

Seed mass, abundance and breeding system among tropical forest species: do dioecious species exhibit compensatory reproduction or abundances?

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Summary

1. Dioecious species may suffer a reproductive handicap compared to sympatric cosexual (hermaphroditic or monoecious) species of equal abundance simply because populations of dioecious species contain fewer seed-producing individuals. To compensate for this population-level disadvantage, natural selection in dioecious populations should favour females that reallocate those reproductive resources, that in cosexual individuals are invested in male function, towards the production of higher quality or more seeds, potentially leading to a higher density of established individuals.

2. We tested for two compensatory fitness advantages (heavier seeds and higher population densities) in dioecious species in the flora of a high-diversity tropical forest in Western Amazonia. Using a phylogenetically corrected generalized linear modelling approach, we examined the phylogenetic dependence (Pagel's λ) of seed mass, abundance, growth form and wood-specific gravity for 641 species from Yasuní National Park, Ecuador. Seed mass was highly correlated with phylogeny, but abundance was not. We then used AIC values to test for models (including breeding system) that best explained seed mass and species abundance, using the maximum likelihood values of λ .

3. Contrary to expectations, dioecious species exhibited no advantage with respect to either seed mass or population density; there was no difference in mean seed mass or abundance between dioecious species and their most closely related cosexual species.

4. We compared our results with those from a similar forest in the Tambopata Wildlife Reserve, Peru. There, dioecious shrubs had larger seeds than hermaphroditic shrubs, but (as for Yasuní) there was no difference between breeding systems in seed size among trees. Differences in the composition of species sampled may have contributed to differences in the results between the two sites.

5. We suggest that other individual fitness advantages, such as reduced inbreeding, increased dispersal, superior seed quality (e.g. better defences) or increased seed number contribute to the persistence of dioecious populations at Yasuní.

6. *Synthesis.* Similarities in the statistical models of seed mass and abundance for plant species in a Western Amazonian rain forest indicate that selective pressures on the seed-producing individuals are similar, despite variation in sexual system. Therefore, breeding system may play a more limited role in community assembly of tropical forests than was previously considered.

Key-words: Amazonia, breeding system, dioecy, hermaphrodite, reproductive biology, seed size

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Introduction

Dioecious plant species divide reproductive function among individuals, with pollen production restricted to males, and seed and fruit production restricted to females. Reported sex ratios in tropical trees are generally male-biased; hence the proportion of seed-producing individuals in a population is usually < 50% (Queenborough *et al.* 2007a). As a result, given equal population densities, populations of dioecious species will have fewer seed-producing individuals than their cosexual (i.e. hermaphroditic or monoecious) counterparts. To maintain *per capita* growth rates that are equal to their cosexual counterparts, female individuals in dioecious populations must exhibit some fitness advantages, which might include: higher fecundity (although without increased dispersal this results in a 'seed shadow handicap' whereby offspring are concentrated in the proximity of a smaller number of maternal plants (Heilbut *et al.* 2001)), earlier ages of reproduction, more frequent reproduction or higher quality offspring (with higher rates of survivorship or greater longevity). Indeed, one recent study has detected higher abundances of dioecious than non-dioecious species among 97 woody species in a Brazilian Atlantic rain forest (Vamosi 2006).

In pure females, selection may be relaxed on those primary or secondary traits that promote male fitness in cosexual individuals. Consequently, resources that are allocated to traits that enhance male function (e.g. anther and pollen production or flowers that are sufficiently attractive, long-lived or rewarding to ensure multiple pollinator visits per flower) may be reallocated towards traits that promote female function (e.g. seed quantity or quality). In other words, relative to cosexual plants, females of dioecious species may invest more resources in seed or fruit production simply by reallocating their reproductive effort. Sex-specific allocation of resources among floral traits – presumably the result of sex-specific selection – has been observed within many species that are polymorphic for sex. For example, in many gynodioecious species, females produce larger, more or higher-quality seeds than cosexuals (Caruso *et al.* 2003; Ramula & Mutikainen 2003; Shykoff *et al.* 2003; Koelewijn & Van Damme 2005; Chang 2006). Similarly, in many dioecious species, males produce larger or more rewarding flowers than females, presumably because males benefit (via pollen dispersal) more from higher attractiveness than females (which do not require many visits per flower to achieve full seed set) (cf. Bell 1985; Geber *et al.* 1999; Vamosi & Otto 2002; Humeau *et al.* 2003; Mitchell & Diggle 2005). Inter-specific investigations of the evolutionary reallocation of resources towards increasing seed size or quality in dioecious species relative to their hermaphroditic counterparts, however, are rare; we are aware of only one other study (Vamosi *et al.* 2008).

Assuming that dioecious species coexist with cosexual species through mechanisms of compensation, it should then be possible to quantify this compensation relative to cosexual species. If n 'female' cosexual individuals invest r resources in seed production, then $n/2$ female dioecious individuals would be predicted to invest $2r$ resources. In terms of seed number,

this would be double the number. In terms of seed quality, it is more difficult to quantify the resources necessary to ensure that each seed produced has a higher chance of survival because of interactions with abiotic factors (Poorter & Rose 2005). We might predict that seeds of dioecious species would be between 50% and 100% heavier, depending on the relationship between individual seed mass and the expected individual fitness of the ensuing seedling (Moles & Westoby 2004).

