Determinants of biased sex ratios and inter-sex costs of reproduction in dioecious tropical forest trees[1]

Simon A. Queenborough,[2,5] David F. R. P. Burslem,[2] Nancy C. Garwood,[3] and Renato Valencia[4]

[2]School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 3UU, UK; [3]Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901 USA; and [4]Department of Biological Sciences, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2148, Quito, Ecuador

Estimates of the sex ratio and cost of reproduction in plant populations have implications for resource use by animals, reserve design, and mechanisms of species coexistence, but may be biased unless all potentially reproductive individuals are censused over several flowering seasons. To investigate mechanisms maintaining dioecy in tropical forest trees, we recorded the flowering activity, sexual expression, and reproductive effort of all 2209 potentially reproductive individuals within 16 species of Myristicaceae over 4 years on a large forest plot in Amazonian Ecuador. Female trees invested >10 times more biomass than males in total reproduction. Flowering sex ratios were male-biased in four species in ≥1 year, and cumulative 4-year sex ratios were male-biased in two species and for the whole family, but different mechanisms were responsible for this in different species. Annual growth rates were equivalent for both sexes, implying that females can compensate for their greater reproductive investment. There was no strict spatial segregation of the sexes, but females were more often associated with specific habitats than males. We conclude that male-biased sex ratios are not manifested uniformly even after exhaustive sampling and that the mechanisms balancing the higher cost of female reproduction are extremely variable.

Key words: dioecious; investment; Myristicaceae; reproduction; sex-ratio; tropical forest; Yasuní.

Dioecious species constitute 16–28% of the tree and shrub species in any one tropical forest site (Ashton, 1969; Ruiz and Arroyo, 1978; Croat, 1979; Bawa et al., 1982; Flores and Schemske, 1984; Bullock, 1985; Ramirez and Brito, 1990; Thomas and LaFrankie, 1993). Effective (i.e., reproductive) population sizes are often very different from total population sizes, and this has bearings on reserve size and design as well as mechanisms of species coexistence, especially in highly diverse ecosystems (Stacy et al., 1997; Laurance, 2005). Many dioecious families are also important as a food source for primate and bird species, and patterns of reproduction have implications for resource use and habitat partitioning by these animals (Di Fiore, 2004; Russo et al., 2005).

Most dioecious plants are not obviously sexually dimorphic, but they often have large inter-sex differences in growth patterns and in the proportional allocation of resources to reproduction (Lloyd and Webb, 1977). There is a greater per gamete cost of reproduction in females than in males (Darwin, 1877; Lloyd and Webb, 1977; Charnov, 1982), and this differential cost of reproduction between the sexes has consequences that are manifested in different ways in different plants. Frequently observed differences include precocious male flowering (Allen and Antos, 1993; Garcia and Antor,

1995), more frequent male flowering (Agren, 1988; Ataroff and Schwarzkopf, 1992), reduced growth, survival, and subsequent reproductive effort in females (Garcia and Antor, 1995; Wheelwright and Logan, 2004), and local habitat preferences (Freeman et al., 1976; Lloyd and Webb, 1977; Bierzychudek and Eckhart, 1988). Alone or in combination, these differences tend to result in male-biased sex ratios.

Previous studies in both the neotropics (Bawa and Opler, 1975; Melampy and Howe, 1977; Opler and Bawa, 1978; Bullock, 1982; Nicotra, 1998) and the paleotropics (Yap, 1982; House, 1992; Thomas and LaFrankie, 1993) have suggested that tropical trees also have these patterns of inter-sex differences. However, these studies have generally not censused all potentially reproductive individuals, nor followed the same trees for several flowering episodes. Here, we present far more extensive data on flowering sex ratios over four reproductive episodes in a long-term permanent forest plot where all stems ≥1 cm diameter at breast height (dbh) have been mapped. We present data for the dioecious family Myristicaceae, which is a common element of lowland tropical rain forests of the Amazon basin and is represented by 16 species on the permanent plot at our study site. Female Myristicaceae produce large animal-dispersed fruit whose biomass is several orders of magnitude greater than their small flowers (Armstrong and Irvine, 1989), and as such the family provides an ideal model with which to study the outcomes of differential costs to reproduction in a single clade.

Studies that have documented sex expression over multiple reproductive episodes have reported great interannual variation in flowering sex ratios (Bullock and Bawa, 1981; Bullock, 1982; Bullock et al., 1983; Clark and Clark, 1987; Wheelwright and Bruneau, 1992; Thomas and LaFrankie, 1993; Nicotra, 1998; Morellato, 2004). However, only two studies have followed the same individuals for more than 2 years (Clark and Clark, 1987; Wheelwright and Bruneau, 1992; Wheelwright and Logan, 2004), and only one previous study has documented sex expression in several coexisting and

closely related species over 2 years (Thomas and LaFrankie, 1993). Multiple censuses allow assessment of reproductive frequency and calculation of cumulative sex ratios, which may estimate total population and seed/seedling sex ratios better than a single census (Thomas and LaFrankie, 1993). It is also essential that all potentially reproductive individuals are censused, especially if sex expression varies as a function of tree size. Most studies (e.g., Ackerly et al., 1990) only include trees ≥10 cm dbh, and so the true flowering sex ratios of species that flower below this threshold is unknown. This study is unique in its length and number of individuals and species studied.

If the distance between the sexes determines reproductive success because of pollen-limitation, then the spatial structure of the population is of particular importance for dioecious species (House, 1992; Cunningham, 1996; Stacy et al., 1996). Aggregation of males and females might aid in pollen transfer by reducing this distance (Bawa and Opler, 1975, 1977). Alternatively, spatial segregation of the sexes (SSS) can permit partitioning of the environment along a resource gradient (Bierzychudek and Eckhart, 1988). In species that do have SSS, it is generally females that predominate under high resource conditions (Freeman et al., 1976; Lloyd and Webb, 1977). Although two thirds of published papers report evidence of segregation (Bierzychudek and Eckhart, 1988), there is little evidence of it among tropical tree and shrub species (Bawa and Opler, 1977; Melampy and Howe, 1977; Bullock, 1982; Armstrong and Irvine, 1989; Nicotra, 1998). However, previous tests have only used the presence or absence of individuals, but segregation or habitat association may instead be apparent in terms of differential growth or fecundity (Bullock, 1982). In this study we examine the spatial patterns of highly fecund and frequently reproducing individuals of both sexes to determine if certain habitats are more conducive to reproductive success than others.

In this report we describe flowering, sex expression, and spatial distributions of 15 species of dioecious and one species of androdioecious trees in the Myristicaceae in a lowland rain forest in Amazonian Ecuador during four successive annual flowering episodes. We made use of a large-scale plot within which all trees ≥10 cm dbh in 50 ha and ≥1 cm dbh in 25 ha were tagged, mapped, and identified, thus ensuring a complete census of each species. Our census of 2209 individuals over 4 years allowed us to address the following questions: (1) Is sex expression fixed in time? (2) Do flowering sex ratios deviate from 1 : 1, and are they consistent between years? (3) What are the proximate causes of biased sex ratios? (4) Are there indirect costs of reproduction? (5) Is there evidence of nonrandom distribution of males and females in relation to each other and in response to habitat variation across the plot?

MATERIALS AND METHODS

Study site—Yasuní National Park and Biosphere Reserve and the adjacent Huaorani Ethnic Reserve cover 1.6 million ha of forest and form the largest protected area in Amazonian Ecuador. Within the park, extensive oil reserves are ceded for prospecting and exploitation. Human influences are currently sparse but increasing; currently <3000 Huaorani indigenous people live in the region, and road and oil sites are localized. Most of the park is undisturbed wilderness covered by unbroken forest. The park is nearly level at about 200 m a.s.l., but is crossed by numerous ridges rising 25–40 m above the intervening streams. At wider intervals, large rivers flow east to meet the Napo and Amazon. The canopy is 10–25 m high but punctuated with emergents to 40 and rarely 50 m tall. Rainfall and temperature are aseasonal at Yasuní (Valencia et al., 2004a). The mean annual rainfall is 2800 mm, and mean monthly rainfall is almost never <100 mm. Mean monthly temperature is 25–27°C.

A 50-ha permanent forest dynamics plot (FDP) is located inside the park (0°41′ S, 76°24′ W), just south of the Tiputini River. It is within a kilometer of the Yasuní Research Station, operated by the Pontificia Universidad Católica del Ecuador (Valencia et al., 2004a). There are a few Huaorani settlements on an oil access road north of the station, and low-intensity hunting occurs near the research station and inside the plot. The 50-ha plot ranges from 216 to 248 m a.s.l: it includes three ridges and an intervening valley that occasionally floods for brief periods.

50-ha plot establishment and measurements—The FDP was fully surveyed in 1995. Between June 1995 and June 2000, all freestanding stems ≥1 cm dbh (1.3 m), excluding lianas, were tagged, mapped, and identified to morphospecies in the western half of the 50 ha (Romoleroux et al., 1997; Valencia et al., 2004a). All stems ≥10 cm dbh were tagged, mapped, and identified in the eastern 25 ha. A second census was undertaken from January 2003 to June 2004. All living stems were remeasured and new recruits mapped, tagged, and identified. We utilized data for the Myristicaceae from both censuses.

