses one year of data from eight species. In the life of a tree, a single reproductive event is trifling, and the conclusions we can draw from these data are necessarily tentative, especially for the rarer species such as *Gomphandra* and *Litsea*. Multiple years of census data (Thomas & LaFrankie 1993) have shown considerable variation in the frequency and intensity of flowering by individual trees. Such flowering patterns will be unobservable in one census. However, the patterns we can observe in one year (e.g. the higher number of males in smaller size classes) generally are consistent from year to year (Queenborough et al. 2007). To fully investigate flowering patterns and lifetime reproductive investment ideally require censuses of multiple reproductive events over many years. With the recent development of large-scale long-term forest plot networks in

which all individuals are mapped, marked and identified such as the Chinese Forest Biodiversity Monitoring Network and the Centre for Tropical Forest Science network, there is an opportunity for multiple censuses of breeding populations of many tree species worldwide. Such detailed, long-term studies of breeding populations from multiple forest communities would shed light on the factors influencing the evolution of plant breeding systems.

CONCLUSIONS

Flowering in a wide range of Chinese dioecious tropical tree species were comparable with patterns found in the Americas and elsewhere. Therefore, it is likely that similar selection pressures drive the evolution and ecology of dioecious species in many ecosystems. Determining these pressures and their associated fitness advantages can help us understand how and why dioecy have evolved numerous times in flowering plants.

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