However, there are other mechanisms of species coexistence that may particularly aid dioecious species to persist. For example, the lower number of dioecious females may benefit from a frequency-dependent advantage (Janzen 1971; Connell 1971; Chesson 2000), or dioecious species may out-compete cosexual species in other aspects of niche-space, such as regeneration, pollination or seed dispersal (e.g. Grubb 1977; Vamosi *et al.* 2007). Alternatively, stochastic processes and dispersal limitation may enable the coexistence of hundreds of species, irrespective of differences in breeding system or any other species trait (Hubbell 2001).

For several reasons, tropical rain forests provide a particularly rich opportunity in which to test the mechanisms that promote the persistence of dioecious species and to detect ecological and/or evolutionary correlates of dioecy. First, due to the high species richness of tropical rain forests, it is possible to compare seed quality and population densities of a taxonomically diverse array of sympatric plant species that differ in breeding system. Secondly, the high diversity of species representing a range of growth forms (e.g. trees, shrubs and lianas) and breeding systems (Bullock 1985; Matallana *et al.* 2005; Queenborough *et al.* 2007a) allows one to explore rigorously the relationship between breeding system and reproductive performance by examining it independently within each of these plant guilds. Thirdly, dioecious and cosexual species and clades have diverged from common ancestors numerous times in tropical floras, resulting in a high local proportion of dioecious species compared to the global proportion of 6% (e.g. Bawa 1980; Renner & Ricklefs 1995; Vamosi & Vamosi 2004). Lastly, the repeated evolutionary divergence in breeding system permits one to test predictions concerning the joint evolution of breeding system with morphological traits such as individual seed mass and ecological traits such as the abundances of individuals of different size or age classes.

In this study, we tested for two compensatory fitness or demographic advantages in dioecious species compared to co-occurring hermaphroditic and monoecious species: (i) higher individual seed mass and (ii) higher densities of established individuals.

In addition to comparing dioecious species to those with cosexual flowers, we compared dioecious and monoecious species. Monoecious species serve as a control because, similar to dioecious species, they produce unisexual flowers (within individuals) but they do not suffer the disadvantage of having fewer seed-producing individuals (Heilbut *et al.* 2001). We therefore predicted that dioecious species should produce larger seeds or persist at higher density than both monoecious and hermaphroditic species, but that monoecious

and hermaphroditic species should not differ consistently with respect to these attributes. First, we tested for phylogenetic dependence in both the dependent and independent variables in order to determine whether we needed to control statistically for non-independence of trait states among closely related species. Secondly, we used a phylogenetically corrected generalized linear modelling approach to ask whether the evolutionary divergence in breeding system between closely related, sympatric species (i.e. divergence between dioecious, monoecious and hermaphroditic species) is associated with either a change in seed size or adult population density as predicted by the arguments above. Specifically, we predicted that dioecious species would have higher individual seed mass and higher densities of adults. In addition, we controlled for the potentially confounding effects of the well-known associations between seed size and growth form (e.g. trees, shrubs, lianas and herbs) by conducting analyses both within and across growth forms.

Because of the well-documented interspecific trade-offs between seed size and other traits (e.g. seed number, mean individual longevity, and growth rate (Swaine & Whitmore 1988; Moles & Westoby 2006; Baraloto & Forget 2007; Rees & Venable 2007)) and given the positive correlations between seed size and plant height (Leishman *et al.* 2000; Moles *et al.* 2004; Wright *et al.* 2007), several components of life history are likely to evolve jointly with seed size, even within growth forms. Moreover, traits such as growth rate and maximum plant height may be strongly correlated with wood density due to the constraints wood density places on the movement of water and on structural support. Indeed, wood-specific gravity (WSG) is a good correlate of longevity and life-history strategy among Neotropical trees (Chave *et al.* 2006). Thus, we sought to isolate and measure the relationship between breeding system and seed size by including WSG as a covariate in our analyses as a proxy for longevity.

Although seed size has primarily been contrasted between functional groups (such as shade-tolerators and light-demanders, represented in our study by wood-specific gravity), the within-group range of seed size is often much larger (Grubb 1998). Within functional groups, a basic trade-off exists between seed size and seedling survival: in species that produce larger seeds the resulting seedlings have a higher tendency to survive. This relationship is often modified by factors such as tolerance of hazards, and competition with established plants and other seedlings (summarized in Coomes & Grubb 2003). Breeding system is a relatively un-examined aspect of variation in seed-size that may subtly modify these well-established relationships.

Finally, to assess the generality of our results, we compare the patterns observed in our analysis of an Ecuadorian rain forest flora with those from a Peruvian rain forest with comparable floristic, ecological and taxonomical diversity that was subject to similar analyses by Vamosi *et al.* (2008). We extend their work by examining the taxonomic composition of and the species abundance within the two forests, as well as frequency distributions of seed size, to understand the potential differences in results between the sites.