Study species—The Myristicaceae is a pantropical family and an important component of Amazonian lowland forests (Pitman et al., 2001). Within the FDP, it is ranked 10th in terms of basal area (Valencia et al., 2004a), and a total of 3351 stems were enumerated in the first plot census. Its life forms range from understorey tree to canopy and emergent tree. All members of the family are dioecious, except some species of *Iryanthera* that are monoecious (Smith, 1937; Ackerly et al., 1990), and so outbreeding is mostly obligatory. Myristicaceae have not been observed to set fruit apomictically (Armstrong and Irvine, 1989; Queenborough, 2005).

Floral morphology conforms closely to the syndrome for dioecy in tropical trees (Bawa and Opler, 1975; Bawa, 1980). Flowers are small (<2 mm in breadth), unspecialized and dull in color, varying from yellow-green in *Compsoneura* and *Iryanthera* to yellow-brown in *Otoba* and *Virola*. They are probably entomophilous, though the pollinators of neotropical taxa are unknown. *Myristica fragrans* Houtt., the commercial nutmeg of Asia, and *M. insipida*, of Australia, are both beetle-pollinated and it is suggested that the other four Myristicaceous genera of Southeast Asia are also beetle-pollinated (Armstrong and Drummond, 1986; Armstrong and Irvine, 1989). No potential pollinators were seen during observations of *I. hostmannii* flowers at Yasuní (S. Queenborough, unpublished data). The fruits are woody capsules, containing a single arillate seed, which are dispersed by various monkeys (*Alouatta seniculus*, *Ateles beelzebuth*, *Lagothrix lagotricha*, and *Pithecia monochus*), toucans (*Ramphastos tucanus*), guans (*Penelope jacquacu* and *Pipile pipile*) and motmots (*Baryphthengus martii*) (Howe, 1983; Roosmalen et al., 1996; A. DiFiore and A. Link, New York University, personal communications; S. Queenborough, unpublished data).

Sixteen species in four genera of Myristicaceae co-occur in the Yasuní FDP: *Compsoneura* (two species); *Iryanthera* (three species); *Otoba* (one species); and *Virola* (10 species). These species are *Compsoneura capitellata* (A.DC.) Warb., *C. sprucei* (A.DC.) Warb., *Iryanthera grandis* Ducke, *I. juruensis* Warb., *I. hostmannii* (Benth.) Warb., *Otoba glycycarpa* (Ducke) W.A. Rodrigues & T.S. Jaram., *Virola dixonii* Little, *V. duckei* A.C. Sm., *V. elongata* (Benth.) Warb., *V. flexuosa* A.C. Sm., *V. mollissima* (A.DC.) Warb., *V. multinervia* Ducke, *V. obovata* Ducke, *V. pavonis* (A.DC.) A.C. Sm., *V. 'microfuzzy'*, and *V.* cf. *calophylla*. Nomenclature follows Rodrigues (1980). A complete set of collections from the plot is held in the Herbarium of the Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCA).

Flowering census—Available phenological evidence (Persson, 2005) suggested that most species of Myristicaceae flowered during the community flowering peak of August–October and fruited during the community fruiting peak of January–March. Consequently, all potentially reproductive stems were visited annually in August–October from 2002 to 2005, and all flowering individuals were recorded. *Compsoneura capitellata* was subsequently observed to flower in May and was therefore visited in May 2003 and 2004. Trees of *V. elongata* and *V. 'microfuzzy'* were observed to flower and fruit sporadically throughout the year, and data for these species are likely to underestimate the total number of reproductive individuals in their populations. Other (rarer) species (e.g., *V. mollissima* and *V. multinervia*) were only

TABLE 1. Flowering and cumulative sex ratios (proportion of males) for 16 tree species of Myristicaceae on the Yasuní Forest Dynamics Plot. dbh = minimum dbh of stem censused; N_{tot} = total no. trees censused; N_{rep} = no. trees that flowered in a given year or set of years. Significance denoted by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (G test for random deviation of sex ratios from 1:1).

Species	dbh (cm)	N_{tot}	Area (ha)	2002		2003		2004		2005		Cumulative	
				Male	N_{rep}	Male	N_{rep}	Male	N_{rep}	Male	N_{rep}	Male	N_{rep}
Compsoneura capitellata	1	109	25	NA	NA	0.57	30	0.92**	12	NA	NA	0.57	30
Compsoneura sprucei	10	13	50	NA	NA	0.33	3	NA	NA	NA	NA	0.25	4
Iryanthera grandis	10	46	50	0.57	7	0.73	15	0.00	1	1.00	3	0.69	16
Iryanthera juruensis†	1	136	25	0.44	9	0.56	18	1.00	1	0.50	2	0.58	24
Iryanthera hostmannii	1	839	25	0.57*	296	0.54	315	0.63***	196	0.58**	323	0.56	380
Otoba glycycarpa	10	491	50	0.59*	207	0.58*	221	0.51	201	0.56	215	0.57*	249
Virola dixonii	10	24	50	0.00	0	1.00	1	0.00	0	0.00	0	0.33	3
Virola duckei	10	146	50	0.51	37	0.44	36	0.32	25	0.58	24	0.50	44
Virola elongata	10	51	50	0.73*	23	0.61	18	0.72*	25	0.73	15	0.71*	28
Virola flexuosa	10	52	50	0.67	3	0.40	5	0.00	0	0.00	0	0.40	5
Virola 'microfuzzy'	10	40	50	0.50	10	0.33	15	0.30	3	0.00	1	0.30	20
Virola mollissima	10	18	50	0.67	3	0.50	4	0.33	3	0.00	2	0.29	7
Virola multinervia	10	14	50	0.00	0	1.00	1	0.00	0	0.00	0	1.00	1
Virola obovata	10	31	50	0.58	12	0.67	18	0.28	7	0.42	7	0.70	20
Virola pavonis	10	124	50	0.47	17	0.57	28	0.07**	14	0.56	16	0.56	32
Virola cf. *calophylla*	10	75	50	0.40	15	0.25	16	0.00**	10	0.25	4	0.31	26
All *Compsoneura*	1	183	25	NA	NA	0.56	32	0.92**	12	NA	NA	0.56	32
All *Iryanthera*	1	1037	25	0.56*	308	0.55	341	0.63***	198	0.58**	328	0.57**	412
All *Virola*	10	591	50	0.55	121	0.49	142	0.36**	87	0.55	69	0.50	186
All Myristicaceae		2209		0.56**	651	0.54*	776	0.54	498	0.57***	616	0.55**	933

† *I. juruensis* proportion = (males/males + monoecious individuals).

occasionally observed in flower or fruit; a more detailed phenological study is required to assess these species fully.

The threshold for censuses was ≥10 cm dbh for all species except *I. hostmannii*, *I. juruensis,* and *Compsoneura*, for which the threshold was ≥1 cm dbh. Sex expression was determined each year from abscised flowers collected from beneath each individual. All females and trees for which flowers could not be collected or that could have been confused with nearby trees were checked again in the fruiting season.

To determine direct investment in reproductive structures, we collected flowering material from a 1 × 1 m quadrat randomly positioned beneath the canopy of every male tree. For *I. hostmannii*, we counted the number of inflorescences in the canopy. We estimated fruit production by counting the number of fallen capsules in sufficient randomly-positioned 1 × 1 m quadrats to cover 10 % of the projected canopy area of every female (range: 1–23). We collected fruit from at least three female trees per species and weighed them after oven drying at 100°C.

Between January 2002 and January 2003, all Myristicaceae stems ≥10 cm dbh, and all *Iryanthera* stems ≥1 cm dbh, were visited and the crown illumination (CI) index (Clark and Clark, 1992) recorded. The CI index quantifies the light available to a tree by estimating the exposure of the crown on a scale of 1–5: 1, no vertical light and minimal lateral light; 2, no vertical light and medium lateral light; 3, crown exposed to some vertical and some lateral light; 4, crown exposed to vertical and some lateral light; and 5, crown completely exposed vertically and laterally.

Data analysis—Sex ratios were expressed as proportions [(males/(males + females)], rather than a strict ratio, because analysis of ratios sensu strictu can lead to errors in interpretation (Wilson and Hardy, 2002). The statistical analysis followed that of Thomas and LaFrankie (1993). Deviations of sex ratios from 1 : 1 were tested using the *G* test for goodness of fit. Variation in size distributions were tested using the Kolmogorov–Smirnov two-sample test, the coefficient of variation (CV: standard deviation/mean), and the Gini coefficient of inequality. The significance of differences between the sexes was tested using a bootstrap approach. Factors affecting the frequency of flowering were examined using a logistic mixed model implemented within SABRE v.4.0 (Software for the Analysis of Binary Recurrent Events, www.cas.lancs.ac.uk/software/sabre/sabre.html, Centre for Applied Statistics, Lancaster University, Lancaster, UK). A full model was run that incorporated five independent variables and a lag parameter (Queenborough, 2005). The explanatory variables

were: tree size (initial dbh), sex (female, male), year (2002–2005), CI index (1–5), and habitat (valley, slope, ridge). Ten species with $N > 15$ were included in this analysis. Interpretation of the model output is complex but is exemplified by *I. juruensis* as follows (Table 3). The parameter estimates for dbh and sex were positive, so flowering probability increased with larger dbh, and male trees flowered more frequently than females (a negative value would indicate females flowered more frequently). For categorical terms with multiple states, the first state is the base against which subsequent states are compared (so the first state appears as zero in Table 3). For example, a significant positive estimate for 2003 within the year term indicates that trees of either sex were more likely to flower in 2003 than 2002, while negative values for 2004 and 2005 indicate that trees were less likely to flower in these years than in 2002. A negative lag term indicates that trees that flowered in year t were less likely to flower in year $t + 1$.