Methods

DATA COLLECTION

Seed mass

Seed sizes were obtained from plant specimens collected in Yasuni National Park, a 1.6×10^6 -ha Biosphere and Ethnic Reserve forest in eastern Amazonian Ecuador. Seeds were collected in terra-firme forest surrounding the Yasuni forest dynamics plot (FDP) in 2000–2007. The Yasuni FDP is a 25-ha permanent plot within which all free-standing stems ≥ 1 cm diameter at breast height (d.b.h. = 1.3 m above the soil surface), excluding lianas, were tagged, mapped and identified to (morpho)species ($0^\circ 41' S$, $76^\circ 24' W$; Valencia *et al.* 2004; additional information is available on the Center for Tropical Forest Science website; www.ctfs.si.edu). We use data from the initial 1996 census. One to several seeds were collected per sample and weighed as a batch on an electronic balance (Sartorius BL150S), dried in an oven at approximately $105^\circ C$ for several days and reweighed. Mean dry individual seed mass was calculated for each species from these samples. Most species are represented by only one collection (sampled from a single individual). Although we aimed to detect sources of variation among species in the investment of resources that directly affect offspring survivorship after dispersal, accessory structures such as wings and plumes were often not removed prior to weighing. We do not expect this to bias our results because very few tropical species are wind-dispersed (Muller-Landau & Hardesty 2005), and a minority of these (2/40 wind-dispersed species in our sample) are dioecious. In species where the seed coats are fused to additional maternal tissue layers (such as the endocarp or mesocarp), these tissues were included in the seed mass. All fleshy parts (e.g. arils) were removed. Voucher specimens are deposited in the Seed and Seedling Project collection of reproductive parts, housed in the Yasuni Scientific Research Station; many are also linked to numbered trees in the FDP (vouchers deposited in the herbarium of the Pontificia Universidad Católica del Ecuador, Quito [QCA]).

Breeding systems

Breeding systems were assigned with reference to, in descending order of use: a treatment of the trees of Peru (Pennington *et al.* 2004), various monographs of the Flora Neotropica (e.g. Gates 1982; Sleumer 1984) and Flora of Panama (e.g. Woodson *et al.* 1976), treatments, family and generic monographs, the Flora of Barro Colorado Island (Croat 1978), primary literature (e.g. Renner & Ricklefs 1995; Lenza & Oliveira 2005; Weckerle & Rutishauser 2005) and web sources (e.g. Watson & Dallwitz 1992 onwards). For many species, multiple sources were available to verify their breeding system. Conflicting reports were resolved with reference to the most recent and/or most comprehensive treatment. As the Yasuni plot contains many new and/or as-yet unidentified species, some (morpho)species were assigned a sexual system based on their genus, if all species recorded to date exhibit a single breeding system.

Growth form

Growth form for the majority of species was assigned based on that of individuals present in the Yasuni FDP (R. Valencia, unpublished data). Other species were assigned growth form from herbarium labels or from the above literature. Growth form could not be assigned unequivocally to 13 species and these were excluded from analyses including this term, along with the 6 herbaceous species for which data were available.

Tree abundance

Numbers of individuals of each tree and shrub species in the Yasuni FDP were calculated for two size classes: 1–10 cm d.b.h. and ≥ 10 cm d.b.h. (data available from www.ctfs.si.edu). The abundances of lianas are not currently available. We used plot data from the initial census (completed 1996). Analyses including abundance were therefore only carried out on species in this subset of the full data set (1–10 cm d.b.h.: number of individuals = 81 481, species = 388, genera = 205, families = 62; ≥ 10 cm d.b.h.: individuals = 11 604, species = 324, genera = 181, families = 55).

Wood specific gravity

Species were assigned (non-transformed) WSG values (data from Chave *et al.* 2006, $N = 172$). Where Yasuni species were not present in the data base, genus-level ($N = 334$) or family-level ($N = 88$) means were used in accordance with the guidelines provided by Chave *et al.* (2006). Nineteen species could not be assigned and were excluded from relevant analyses.

Seed size data from Tambopata Wildlife Reserve, Peru

We compared the data from Yasuni with data from the Tambopata Wildlife Reserve (Vamosi *et al.* 2008). Seed sizes of the species sampled at Tambopata were estimated from seed volume (mm^3) rather than seed mass, but the patterns revealed are comparable. Seed volumes and breeding systems are available for 972 species in 104 families. See Vamosi *et al.* (2008) for methods of data collection, analysis, etc.

STATISTICAL ANALYSES

We employed an evolutionary (hereafter phylogenetic) approach to ask: Where there is evolutionary divergence between closely related species in breeding system, is there a correlated change in seed size? And, if so, do dioecious species produce larger seeds than their cosexual counterparts within and across growth forms? In the current study, we predict that relative to closely related hermaphrodites, dioecious species should produce larger seeds. This prediction applies regardless of whether the dioecious species included in these analyses are derived from, or give rise to, the hermaphroditic species to which they are directly compared. Similarly (see below), we examined whether differences in population densities between species that differ in breeding system are consistent with the prediction that the evolution of dioecy will result in a compensatory increase in population density. This prediction does not imply that population density is an inherited trait (such as seed size or dioecy itself, for that matter), but rather that a higher population density is a predicted ecological consequence of the evolution of (unmeasured) traits in dioecious species that confer enhanced rates of survivorship and recruitment relative to their hermaphroditic counterparts.

To examine the joint evolution of breeding system and seed mass, and their association with ecological abundances, we assessed and examined the relationships between these traits whilst taking account of their evolutionary history (Felsenstein 1985; Harvey & Pagel 1991; see also Moles *et al.* 2005a; Vamosi *et al.* 2008). To identify phylogenetic relationships among the sampled species, we used *Phyloomatic* (Webb & Donoghue 2005), a software utility that constructs a hypothesized phylogeny that includes the angiosperm species (which may be members of a given habitat or community) provided by the user. The relationships assigned to the listed species are based on the dynamic angiosperm phylogeny available on-line (Stevens 2004). Specifically, we used the

maximally resolved seed plant tree designated 'R20040402'. The limitation to this approach is that, because the species included in any given list (such as the one we provided from Yasuni) comprise only a subset of the families and genera to which they belong, any phylogenetic tree constructed is likely to be highly incomplete. An advantage of the statistical analysis approach adopted below is that, unlike independent contrasts that only compare sister species at defined nodes, our approach includes all species. The approach we take is to use the lambda transformation suggested by Pagel (1999). This allows us to determine whether the available phylogeny improves the statistical description of the data relative to treating all data points as independent, as well as to optimize the level of phylogenetic correction in the case of uncertain or approximate phylogenetic information.

To test whether we needed to account for phylogenetic autocorrelation in the subsequent analyses, we initially examined the strength of phylogenetic signal of each variable across the Yasuni phylogeny. The phylogenetic signal for seed size, $\ln(\text{seed mass})$, abundance, $\ln(\text{abundance})$, WSG (g cm^{-3}), breeding system (dioecious, mono-ecious or hermaphroditic) and growth form (liana, shrub or tree) were estimated via a generalized least squares approach (Grafen 1989; Martins & Hansen 1997; Pagel 1999), implemented in the R environment (R Development Core Team 2008). The influence of phylogenetic non-independence on each of these variables was modelled by incorporating the phylogenetic covariance matrix in a generalized least squares model. The phylogenetic covariance structure was multiplied by a phylogenetic signal value (λ), ranging from 0 (no phylogenetic autocorrelation) to 1 (maximum phylogenetic autocorrelation), and the log-likelihood of each run was recorded; from the resulting likelihood surface a maximum likelihood phylogenetic signal value of λ was obtained (Pagel 1999). λ measures the degree to which the variation/covariation of traits across a tree agrees with the Brownian process (Freckleton *et al.* 2002). In the context of analysing seed mass, a value of $\lambda = 0$ implies that seed mass is distributed among species at random with respect to phylogeny. A value of $\lambda = 1$ indicates that seed mass is phylogenetically conserved; that is, closely related groups have more similar seed masses than would be expected by chance. Approximate confidence intervals for the maximum likelihood value of λ were calculated via likelihood ratio tests (Freckleton *et al.* 2002) on values derived from the likelihood surface. Following estimation of the phylogenetic dependence for each variable, we used a similar approach when examining the relationships between seed mass, breeding system and co-varying ecological variables (detailed below). We carried out each analysis using the maximum likelihood value of λ (Table 1).

We adopted a simple information theoretic approach, using the Akaike Information Criterion (AIC), to determine whether a simpler model performed less well than a more complex one (Burnham & Anderson 2004). All statistical analyses were conducted in the R environment (R Development Core Team 2008), and phylogenetic manipulations utilized the APE package (Paradis *et al.* 2004). The code used is available from the authors on request.

Seed mass

In order to maximize sample size, we carried out two model comparisons. First, to examine the relationship between breeding system and individual seed mass accounting for growth form, we examined three candidate models (Table 2): seed mass solely as a function of breeding system, seed mass as a function of breeding system + growth form, and then the model including the interaction between breeding system and growth form. Secondly, for trees and shrubs for which data were available, we included WSG as a covariate in these models. This controls for

Table 1. Phylogenetic signal across a phylogeny of > 500 tropical liana, shrub and tree species from Yasuní, Amazonian Ecuador

Trait	λ	95% CI	χ^2 test if λ is different from 0 or 1	
			0	1
Seed mass (LN)	0.99	0.99–0.99	0	0
Wood specific gravity	0.98	0.97–0.99	0	0
Abundance 1–10 cm d.b.h. (LN)	0.01	0–0.29	0.88	0
Abundance >10 cm d.b.h. (LN)	0.04	0–0.17	0.2	0
Breeding system	0.99	0.98–0.99	0	0
Growth form	0.95	0.92–0.97	0	0

Note: the maximum likelihood value of λ is given along with confidence intervals for this value, and the significance (P -values) of the difference from $\lambda = 0$ and $\lambda = 1$ (see 'Methods').

Table 2. The models tested for effect on the natural logarithm (LN) of seed mass. The 'best' model is indicated by the lowest AIC value (in bold). Δ_{AIC} values indicate the difference in AIC of each model from this model. Values > 2 indicate substantial differences in model fit (Burnham & Anderson 2004)

Model	λ	AIC	Δ_{AIC}	R^2
(a) All species ($N = 623$)				
Breeding system	0.99	2237.04	11.37	0
Breeding system + growth form	0.99	2234.75	9.08	0.02
Breeding system \times growth form	0.99	2225.67	0.00	0.06
(b) Trees and shrubs pooled ($N = 585$)				
Growth form	0.99	2228.26	19.06	0.02
Wood specific gravity	0.99	2218.12	8.92	0.03
Breeding system	0.99	2235.16	25.96	0
Breeding system + growth form	0.99	2232.85	23.65	0.02
Breeding system \times growth form	0.99	2223.88	14.68	0.05
Breeding system + wood specific gravity	0.99	2222.95	13.75	0.03
Breeding system \times wood specific gravity	0.99	2227.06	17.86	0.03
Breeding system + growth form + wood specific gravity	0.99	2218.64	9.44	0.05
Breeding system \times wood-specific gravity + growth form	0.99	2222.35	13.15	0.05
Breeding system \times growth form + wood specific gravity	0.98	2209.20	0.00	0.09
Breeding system \times growth form \times wood specific gravity	0.98	2221.93	12.73	0.11

Note: coefficients for model with lowest AIC can be found in Table S1.

variation in seed size among species that is associated with variation in longevity (for which WSG is a proxy). We examined nine candidate models, comparing the full model of breeding system + growth form + WSG and all second-order interactions against eight simpler models (Table 2). All of these models were run accounting for phylogeny, using the maximum likelihood value of λ .