The spatial association between the distributions of the two sexes of each species was tested by a method of bivariate second-order spatial pattern analysis based on Ripley's *K* function corrected for edge effects (Ripley, 1976). Methods were implemented using SPPA 2.0.3 (Haase, 1995). When $L(d)$ exceeds the confidence envelope with positive values, the distributions are inferred as significantly attracted or associated, and with negative values, they are inferred as significantly repelled or complementary. All calculations were conducted using data from the whole 50-ha FDP, except in the cases of *I. hostmannii*, *I. juruensis,* and *Compsoneura*, when the western 25 ha was used, because individuals begin reproducing at <10 cm dbh. Eight species with $N > 25$ were analyzed (*C. capitellata*, *I. hostmannii*, *I. juruensis*, *O. glycycarpa*, *V. duckei*, *V. elongata*, *V. pavonis*, and *V.* cf. *calophylla*).

Annual growth rates of diameter (dbh) were calculated as (dbh$_2$ − dbh$_1$)/(time$_2$ − time$_1$), where subscripts 1 and 2 refer to the first and second censuses respectively. Annual mortality rates were not calculated because too few mature trees died in the census period.

Differences in annual growth rates (mm·yr^{-1}) between males and females in different habitats were tested using ANCOVA. The explanatory variables were habitat (categorical: ridge, slope, valley) and sex (categorical: male, female), and dbh was the covariate. The best-fit model from the full model of habitat, sex and dbh, the interactions between them, and all sequential deletions was selected using Akaike's information criterion values (Sakamoto et al., 1986). The AIC values, the estimates of the parameters for two models (sex × dbh and habitat × dbh), and the parameter estimates of the model with the lowest AIC value are shown in Appendixes S1–S3 (see Supplemental Data accompanying online version of this article). The ANCOVA tested the null hypotheses that (1)

TABLE 2. Frequency distributions of stem diameters (dbh) by sex in species of Myristicaceae on the Yasuní Forest Dynamics Plot. Values detail size-category specific flowering sex ratios and significance of associated binomial tests (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Data are for cumulative (4-yr) sex determinations. NA indicates specific size classes that were not censused for certain species.

Taxon and size class (mm)	Reproductive state			
	Non-repro	Male	Female	Male proportion
Compsoneura capitellata				
10–100	51	1	3	0.25
101–300	6	16	9	0.64
>300	0	0	0	
Compsoneura sprucei				
10–100	36	1	0	1.00
101–300	9	1	3	0.25
>300	0	0	0	
Iryanthera grandis				
10–100	38	0	0	
101–300	26	8	3	0.73
>300	3	3	2	0.60
Iryanthera hostmannii				
10–100	488	189	156	0.55
101–300	1	2	3	0.40
>300	0	0	0	
Iryanthera juruensis				
10–100	110	14	4	0.78*
101–300	2	0	6	0.00*
>300	0	0	0	
Otoba glycycarpa				
10–100	NA	NA	NA	
101–300	205	64	25	0.72***
>300	31	78	81	0.49
Virola dixonii				
10–100	NA	NA	NA	
101–300	21	0	1	0.00
>300	0	1	1	0.50
Virola duckei				
10–100	NA	NA	NA	
101–300	86	1	2	0.33
>300	13	21	20	0.51
Virola elongata				
10–100	NA	NA	NA	
101–300	21	13	3	0.81*
>300	1	7	4	0.64
Virola flexuosa				
10–100	NA	NA	NA	
101–300	37	0	0	
>300	8	2	3	0.40
Virola 'microfuzzy'				
10–100	NA	NA	NA	
101–300	18	2	4	0.33
>300	1	4	10	0.29
Virola mollissima				
10–100	NA	NA	NA	
101–300	11	0	4	0.00
>300	0	2	1	0.67
Virola multinervia				
10–100	NA	NA	NA	
101–300	10	0	0	
>300	3	1	0	1.00
Virola obovata				
10–100	NA	NA	NA	
101–300	12	13	4	0.76*
>300	0	1	0	1.00

TABLE 2. Continued.

Taxon and size class (mm)	Reproductive state			
	Non-repro	Male	Female	Male proportion
Virola pavonis				
10–100	NA	NA	NA	
101–300	80	5	0	1.00
>300	11	13	14	0.48
Virola cf. *calophylla*				
10–100	NA	NA	NA	
101–300	42	2	4	0.33
>300	7	6	11	0.35
Virola				
10–100	NA	NA	NA	
101–300	345	37	22	0.63
>300	44	58	64	0.48
Compsoneura				
10–100	87	2	3	0.40
101–300	12	16	10	0.62
>300	0	0	0	
Iryanthera				
10–100	636	203	160	0.56*
101–300	17	7	10	0.41
>300	2	1	1	0.50
Myristicaceae				
10–100	750	205	159	0.56*
101–300	627	141	72	0.66***
>300	79	140	147	0.49

when differences in dbh were taken into account, trees of different sexes and in different habitats had equal mean growth rates and that (2) the relationship between growth rate and dbh were equal between habitats and sexes (i.e., there was no interaction between habitat or sex and dbh).

Habitat associations were tested using a torus translation method (Harms et al., 2001; Debski et al., 2002). Habitats were defined with topographic information only, measured at each 20×20 m grid-point, because this was the basis for prior hypotheses about tree distribution. Subplots were divided into three topographic habitats (valley, slope, and ridge) by splitting each plot around median values of elevation and slope and around zero convexity. For a detailed explanation of the methods and distributions of habitats in the western 25 ha, see Valencia et al. (2004b).

The torus-translation procedure consists of generating a null distribution of stem densities in each habitat by shifting the true habitat map about a two-dimensional torus by 20-m increments in the four cardinal directions. As strips of quadrats are moved beyond a border of the plot, they are placed inside the opposite border. For the tests of association, each simulated map was overlaid by the observed distributions of trees, and the relative density of males and females was calculated for each species and habitat to give frequency distributions of relative-density estimates for each sex. If the relative density of a sex determined from the true habitat map was more extreme than at least 97.5% of the simulated relative densities (i.e., $\alpha = 0.05$ level of significance for a two-tailed test), then it was considered to be statistically associated (either positively or negatively) with the habitat. Torus-translation tests were carried out for male and female individuals of species with >25 reproductive individuals, as described previously.

RESULTS

Constancy of sex expression—No individuals changed sex over the four study years. However, several trees of *I. hostmannii* bearing many male flowers subsequently produced a few fruit. Small (<10 cm dbh) *I. juruensis* had only male inflorescences on outer branches, but larger individuals also

TABLE 3.   Factors affecting the flowering frequency of 10 species of Myristicaceae tree on the Yasuní Forest Dynamics Plot from 2002 to 2005. Data shown are the estimate ± SE of parameters in logistic mixed models (*I. hostmannii, I. juruensis, O. glycycarpa*) or logistic regression models (all other species). The variables included in the models were tree diameter (dbh), tree sex (female, male), year, canopy exposure (1 = understorey; 5 = emergent), and topographical habitat. A lag term was included in the logistic mixed model, and the scale term shows whether any unobserved heterogeneity was present in the model (and hence a logistic mixed model was valid—if this term was not significant, the model was reduced to a logistic regression). Estimates in **bold** are significant ($P < 0.05$). CI = crown illumination.