We then conducted non-phylogenetically-corrected weighted ANOVAs (i.e. species values were weighted by their abundances) to detect differences among breeding systems with respect to the mean seed mass of all co-occurring individuals. This analysis was restricted to trees and shrubs present in the Yasuní plot and it evaluated whether the mean individual seed mass of censused dioecious *individuals* (treating all established individuals as equals regardless of their sex or species) differed from that of their cosexual counterparts.

Abundance

To detect compensatory increases in the demographic performance (leading to greater adult abundances) of dioecious species relative to their cosexual counterparts, we tested the prediction that, independent of seed mass, dioecious species are more abundant than cosexual species. This analysis was also restricted to tree and shrub species. We tested whether there was covariation between evolutionary divergence in

breeding system and divergence in ecological densities. We also examined the relationships between abundances and seed mass to evaluate the idea that, in order for species representing six orders of magnitude in seed mass to coexist, seed mass should be neutral with respect to its effects on abundances. Again, we compared the full model of log abundance (of stems 1–10 cm d.b.h., stems > 1 cm d.b.h., and stems > 10 cm d.b.h.) as a function of breeding system + seed mass + the interaction, against simpler models. Because abundance was independent of phylogeny (Table 1), there was no need to account for phylogenetic dependence in these analyses.

Results

The sample for which seed mass data were available included hermaphroditic (378 species), monoecious (74) and dioecious (189) breeding systems. Therefore, the incidence of dioecy (29.2%) is comparable to that in similar analyses of breeding systems in tropical forests (Queenborough *et al.* 2007a). Four different growth forms were encountered: herbs (6), lianas (111), shrubs (99) and trees (412), while thirteen species were unassigned. Thirty genera (of 293) had > 1 growth form within the genus.

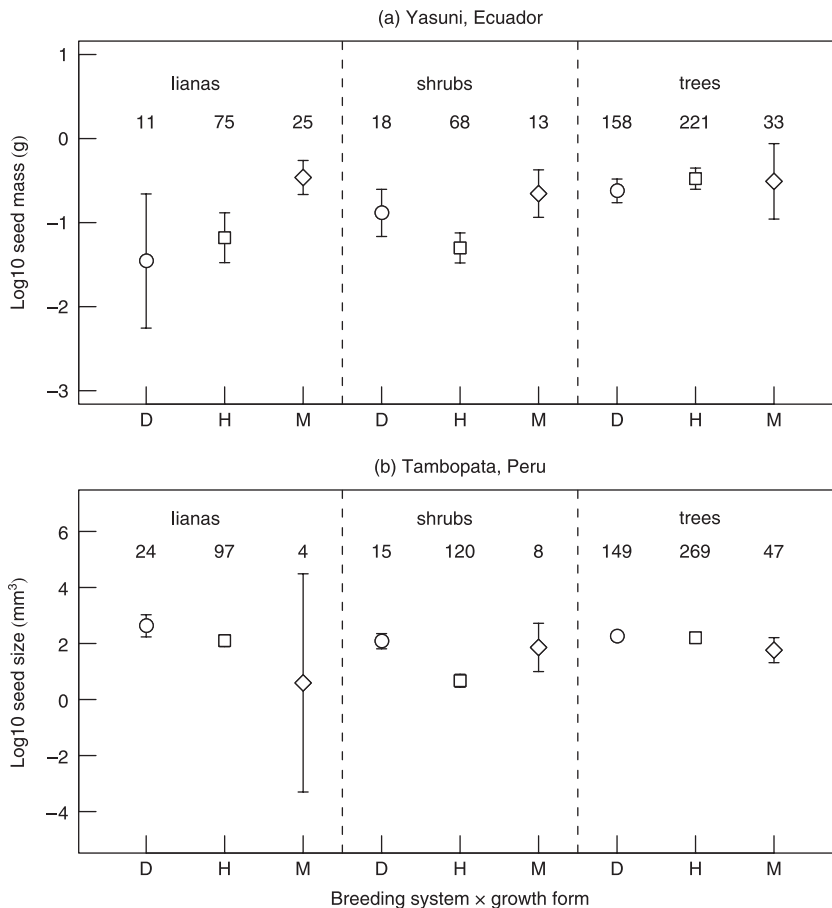


Fig. 1. Mean seed size according to growth form for plant species from two lowland tropical rain forests: Yasuni, Ecuador and Tambopata, Peru. D = dioecious, M = monoecious, H = hermaphroditic. Sample sizes listed below growth form. Error bars = 95% confidence intervals. Note the log scale of the y-axes. Data for Tambopata from Vamosi *et al.* (2008).

PHYLOGENETIC SIGNAL

There was significant phylogenetic dependence in the key variables of seed mass, breeding system and growth form (Table 1). The covariate WSG also showed a strong phylogenetic signal. However, species abundance was unrelated to phylogeny and had a λ that was not significantly different from 0. For all variables, λ was significantly different from 1.

SEED MASS

There was a large range in seed mass among the species sampled from Yasuni (0.00002–38.0 g, mean = 1.2 g, SD = 3.4 g). The model constructed to detect significant sources of variation in seed mass with the lowest AIC value included breeding system, growth form and their interaction (Table 2a). This was driven largely by the interaction term, which caused a large drop in AIC. For all species combined, trees produced significantly heavier seeds than lianas and shrubs (see Table S1 in Supporting Information). Within growth forms, however, dioecious species did not consistently produce heavier seeds than non-dioecious species, when accounting for phylogeny. Among both trees and shrubs, seeds of dioecious species were heavier than those of monoecious species, but dioecious and hermaphroditic species did not differ significantly with respect to mean seed mass (Table S1). Among lianas, dioecious and hermaphroditic species

produced significantly lighter seeds than monoecious species (Table S1). These differences can be obscured if phylogeny is not taken into account (Fig. 1).

When species were weighted by their abundances, breeding systems differed with respect to mean seed mass (Fig. S1), but not in the direction we predicted. With respect to small trees (1–10 cm d.b.h.) there were no differences in seed mass among individuals of different breeding systems, but when trees > 10 cm d.b.h. were included in the analysis, dioecious species had lower seed mass than cosexual species.

ABUNDANCE

Species ranged in abundance from 1 to 4580 individuals (mean = 236, SD = 443). An evolutionary divergence in breeding system had very little effect on abundance and was only present in one candidate model for the number of stems 1–10 cm d.b.h. (Table 3). Stems 1–10 cm d.b.h. of monoecious trees and shrubs were significantly less abundant than stems of dioecious and hermaphroditic trees and shrubs (Table S2, Fig. S2).

WOOD-SPECIFIC GRAVITY

There was a significant positive relationship between seed mass and WSG (linear regression, $F = 22.49$, d.f. = 497, $P < 0.001$, $R^2 = 0.04$, $y = -1.5 + 1.4x$); species with denser wood produce

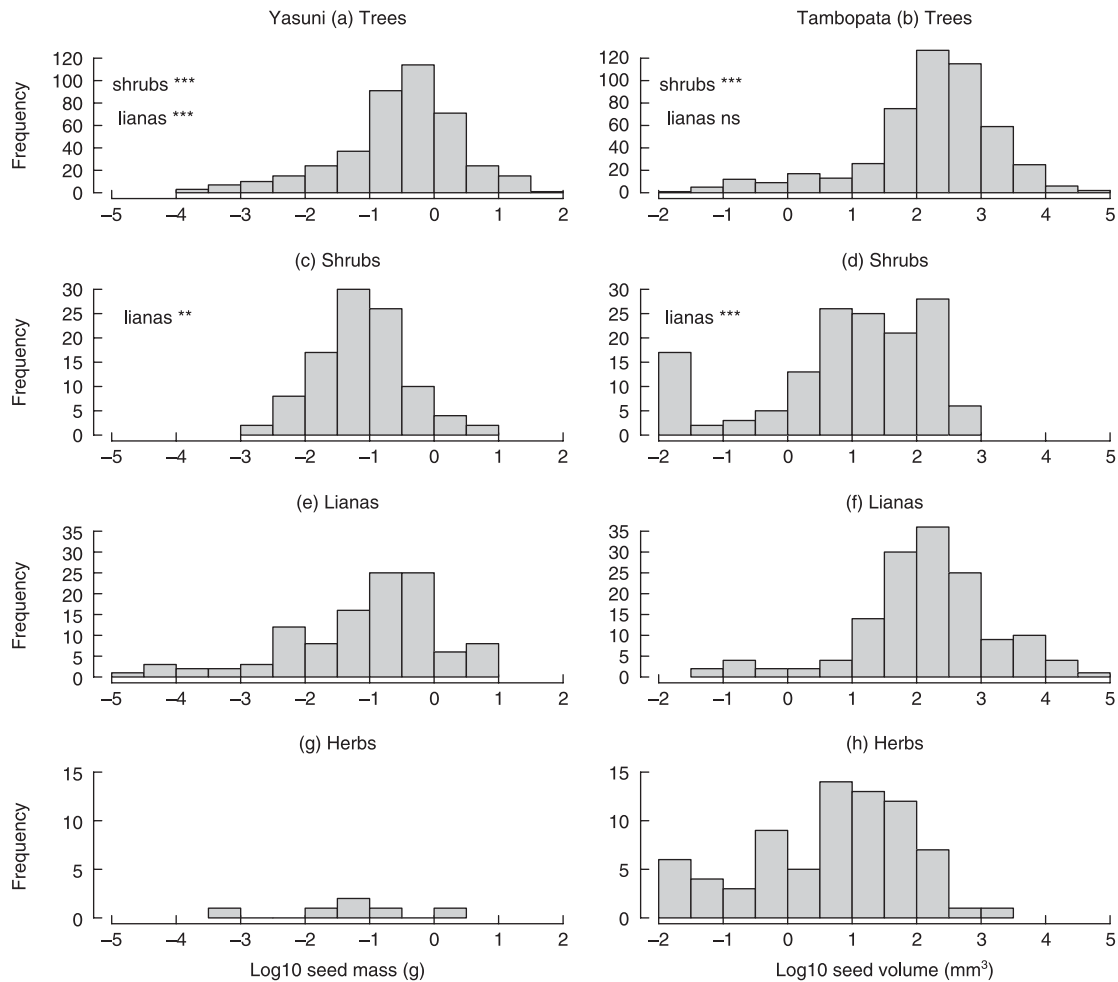


Fig. 2. Frequency distributions of seed size (mass or volume) for plant species from two lowland tropical rain forests: Yasuni, Ecuador and Tambopata, Peru. Data for Tambopata from Vamosi *et al.* (2008). The significance of intra-site comparisons of the frequency distributions are indicated by asterisks (Two-sample Kolmogorov–Smirnov test, *** $P < 0.001$, ** $P < 0.01$, ns = not significant).