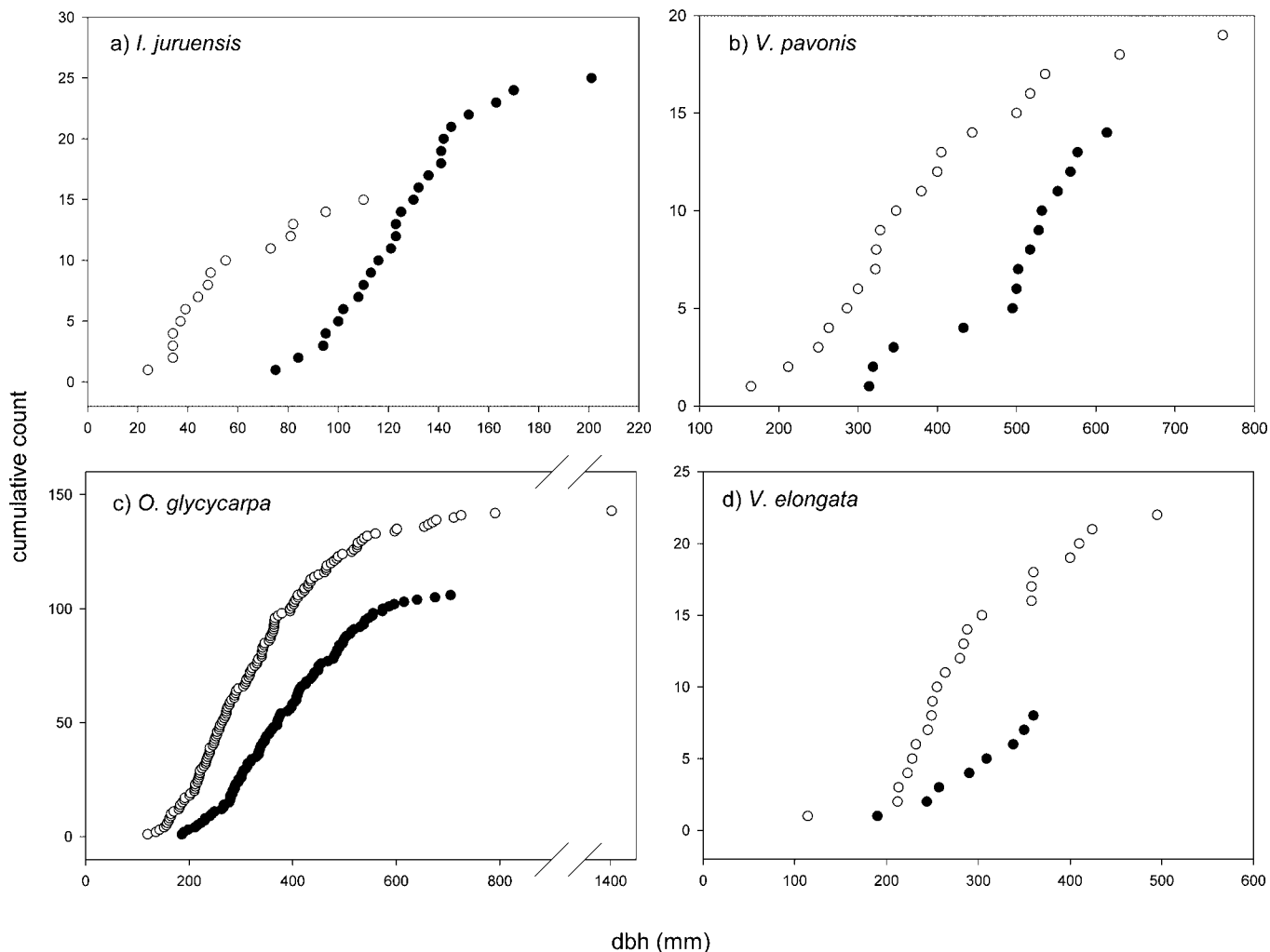|					Species					
Coefficient	Iryanthera grandis	Iryanthera hostmannii	Iryanthera juruensis	Otoba glycycarpa	Virola duckei	Virola elongata	Virola 'microfuzzy'	Virola obovata	Virola pavonis	Virola cf. calophylla
Intercept	−4.84 ± 39.7	**−1.31** ± 0.4	**−0.82** ± <0.01	−1.48 ± 1.4	−4.92 ± 37.6	2.03 ± 1.3	0.65 ± 1.2	2.11 ± 1.4	−1.63 ± 1.2	−5.97 ± 35.3
dbh	<0.01 ± <0.01	**0.04** ± <0.01	**0.01** ± <0.01	**0.01** ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	<0.01 ± <0.01	**<0.01** ± <0.01	**0.01** ± <0.01
Sex	0.21 ± 0.5	**0.60** ± 0.2	**0.29** ± <0.01	−0.95 ± 0.5	0.28 ± 0.2	−0.45 ± 0.4	0.32 ± 0.5	**−1.55** ± 0.5	−0.41 ± 0.3	−0.39 ± 0.3
Year 2002	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2003	5.13 ± 39.7	NA	**0.21** ± <0.01	NA	−0.13 ± 0.3	**−1.18** ± 0.5	0.44 ± 0.5	**1.26** ± 0.6	**1.03** ± 0.4	0.03 ± 0.4
2004	**−1.72** ± 0.7	**−1.22** ± 0.2	**−2.40** ± <0.01	**−0.63** ± 0.3	**−0.94** ± 0.3	−0.23 ± 0.6	**−1.49** ± 0.5	−0.82 ± 0.5	−0.52 ± 0.4	−0.66 ± 0.4
2005	−1.04 ± 0.6	0.01 ± 0.2	**−2.10** ± <0.01	−0.27 ± 0.3	**−0.96** ± 0.3	**−1.69** ± 0.5	**−2.32** ± 0.7	−0.86 ± 0.5	−0.23 ± 0.3	**−1.54** ± 0.4
CI index 1		0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
2		**0.46** ± 0.2	**0.06** ± <0.01	1.90 ± 1.0	4.74 ± 37.6		0.12 ± 0.5	0.39 ± 0.5	0.77 ± 0.8	4.72 ± 35.3
3		0.35 ± 0.2	**0.56** ± <0.01	**2.35** ± 1.1	5.25 ± 37.6	0.00	0.26 ± 0.7	0.02 ± 1.0	0.92 ± 0.8	4.28 ± 35.3
4		0.01 ± 1.2	−1.87 ± 2.4	**2.70** ± 1.1	6.03 ± 37.6	−0.08 ± 0.8			1.08 ± 0.9	6.60 ± 35.3
5		NA		**3.58** ± 1.6		0.72 ± 1.0				
Habitat—Valley	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Slope	4.83 ± 39.7	0.20 ± 0.2	**0.70** ± <0.01	**1.43** ± 0.7	0.49 ± 0.4	**1.09** ± 0.8	**1.04** ± 0.7	−0.12 ± 0.6	**0.59** ± 0.3	−0.33 ± 0.5
Ridge	4.70 ± 39.7	0.04 ± 0.2	−0.04 ± <0.01	0.88 ± 0.5	0.63 ± 0.4	**0.56** ± 0.4	−0.38 ± 0.5	0.65 ± 0.7	**0.71** ± 0.3	−0.36 ± 0.4
Lag	NA	−0.09 ± 0.2	**−0.32** ± <0.01	**−0.98** ± 0.4	NA	NA	NA	NA	NA	NA
Scale	NA	**0.72** ± 0.2	**0.18** ± <0.01	**2.55** ± 0.6	NA	NA	NA	NA	NA	NA

Fig. 1.   Cumulative distributions of male and female trees of four species of Myristicaceae on the Yasuní Forest Dynamics Plot in relation to stem diameter (dbh). (a) *Iryanthera juruensis*, (b) *Virola pavonis*, (c) *Otoba glycycarpa*, (d) *Virola elongata*. Filled circles = female, empty circles = male. Note the different scales of the *x*- and *y*-axes.

had cauliflorous female inflorescences, and the species is therefore androdioecious.

Flowering and cumulative sex ratios—A total of 907 trees flowered in at least one of the four study years (Table 1). More trees flowered in 2003 than in the other three years, 278 more trees than flowered in 2004, the poorest year. In every year, over half the reproductively mature trees flowered. The number of flowering male trees exceeded the number of flowering female trees in 2002, 2003, and 2005 for most species. In 2004, however, more males flowered in only four of 11 species. Significant male-biased populations occurred in four species: *C. capitellata* (2004), *I. hostmannii* (2002, 2004, 2005), *O. glycycarpa* (2002, 2003), and *V. elongata* (2002, 2004). Significantly female-biased sex ratios were observed in two species in 2004 (*V. pavonis* and *V.* cf. *calophylla*). Cumulative sex ratios were generally intermediate between those of specific years or toward the lower end of the range for all species except one (*V. mollissima*), for which the ratio was lower than the lowest yearly value (least male-biased).

Genus-specific sex ratios were significantly male-biased in *Iryanthera* in all years except 2003 and for all *Compsoneura* in 2004. *Virola* was significantly female-biased also in this year. Over the whole family, the sex ratio was male-biased in all years except 2004. The most skewed sex ratios were found in 2004 when the fewest trees flowered. The cumulative sex ratio of the family was significantly male-biased.

Size distributions of male and female trees—Sex ratios were male-biased in smaller size classes of *I. juruensis*, *O. glycycarpa*, *V. elongata,* and *V. obovata*, but this bias disappeared in larger size classes and was not apparent in other species (Table 2). In *Iryanthera*, and the Myristicaceae as a whole, sex ratios were male-biased in the 10–100 mm (male proportion 0.56) and 101–300 mm dbh size classes (male proportion 0.66) but not in the >300 mm size class (male proportion 0.49). The few larger but nonreproductive individuals were usually liana towers or damaged, resprouting trees.

Relative size variation was greater in males than females for four species (*I. juruensis, O. glycycarpa, V. elongata,* and *V.*
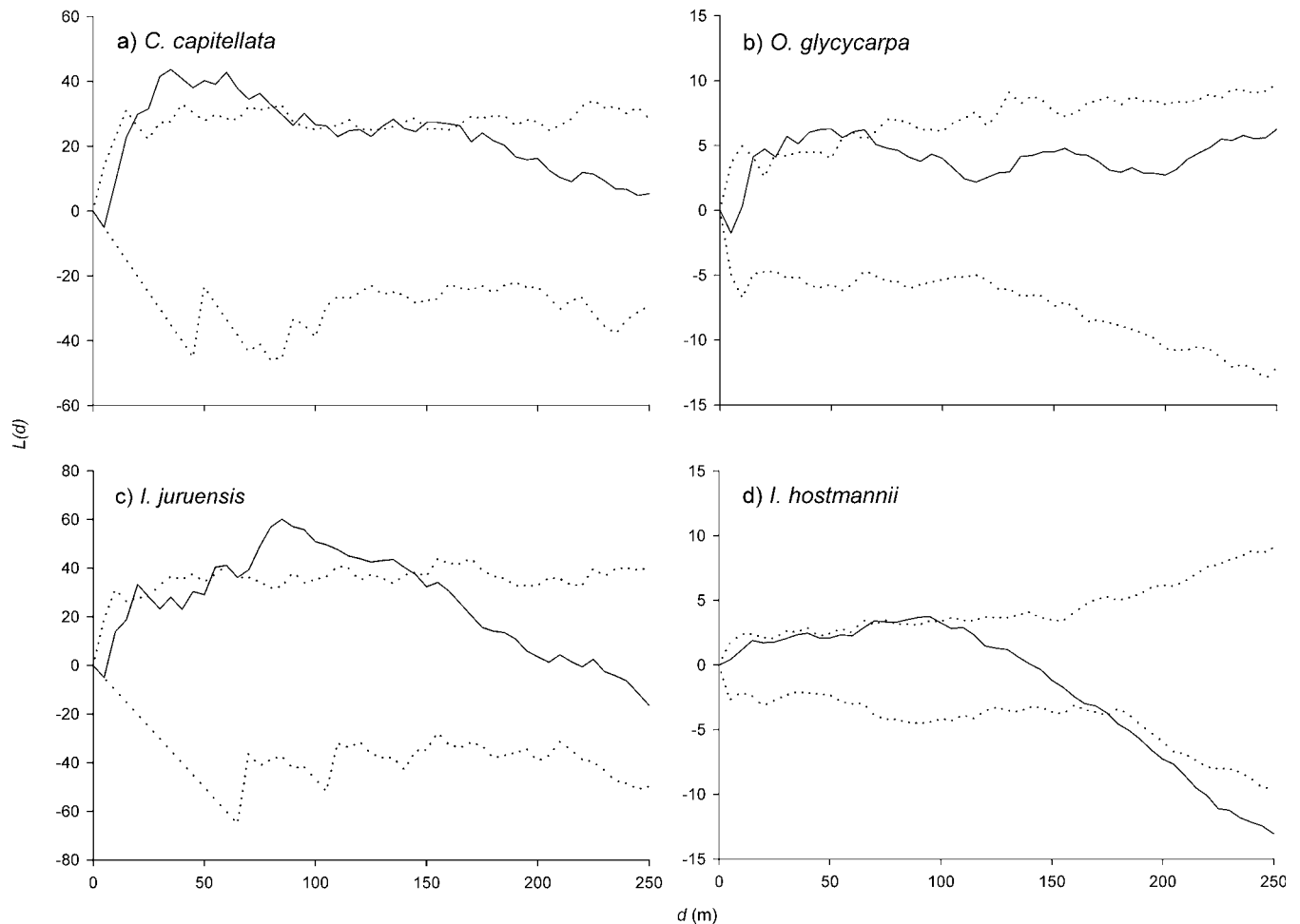
Fig. 2. The spatial distribution of male and female trees of four species of Myristicaceae on the Yasuní Forest Dynamics Plot, using a bivariate Ripley's K spatial analysis. The x-axis is distance; y-axis is $L(d)$ (see data analysis section for details). Solid lines show test statistic $L(d)$; dashed lines show 99% confidence envelopes. (a) *Compsoneura capitellata*, (b) *Otoba glycycarpa*, (c) *Iryanthera juruensis*, (d) *Iryanthera hostmannii*.

pavonis; Fig. 1; Appendix S4 [see Supplemental Data accompanying online version of this article]), but there was no difference in size variation for any genus or the family. *Iryanthera juruensis* and *O. glycycarpa* had more small males, while *V. pavonis* had more males that were both larger and smaller than females. The Kolmogorov–Smirnov test failed to detect the inter-sex difference in size variation in *V. elongata* and *V. pavonis*.

Flowering frequency—The logistic mixed model was appropriate for three species (*I. hostmannii, I. juruensis,* and *O. glycycarpa*). For the remaining seven species, a standard logistic regression model was used (Table 3). Increasing tree size (dbh) had a significantly positive impact on flowering frequency in five species. Male trees flowered significantly more frequently in *I. hostmannii* and *I. juruensis*, but significantly less frequently in *V. obovata*. In many years following 2002, fewer trees flowered; and individual trees were less likely to flower following a flowering year in *I. juruensis* and *O. glycycarpa*, indicated by the significant lag term. Trees with access to higher light levels were also more likely to flower in three species (*I. hostmannii, I. juruensis*, and *O. glycycarpa*). In two species (*I. juruensis* and *O. glycycarpa*),

trees on slopes flowered more frequently than trees in valleys. Compared to trees in valleys, those on ridges flowered less frequently in *I. juruensis* and more frequently in *V. pavonis*.

Spatial distribution and habitat associations—Four of the eight species analyzed using Ripley's K had evidence of aggregation of the sexes at some spatial scales (*C. capitellata, I. juruensis, I. hostmannii,* and *O. glycycarpa*; Fig. 2). *Iryanthera juruensis* had the most aggregated distribution of males and females. In *I. hostmannii* at distances >180 m, males were overdispersed with respect to females. The remaining four *Virola* species showed no evidence of aggregation or overdispersion.

Significant habitat associations were found for females in five and for males in two of the eight species tested (Table 4). All but one species had a negative or a positive association with the valley habitat. In females, *O. glycycarpa* and *V. pavonis* were positively associated with valleys, and *V. duckei* and *V. elongata* were negatively associated. *Iryanthera juruensis* had a negative association for the slope habitat and a positive association for the ridge habitat. In males, *C. capitellata* and *I. juruensis* had negative associations with the valley habitat. There were no reciprocal habitat associations

TABLE 4. Habitat associations of male and female individuals of eight species of Myristicaceae in the Yasuní Forest Dynamics Plot. Values are the number of individuals in each habitat (*N*) and whether this is significantly different from a null distribution of stem densities using a torus translation test, which shows positive (+), negative (−) or no (0) habitat association: (+) or (−) = $P < 0.1$; + or − = $P < 0.05$; ++ or −− = $P < 0.01$. Habitats are from Valencia et al. (2004b).

| | Habitat | | | | | | |
| | Valley | | Slope | | Ridge | | |
Species	*N*	*P*	*N*	*P*	*N*	*P*	Total *N*
Females							
Compsoneura capitellata	3	0	3	0	13	0	19
Iryanthera juruensis	2	−	2	−	22	+	26
Iryanthera hostmannii	26	0	57	0	73	0	156
Otoba glycycarpa	30	++	33	0	42	0	105
Virola duckei	1	−	9	0	15	0	25
Virola pavonis	6	+	4	0	5	0	15
Virola elongata	0	−	1	0	8	0	9
Virola cf. *calophylla*	6	(+)	4	0	9	0	19
Males							
Compsoneura capitellata	0	−	7	0	22	(+)	29
Iryanthera juruensis	0	−	3	0	12	0	15
Iryanthera hostmannii	41	0	53	0	97	0	191
Otoba glycycarpa	37	0	42	0	63	0	142
Virola duckei	4	0	8	0	10	0	22
Virola pavonis	6	0	7	0	6	0	19
Virola elongata	7	0	3	0	12	0	22
Virola cf. *calophylla*	4	(+)	1	0	3	0	8

between males and females within a species, but in several species the habitat association was expressed only in females.

Significant habitat associations for females that produced above-average amounts of fruit per species were found only in *V. pavonis* (positive for valley), which replicated the earlier finding based on all female stems.

Trees of both sexes that flowered every year also had few habitat associations. *Virola duckei* and *V.* 'microfuzzy' had negative and positive associations with the valley habitat, respectively, and *V. elongata* had a negative association with the slope habitat.

Investment in reproductive structures—Females and males differed greatly in the energy invested in their respective

reproductive structures (Table 5). Individual fruits of *I. hostmannii* had over 1000 times the mass of male flowers, and females invested over 60 times the amount of dry mass in reproduction per tree than males. In *Virola* and *Otoba*, female trees produced 8–30 times as much dry mass of fruit per square meter of canopy than males produced flowers.

Growth rate as an indirect measure of the cost of reproduction—For many species habitat, sex, and tree size had little or no effect on growth rates (Appendix S1, see Supplemental Data accompanying online version of this article). In five species, the model with the lowest AIC had no parameters. In two species (*O. glycycarpa* and *V. obovata*), the model with no parameters had an AIC value <0.1 greater

TABLE 5. Mass of the reproductive structures in six species of Myristicaceae on the Yasuní Forest Dynamics Plot.

| | Male reproduction | | Female reproduction | | | |
| | Flower mass·m^{-2} (g) | | No. fruits·m^{-2} | | | |
Species	Mean	SD (*N*)	Mean	SD (*N*)	Mean dry mass of fruit (g)	Mean fruit mass·m^{-2} (g)
Otoba glycycarpa	3.60	5.60 (128)	16.6	19.2 (149)	6.1	101.3
Virola duckei	4.00	7.46 (16)	12.3	25.6 (27)	3.3	40.6
Virola pavonis	5.61	8.99 (16)	11.8	16.4 (16)	5.5	64.9
Virola obovata	1.61	1.80 (12)	4.3	3.4 (11)	3.0	12.9
Virola cf. *calophylla*	3.05	3.55 (4)	9.0	17.3 (20)	10.5	94.7
			No. fruits per tree			
	Mean	SD (*N*)	Mean	SD (*N*)	Mean dry mass of fruit (g)	Mean fruit mass per tree (g)
Iryanthera hostmannii			56.9	94.7 (190)	1.6	91.0
Flowers per inflorescence	56	29 (103)				
Inflorescences per tree	52.3	88.5 (170)				
Mass per flower	0.000477	NA (404)				
Flower mass per tree (g)	1.40	NA				

than the best-fit model. Tree size as the sole term had the best fit for three species and all stems. Sex as the only term had the best fit in *O. glycycarpa*. Models including habitat and tree size were the best-fit models in three species (*I. grandis, V. mollissima,* and *V.* cf. *calophylla*). In *I. grandis* the full model had the lowest AIC value.