Table 3. Models tested for effect on species abundance. The ‘best’ model is indicated by the lowest AIC value (in bold)

Model	λ	AIC	Δ_{AIC}	R^2	P
(a) 1–10 cm d.b.h. ($N = 388$)					
Breeding system	0.01	1334.40	2.19	0.02	*
Seed mass	< 0.01	1332.68	0.47	0.01	*
Breeding system + seed mass	< 0.01	1332.21	0.00	0.03	
Breeding system \times seed mass	< 0.01	1336.25	4.04	0.04	ns
(b) > 10 cm d.b.h. ($N = 324$)					
Breeding system	0.39	1259.51	9.61	0.01	ns
Seed mass	0.32	1249.90	0.00	0.03	***
Breeding system + seed mass	0.19	1252.47	2.57	0.04	
Breeding system \times seed mass	0.19	1252.99	3.09	0.06	ns
(c) > 1 cm d.b.h. ($N = 394$)					
Breeding system	0.04	1248.38	6.67	0.01	ns
Seed mass	0.01	1241.71	0.00	0.02	*
Breeding system + seed mass	0.02	1246.00	4.29	0.02	
Breeding system \times seed mass	0.02	1246.54	4.83	0.04	ns

Note: significance values from the full model ANOVA are indicated by asterisks (* $P < 0.05$, *** $P < 0.001$; coefficients in Table S2).

larger seeds. Thus, we were justified in including WSG as a covariate in our analyses of seed mass. However, although the probable model included WSG, it did not include any interactions between WSG and breeding system or growth form (Table 2). The effect of WSG on seed mass did not differ among breeding systems or growth forms, even though lianas had significantly higher WSG than shrubs and trees (ANOVA, $F = 4.33$, d.f. = 570, $P = 0.0049$).

COMPARISON OF YASUNÍ WITH TAMBOPATA, PERU

Among shrubs and lianas at Tambopata, dioecious species produced larger seeds than cosexual species (monoecious and hermaphrodites combined), but this pattern did not hold for trees (Figs 1 and 2).

The distributions of seed size in trees and lianas are strikingly similar at both sites (Fig. 2). Herbs were undersampled at Yasuni (and in any case were not included in our analyses). Differences in the communities are apparent in shrubs. At Tambopata, there are many shrubs with very tiny seeds

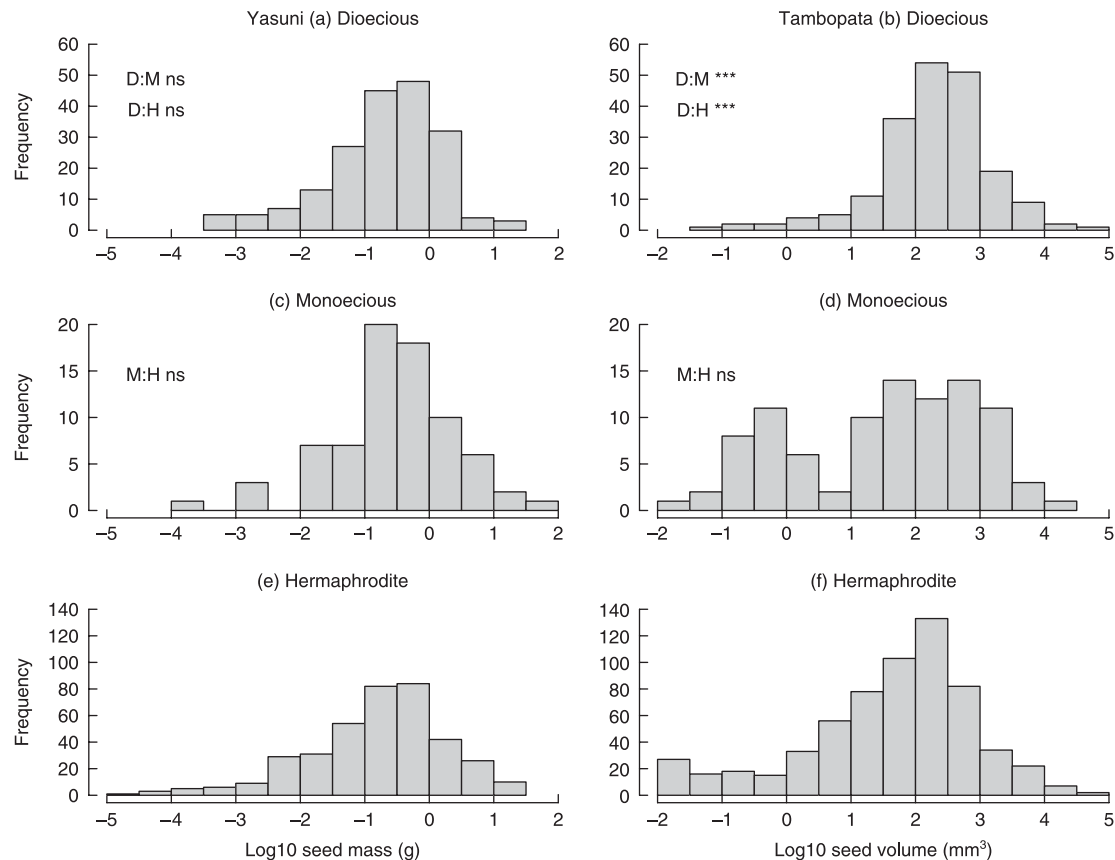


Fig. 3. Frequency distributions of seed size (mass or volume) according to breeding system for plant species from two lowland tropical rain forests: Yasuni, Ecuador and Tambopata, Peru. Data for Tambopata from Vamosi *et al.* (2008). The significance of intra-site comparisons of the distributions are indicated by asterisks (Two-sample Kolmogorov–Smirnov test, *** $P < 0.001$, ns = not significant).