The lack of significant effects of habitat type and sex on tree growth is borne out in the details of the two models that include the interaction terms (Appendix S2, see Supplemental Data accompanying online version of this article). Growth rates differed between habitats in only *O. glycycarpa* and *V.* cf. *calophylla*. In no species was there a significant difference between habitats or sex in the model with the lowest AIC (Appendix S3, see Supplemental Data accompanying online version of this article). AIC values are generally conservative (Crawley, 2002), and so it seems likely that sex and habitat have no impact on growth rates in most species.

DISCUSSION

Sex expression—Small individuals of *I. juruensis* had only male flowers, while trees ≥10 cm dbh had female flowers. It is assumed that as individuals increase in size, they switch from producing solely male flowers to female flowers as well. This species is therefore androdioecious. Other species of *Iryanthera* are monoecious (Smith, 1937; Ackerly et al., 1990). Sex lability is common in dioecious herbs but has not been well documented in woody plants (Schlessman, 1991; Korpelainen, 1998) and has only been found in (sub)tropical forests in *Bischofia javanica* (Yamashita and Abe, 2002).

Some individual male trees of *I. hostmannii* produced a few flowers of the opposite sex. This "leaky" dioecy is not uncommon in plants and has been reported in cultivated *Myristica fragrans* (Flach, 1966) and in wild *M. insipida* by Armstrong and Irvine (1989) and could be related to inflorescence morphology (Armstrong and Tucker, 1986). All the previous observations have been interpreted as evidence that monoecy is the ancestral condition from which dioecy evolved in the Myristicaceae (Rodrigues, 1980; Armstrong, 1997). In an analysis of all angiosperms, the presence of monoecy in a family was the strongest predictor of dioecy (Renner and Ricklefs, 1995). However, whether monoecy is basal within the Myristicaceae is unclear because in the only phylogenetic analysis of the family, a lack of molecular variation means that intergeneric relationships are poorly resolved (Sauquet et al., 2003).

Sex ratios—The sex ratios of flowering trees were male-biased in over half the species studied and significantly so in at least 1 year in four species. These data support the general finding of male-biased sex ratios in tropical dioecious tree species in other families, including Boraginaceae, Erythroxylaceae, Polygonaceae, Sapindaceae, Rubiaceae, and Zanthoxylaceae (Opler and Bawa, 1978), Euphorbiaceae (Thomas and LaFrankie, 1993), Meliaceae (Bullock et al., 1983), Lauraceae and Ebenaceae (House, 1992), Zamiaceae (Clark and Clark, 1987), and Siparunaceae (Nicotra, 1998). Female-biased sex ratios in tropical forest trees have only been observed in two species (*Coccoloba caracasana* and *Triplaris americana*; Polygonaceae [Melampy and Howe, 1977; Opler and Bawa, 1978]). Unbiased sex ratios are also encountered (Bullock,

1982; Bullock and Bawa, 1981; Bullock et al., 1983; Thomas and LaFrankie, 1993; Morellato, 2004).

The sex ratios of flowering Myristicaceae are therefore lower at Yasuní than at other sites. There are several possible reasons for this. First, female flowers abscise singly and are consequently harder to find than the male inflorescences, that fall whole. In this study, we confirmed the sex of trees by checking for fruit, thus ensuring accurate sexing of trees. Second, we found that sex ratios were more male-biased in years in which fewer trees flowered. Both Ackerly et al. (1990) and Armstrong and Irvine (1989) studied only one flowering episode. These may have been years of low community flowering and therefore provide a misleading impression of the true population-level sex ratio. However, in *I. macrocarpa* (Ackerly et al., 1990), virtually the whole population flowered. Third, in diphasic *Iryanthera*, species may differ in the size at which individual males switch to female. That the sex ratio of *I. macrocarpa* is more male-biased than *I. juruensis* in this study suggests that either the size at which it switches is larger or that the proportion of the population below that size is higher. Correct estimation of reproductive population sizes in undisturbed ecosystems is necessary when considering minimum population sizes, especially of rare species or those that also occur in anthropogenically disturbed and fragmented areas.

The possible proximate causes of male-biased effective sex ratios include precocious male flowering (Melampy and Howe, 1977; Opler and Bawa, 1978; Bullock and Bawa, 1981; Thomas and LaFrankie, 1993; Nicotra, 1998), more frequent flowering of males than females (Bullock and Bawa, 1981; Bullock, 1982; Bullock et al., 1983; Thomas and LaFrankie, 1993; Nicotra, 1998), higher female mortality (Meagher and Antonovics, 1982; Agren, 1988; Bierzychudek and Eckhart, 1988), and inter-sex differences in local habitat preferences (Cox, 1981; Bierzychudek and Eckhart, 1988). Data from tropical forest trees have supported precocious and more frequent, male flowering (Thomas and LaFrankie, 1993). We found no significant male-bias in large diameter trees, indicating that females are unlikely to have higher mortality rates (males and females had similar growth rates and so their age vs. size profiles should be similar). We did find that male trees flowered more frequently than females in two species. We also found that males flowered at a smaller size than females in four species and that males were significantly smaller than females in three species.

Whether small males that produce very few flowers actually have any reproductive success is unknown. Although most males produce relatively few inflorescences, large males can produce many more and may swamp the small quantity of pollen produced by small males. About 80% of male *O. glycycarpa* produce <5 g dry mass of inflorescence per square meter canopy, but large males can produce six times this amount. Equally, 80% of male *I. hostmannii* produce <100 inflorescences, but large males can produce up to 600. Number of inflorescences in *I. hostmannii* scales with dbh (linear regression, slope = 3.039, r^2 = 0.28, P < 0.001; S. Queenborough, unpublished data). Nevertheless, the selective pressure for precocious flowering may be that it provides rare but important opportunities for pollination of flowers on nearby females. Females may also be under selection pressure to produce increased numbers of flowers if pollination is secured by deceit (Armstrong, 1997).

However, reproductive success may ultimately depend on

the spatial arrangement of males and females as well as their sizes (Ghazoul, 2005). We have demonstrated elsewhere that fruit production is pollen limited at the branch level in *I. hostmannii* and that local male density and flowering intensity are important factors determining fruit production in several other species of Myristicaceae at Yasuní (Queenborough, 2005).

Costs of reproduction—The five species for which we measured direct investment in reproduction all had much greater investment by females than males. Fruits were much more costly to produce than flowers, and female investment per unit area of canopy was generally an order of magnitude greater than that of males. There is therefore a substantial direct cost to reproduction in females. Our analyses of the differential costs of reproduction do not account for the investment by females in unfertilized flowers, which in *I. hostmannii* have 2.8 times more dry mass than male flowers (S. Queenborough, unpublished data), as well as the energy-rich fatty seed aril which may add greatly to the costs imposed on females. Australian female *M. insipida* invested four times as much biomass in reproductive structures per unit branch length than males (Armstrong and Irvine, 1989), which is less than our estimate of 8–30 times the biomass per unit canopy area.

We found no evidence of inter-sex differences in growth rates in 10 of the 12 species assessed. In two species, low AIC values hinted at a difference, but this was not significant when the model was examined in detail. We also found no evidence that intensity of reproduction affects future reproductive output: females that produce many fruit are no less likely to have high fruit production the next year than less fecund females (Queenborough, 2005). There appear to be no delayed costs to being female in terms of growth or future reproduction within the Myristicaceae at Yasuní.

Previous studies of dioecious species have inferred costs of reproduction from reduced female photosynthesis (Wheelwright and Logan, 2004), reduced female growth rates (Popp and Reinartz, 1988; Garcia and Antor, 1995; Nicotra, 1999a; Wheelwright and Logan, 2004), reduced female survival (Meagher and Antonovics, 1982; Agren, 1988; Bierzychudek and Eckhart, 1988; Lovett Doust and Lovett Doust, 1988), lower frequency and/or intensity of reproductive episodes in females (Bullock and Bawa, 1981; Bullock, 1982; Meagher and Antonovics, 1982; Agren, 1988; Oyama, 1990; Cipollini and Stiles, 1991; Ataroff and Schwarzkopf, 1992; Nicotra, 1998), and smaller size of initial reproduction in males (Opler and Bawa, 1978; Bullock and Bawa, 1981; Armstrong and Irvine, 1989; Thomas and LaFrankie, 1993). In our study too few mature individuals died to analyze inter-sex differences in mortality. Sex-specific mortality is much less apparent in trees than in herbs because mortality rates are lower and trees are more likely to become nonreproductive than to die (Nicotra, 1998). More frequent flowering of males occurred in two species, and males flowered at smaller sizes than females in four species. There was no evidence for an impact of reproduction on growth rates.

This pattern of equivalent growth despite greater reproductive allocation has been identified in a wide range of dioecious species (Nicotra, 1999b and references therein). The ability of females to account for reproductive investment could be due to factors such as differences in allocation patterns, longer leaf life span in females and thus increased carbon gain per leaf, or

higher rates of assimilation in females (Nicotra, 1999b). Few studies have investigated these factors.

Spatial segregation of the sexes—We found no strict spatial segregation of the sexes (SSS) among the Myristicaceae at Yasuní. To demonstrate SSS, reciprocal associations of the sexes in different microhabitats must be shown. By contrast, the sexes were spatially aggregated in four of the eight species studied here and randomly distributed in the remaining four. The complimentary distribution of male and female *I. hostmannii* at distances >180 m was also found in the distribution of all stems and might be caused by the ridge–valley system within the FDP (Queenborough, 2005).

We did find that females had more habitat associations than males, with significant associations in five species for females and in only two species for males. In species that do have SSS, it is often the females that dominate in high quality environments, while males dominate in low quality habitats (Lloyd and Webb, 1977). Previous analyses of tropical rain forest habitat associations have shown relatively coarse-grained partitioning of topographic environments among species (Harms et al., 2001; Valencia et al., 2004b; Queenborough, 2005). At Yasuní, species associate with the ridge or valley habitat, or they have widespread distributions. Whether topography is a surrogate for resource availability is questionable, because soil nutrient concentrations at Yasuní do not correlate with topography (J. Dalling, University of Illinois, personal communication).

Light is a more common limiting resource in tropical forests (Chazdon and Fetcher, 1984). However, SSS is most likely in environments where a critical resource is distributed along a gradient with stable extremes (Dawson and Bliss, 1989; Nicotra, 1998). This condition is not satisfied for the light climates of tropical forests, which are spatially and temporally heterogeneous (e.g., Chazdon et al., 1996). Segregation or habitat associations may be expressed in terms of higher growth or greater reproductive output in high quality habitats rather than by higher mortality or reduced recruitment of stems in low quality habitats (Bullock, 1982). However, while light is an important factor affecting reproductive output in the Myristicaceae here, topographic habitat is not. There were fewer habitat associations among trees with high fecundity or high frequency of flowering than among reproductive trees as a whole, and neither habitat nor sex were significant factors affecting the growth rate of mature trees.

Rare dioecious species in a system where inter-tree pollen movement is essential for reproductive success are much less likely to undergo selection for SSS that would further decrease offspring output. It may be productive to consider whether selection for male-biased sex ratios acts to decrease mean male–female distance and thereby help to overcome pollen-limited reproductive output.

Conclusions—Understanding the factors affecting the distribution and reproduction of dioecious species in tropical forests has wider implications for resource partitioning by animals, estimation of minimum population sizes and also for mechanisms of species coexistence, if only about half the reproductive population produces fruit.

We have demonstrated a large differential cost of reproduction between females and males in species of dioecious tropical forest tree. Female trees invested over 10 times more biomass in reproduction than male trees. The effects of this difference

were expressed in several ways. Previous workers have often examined a single species over one or two reproductive episodes, which has led to conclusions about general patterns. However, here we studied a group of coexisting closely related species over four reproductive episodes, and so we were able to identify different strategies adopted by each species. In *I. hostmannii,* male-biased sex ratios were caused solely by more frequent flowering of males. In *O. glycycarpa* and *V. elongata,* size variation was greater in males than females, and males were more numerous in smaller size classes, but males did not flower more frequently than females. Females in these two species had positive and negative associations respectively with the valley habitat. The highly skewed sex ratio of *C. capitellata* in 2004 was not caused by any of the factors examined in this study. There was also no obvious explanation for the female-biased sex ratios of *V. pavonis* and *V.* cf. *calophylla* in 2004, as male *V. pavonis* trees had greater size variation than females. Inter-sex differences in flowering frequency and minimum reproductive size were observed in other species but with no significant sex ratio bias. Male *I. juruensis* were more common in small size classes and flowered more frequently, and females had several habitat associations, but the androdioecious nature of this species complicates interpretation. Male *V. obovata* were also more common at smaller sizes, but females flowered more frequently. The high expenditure on reproduction by females was not expressed as a difference between the sexes in terms of growth rate or in reducing future fruit output; however, flowering in *I. juruensis* and *O. glycycarpa* decreased the probability of flowering the following year. Long-term individual-based studies are few in tropical ecosystems. This continuing study first confirmed observations from previous studies conducted elsewhere, but also emphasized the diversity of reproductive strategies that have evolved within one taxon. Evidently, there is no consistent mechanism for balancing the costs of reproduction even among the species of a single clade of coexisting tropical forest trees, and studies that conduct relatively limited sampling of a small number of relatively common species should not be used as a basis for generalization.

LITERATURE CITED

ACKERLY, D., J. RANKIN-DE-MERONA, AND W. RODRIGUES. 1990. Tree densities and sex ratios in breeding populations of dioecious central Amazonian Myristicaceae. *Journal of Tropical Ecology* 6: 239–248.

AGREN, J. 1988. Between-year variation in flowering and fruit set in frost-prone and frost-sheltered populations of dioecious *Rubus chamaemorus. Oecologia* 76: 161–169.

ALLEN, G., AND J. ANTOS. 1993. Sex ratio variation in the dioecious shrub *Oemleria cerasiformis. American Naturalist* 141: 537–553.

ARMSTRONG, J. 1997. Pollination by deceit in nutmeg (*Myristica insipida,* Myristicaceae): floral displays and beetle activity at male and female trees. *American Journal of Botany* 84: 1266–1274.

ARMSTRONG, J., AND B. DRUMMOND. 1986. Floral biology of *Myristica fragrans* Houtt. (Myristicaceae), the nutmeg of commerce. *Biotropica* 18: 32–38.

ARMSTRONG, J., AND A. IRVINE. 1989. Flowering, sex ratios, pollen–ovule ratios, fruit set, and reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different rain forest communities. *American Journal of Botany* 76: 74–85.

ARMSTRONG, J., AND S. TUCKER. 1986. Floral development in *Myristica* (Myristicaceae). *American Journal of Botany* 73: 1131–1143.

ASHTON, P. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* 1: 155–196.

ATAROFF, M., AND T. SCHWARZKOPF. 1992. Leaf production, reproductive patterns, field germination, and seedling survival in *Chamaedorea bartlingiana,* a dioecious understorey palm. *Oecologia* 92: 250–256.

BAWA, K. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11: 15–39.

BAWA, K., AND P. OPLER. 1975. Dioecism in tropical forest trees. *Evolution* 29: 167–179.

BAWA, K., AND P. OPLER. 1977. Spatial relationships between staminate and pistillate plants of dioecious tropical forest trees. *Evolution* 31: 64–68.

BAWA, K., D. PERRY, AND J. BEACH. 1982. Reproductive biology of tropical lowland forest trees. I. Sexual systems and incompatibility mechanisms. *American Journal of Botany* 72: 331–345.

BIERZYCHUDEK, P., AND V. ECKHART. 1988. Spatial segregation of the sexes of dioecious plants. *American Naturalist* 132: 34–43.

BULLOCK, S. 1982. Population structure and reproduction in the neotropical dioecious tree *Compsoneura sprucei. Oecologia* 55: 238–242.

BULLOCK, S. 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. *Biotropica* 17: 287–301.

BULLOCK, S., AND K. BAWA. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. *Ecology* 62: 1494–1504.

BULLOCK, S., J. BEACH, AND K. BAWA. 1983. Episodic flowering and sexual dimorphism in *Guarea rhopalocarpa* in a Costa Rican rain forest. *Ecology* 64: 851–861.

CHARNOV, E. 1982. The theory of sex allocation. Princeton University Press, Princeton, New Jersey, USA.

CHAZDON, R., AND N. FETCHER. 1984. Light environments of tropical forests. *In* E. Medina, H. Mooney, and C. Vasquez-Yanes [eds.], Physiological ecology of plants in the wet tropics, 27–36. Dr. W. Junk Publishers, The Hague, Netherlands.

CHAZDON, R., R. PEARCY, D. LEE, AND N. FETCHER. 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. *In* S. Mulkey, R. Chazdon, and A. Smith [eds.], Tropical forest plant ecophysiology, 5–55. Chapman and Hall, New York, New York, USA.

CIPOLLINI, M., AND E. STILES. 1991. Costs of reproduction in *Nyssa sylvatica*: sexual dimorphism in reproductive frequency and nutrient flux. *Oecologia* 86: 585–593.

CLARK, D., AND D. CLARK. 1987. Temporal and environmental patterns of reproduction in *Zamia skinneri,* a tropical rain forest cycad. *Journal of Ecology* 75: 135–149.

CLARK, D., AND D. CLARK. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* 62: 315–344.

COX, P. 1981. Niche partitioning between sexes of dioecious plants. *American Naturalist* 117: 295–307.

CRAWLEY, M. 2002. Statistical computing: an introduction to data analysis using S-Plus. John Wiley, Chichester, UK.

CROAT, T. 1979. The sexuality of the Barro Colorado Island flora (Panama). *Phytologia* 42: 319–348.

CUNNINGHAM, S. 1996. Pollen supply limits fruit initiation by a rain forest understorey palm. *Journal of Ecology* 84: 185–194.

DARWIN, C. 1877. The different forms of flowers on plants of the same species. John Murray, London, England.

DAWSON, T., AND L. BLISS. 1989. Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. *Oecologia* 79: 332–343.

DEBSKI, I., D. BURSLEM, P. PALMIOTTO, J. LAFRANKIE, H. LEE, AND N. MANOKARAN. 2002. Habitat preferences of *Aporosa* in two Malaysian forests: implications for abundance and coexistence. *Ecology* 83: 2005–2018.

DI FIORE, A. 2004. Diet and feeding ecology of woolly monkeys in a western Amazonian rain forest. *International Journal of Primatology* 25: 767–801.

DOYLE, J., H. SAUQUET, T. SCHARASCHKIN, AND A. LE THOMAS. 2004. Phylogeny, molecular and fossil dating, and biogeographic history of

Annonaceae and Myristicaceae (Magnoliales). *International Journal of Plant Sciences* 165: S55–S67.

FLACH, M. 1966. Nutmeg cultivation and its sex problem. *Meded. Landbouwhogeschool (Wageningen)* 66: 1–85.

FLORES, S., AND D. SCHEMSKE. 1984. Dioecy and monoecy in the flora of Puerto Rico and the Virgin Islands: ecological correlates. *Biotropica* 16: 132–139.

FREEMAN, D., L. KLIKOFF, AND K. HARPER. 1976. Differential resource utilization by the sexes of dioecious plants. *Science* 193: 597–599.

GARCIA, M., AND R. ANTOR. 1995. Age and size structure in populations of a long-lived dioecious geophyte: *Borderea pyrenaica* (Dioscoreaceae). *International Journal of Plant Sciences* 156: 236–243.

GHAZOUL, J. 2005. Implications of plant spatial distribution for pollination and seed production. *In* D. Burslem, M. Pinard, and S. Hartley [eds.], Biotic interactions in the tropics: their role in the maintenance of species diversity, 241–266. Cambridge University Press, Cambridge, UK.

HAASE, P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. *Journal of Vegetation Science* 6: 575–582.

HARMS, K., R. CONDIT, S. HUBBELL, AND R. FOSTER. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.

HOUSE, S. 1992. Population density and fruit set in three dioecious tree species in Australian tropical rain forest. *Journal of Ecology* 80: 57–69.

HOWE, H. 1983. Annual variation in a neotropical seed-dispersal system. *In* S. Sutton, T. Whitmore, and A. Chadwick [eds.], Tropical rain forests: ecology and management, 211–227. Blackwell, Oxford, UK.

KORPELAINEN, H. 1998. Labile sex expression in plants. *Biological Reviews* 73: 157–180.

LAURANCE, W. F. 2005. When bigger is better: the need for Amazonian mega-reserves. *Trends in Ecology and Evolution* 20: 645–648.

LLOYD, D., AND C. WEBB. 1977. Secondary sex characters in plants. *Botanical Review* 43: 177–215.

LOVETT DOUST, J., AND L. LOVETT DOUST. 1988. Modules of reproduction in a dioecious clonal shrub *Rhus typhina*. *Ecology* 69: 741–750.

MEAGHER, T., AND J. ANTONOVICS. 1982. The population biology of *Chamaelirium luteum* a dioecious member of the lily family: life history studies. *Ecology* 63: 1690–1700.

MELAMPY, M., AND H. HOWE. 1977. Sex ratio in the tropical tree *Triplaris americanus* (Polygonaceae). *Evolution* 31: 867–872.

MORELLATO, L. 2004. Phenology, sex ratio, and spatial distribution among dioecious species of *Trichilia* (Meliaceae). *Plant Biology* 6: 491–497.

NICOTRA, A. 1998. Sex ratio variation and spatial distribution of *Siparuna grandiflora*, a tropical dioecious shrub. *Oecologia* 115: 102–113.

NICOTRA, A. 1999a. Reproductive allocation and the long-term costs of reproduction in *Siparuna grandiflora*, a dioecious neotropical shrub. *Journal of Ecology* 87: 138–149.

NICOTRA, A. 1999b. Sexually dimorphic growth in the dioecious tropical shrub, *Siparuna grandiflora*. *Functional Ecology* 13: 322–331.

OPLER, P., AND K. BAWA. 1978. Sex ratios in tropical forest trees. *Evolution* 32: 812–821.

OYAMA, K. 1990. Variation in growth and reproduction in the neotropical dioecious palm *Chamaedorea tepejilote*. *Journal of Ecology* 78: 648–663.

PITMAN, N., J. TERBORGH, M. SILMAN, P. NUNEZ V., D. NEILL, C. CERON, W. PALACIOS, AND M. AULESTIA. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82: 2101–2117.

POPP, J., AND J. REINARTZ. 1988. Sexual dimorphism in biomass allocation and clonal growth of *Xanthoxylum americanum*. *American Journal of Botany* 75: 1732–1741.

QUEENBOROUGH, S. 2005. Coexistence of the Myristicaceae in an Amazonian rain forest. Ph.D. dissertation, University of Aberdeen, Aberdeen, UK.

RAMIREZ, N., AND T. BRITO. 1990. Reproductive biology of a tropical palm

swamp community in the Venezuelan llanos. *American Journal of Botany* 77: 1260–1271.

RENNER, S., AND R. RICKLEFS. 1995. Dioecy and its correlates in the flowering plants. *American Journal of Botany* 82: 596–606.

RIPLEY, B. 1976. The second-order analysis of stationary processes. *Journal of Applied Probability* 13: 255–266.

RODRIGUES, W. 1980. Revisao taxonomica das especies de *Virola* Aublet (Myristicaceae) do Brasil. Acta Amazonica 10(1, Supplement): 1–127.

ROMOLEROUX, K., R. FOSTER, R. VALENCIA, R. CONDIT, H. BALSLEV, AND E. LOSOS. 1997. Arboles y arbustos (dap >1 cm) encontrados en dos hectareas de un bosque de la Amazonia ecuatoriana. *In* R. Valenica and H. Balslev [eds.], Estudios sobre diversidad y ecología de plantas: memorias del II Congreso Ecuatoriano de Botánica Realizado en la Pontifica Universidad Católica del Ecuador, 189–215. PUCE, Quito, Ecuador.

ROOSMALEN, M., P. M. D. P. BARDALES, AND O. M. D. C. GARCIA. 1996. Frutos da floresta Amazonica. Parte I: Myristicaceae. *Acta Amazonica* 25: 209–264.

RUIZ, Z., AND M. ARROYO. 1978. Plant reproductive ecology of a secondary tropical deciduous forest in Venezuela. *Biotropica* 10: 221–230.

RUSSO, S. E., C. J. CAMPBELL, J. L. DEW, P. R. STEVENSON, AND S. A. SUAREZ. 2005. A multi-forest comparison of dietary preferences and seed dispersal by *Ateles* spp. *International Journal of Primatology* 26: 1017–1037.

SAKAMOTO, Y., M. ISHIGURO, AND G. KITAGAWA. 1986. Akaike information criterion statistics. Reidel Publishing, Dordrecht, Netherlands.

SAUQUET, H., J. DOYLE, T. SCHARASCHKIN, T. BORSCH, K. HILE, L. CHATROU, AND A. LE THOMAS. 2003. Phylogenetic analysis of Magnoliales and Myristicaceae based on multiple data sets: implications for character evolution. *Botanical Journal of the Linnean Society* 142: 125–186.

SCHLESSMAN, M. 1991. Size, gender, and sex-change in dwarf ginseng, *Panax trifolium* (Araliaceae). *Oecologia* 87: 588–595.

SMITH, A. 1937. The American species of Myristicaceae. *Brittonia* 2: 393–510.

STACY, E., J. HAMRICK, J. NASON, S. HUBBELL, R. FOSTER, AND R. CONDIT. 1996. Pollen dispersal in low-density populations of three neotropical tree species. *American Naturalist* 148: 275–298.

THOMAS, S., AND J. LAFRANKIE. 1993. Sex, size, and interyear variation in flowering among dioecious trees of the Malayan rain forest. *Ecology* 74: 1529–1537.

VALENCIA, R., R. CONDIT, R. FOSTER, K. ROMOLEROUX, G. VILLA MUNOZ, J.-C. SVENNING, E. MAGARD, M. BASS, E. LOSOS, AND H. BALSLEV. 2004a. Yasuní forest dynamics plot, Ecuador. *In* E. Losos and E. Leigh [eds.], Tropical forest diversity and dynamism: findings from a large-scale plot network, 609–620. University of Chicago Press, Chicago, Illinois, USA.

VALENCIA, R., R. FOSTER, G. VILLA, R. CONDIT, J.-C. SVENNING, C. HERNANDEZ, K. ROMOLEROUX, E. LOSOS, E. MAGARD, AND H. BALSLEV. 2004b. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92: 214–229.

WHEELWRIGHT, N., AND A. BRUNEAU. 1992. Population sex ratios and spatial distribution of *Ocotea tenera* (Lauraceae) trees in a tropical forest. *Journal of Ecology* 80: 425–432.

WHEELWRIGHT, N., AND B. LOGAN. 2004. Previous-year reproduction reduces photosynthetic capacity and slows lifetime growth in females of a neotropical tree. *Proceedings of the National Academy of Sciences, USA* 101: 8051–8055.

WILSON, K., AND I. HARDY. 2002. Statistical analysis of sex ratios: an introduction. *In* I. Hardy [ed.], Sex ratios: concepts and research methods, 48–92. Cambridge University Press, Cambridge, UK.

YAMASHITA, N., AND T. ABE. 2002. Size distribution, growth and inter-year variation in sex expression of *Bischofia javanica*, an invasive tree. *Annals of Botany* 90: 599–605.

YAP, S. 1982. The phenology of some fruit tree species in a lowland forest. *Malaysian Forester* 45: 21–35.