(< 0.1 mm³) that are not present within the sampled Yasuni flora. Examining how seed size is distributed by breeding system, it can be seen that most of these very tiny-seeded shrubs are monoecious or hermaphroditic (Fig. 3). There is a long tail in the distribution of hermaphroditic species at Yasuni also, but it is much thinner and is comprised of fewer species than at Tambopata.

Discussion

The evolution and ecology of seed size (e.g. Kelly 1995; Lord *et al.* 1997; Moles *et al.* 2005a,b) and breeding systems (Yampolsky & Yampolsky 1922; Renner & Ricklefs 1995; Heilbuth 2000) are only two of the many functional reproductive traits in angiosperms that have a long history of study, but few authors have considered both traits simultaneously (Ibarra-Manriquez & Oyama 1992; Carpenter *et al.* 2003; Vamosi *et al.* 2008). In addition, while many studies of breeding system evolution have aimed to identify the selective forces that promote the evolution of relatively uncommon phenomena such as dioecy (Bawa & Opler 1975; Charlesworth & Charlesworth 1978; Bawa 1980; Givnish 1980; Thomson & Barrett 1981; Sakai *et al.* 1995; Dorken *et al.* 2002), few have aimed to identify the process or study the outcome of selective forces that occur in populations as a result of dioecy (but see Heilbuth

et al. 2001; Vamosi & Otto 2002; Vamosi *et al.* 2003, 2006). In other words, as dioecy becomes established in a population or species, are there traits that evolve differently from their cosexual sister species?

In this article, we surveyed species in a highly diverse tropical forest in Ecuador in order to (i) examine associations between seed size, breeding system, growth form and regeneration strategy and (ii) test specific predictions concerning the evolutionary and ecological consequences of dioecy. Our results were not entirely consistent with those of previous studies. Ibarra-Manriquez & Oyama (1992) found no difference in seed mass between breeding systems; Carpenter *et al.* (2003) found bigger seeds in dioecious species (in ‘larger tree species’); Matallana *et al.* (2005) found that dioecy was disproportionately represented among the 43 most abundant woody plant species relative to the remainder of the flora; Vamosi (2006) found a marginally higher density of dioecious species than non-dioecious species; and Vamosi *et al.* (2008) found bigger seeds in dioecious than in cosexual species in certain growth forms. First, we did not find that dioecious species produce heavier seeds than hermaphroditic species, in lianas, shrubs or trees. We did find that monoecious species produce heavier seeds than dioecious and hermaphroditic species in lianas, but lighter seeds in shrubs and trees. Secondly, although our analyses corroborated the positive relationship between seed

size and WSG (which is, in turn, positively correlated with longevity (Chave *et al.* 2006)), we found no significant interaction between WSG and breeding system. We found no difference between the WSG of shrubs and trees, but within both of these growth forms life-history strategy varies enormously, so the absence of a significant difference between them is unsurprising.

There is a strong phylogenetic signal in the distributions of seed mass, breeding system and growth form. All three traits are highly phylogenetically conserved, with λ values significantly different from 0 and very close to 1. This is as expected (see also Vamosi *et al.* 2003). By contrast, species abundances were distributed at random with respect to phylogenetic relatedness. Although there is no reason from an evolutionary perspective to expect that species abundances would appear to be phylogenetically conserved, if adult densities were determined by traits that were strongly correlated with dioecy, and if the persistence of dioecious species required that they maintain higher population densities, then abundances could be strongly correlated with breeding system, appearing to 'co-evolve' with dioecy when examined on a phylogenetic tree. In contrast to our prediction that dioecious species should exhibit evidence of a demographic advantage that compensates for the lower

proportion of seed-bearing individuals, we found no evidence for this kind of joint change in breeding system and abundance.

DIFFERENCES BETWEEN YASUNÍ AND TAMBOPATA

Here, we compare our results with those from another diverse Neotropical forest in the Tambopata Wildlife Reserve of Peru (Vamosi *et al.* 2008). In that study, the authors found evidence for the association between seed size and breeding system described above and, as in this study, the association varied according to growth form (Fig. 1): Dioecious lianas and shrubs, but not trees, were found to have larger seeds. What are the differences between these two forests that might explain these patterns? And why is the predicted pattern of larger seed size in dioecious species not found among the tree species at either site?

The distribution of seed size in the two communities is different (Figs 2 and 3). There are many more smaller-seeded shrubs at Tambopata than Yasuní. The species that make up the forest communities from which seed size was sampled are also different (although half of the 15 largest-seeded species in each flora belong to the same four families: Arecaceae, Chrysobalanaceae, Fabaceae and Lecythidaceae; Table 4). For instance, *Cecropia* contributes six species to the Yasuní data set,

Table 4. A comparison of the 15 largest-seeded species in Yasuní, Ecuador (current study) and Tambopata, Peru (Vamosi *et al.* 2008). Note that the units are different for the two floras. Code abbreviations: BS = breeding system, GF = growth form. The same four families (in bold) are disproportionately represented among the largest-seeded species in both floras

Forest	Family	Genus	Species	BS	GF	Seed size
Yasuní, Ecuador						Mass (mg)
	Arecaceae	<i>Attalea</i>	<i>insignis</i>	M	Tree	38.00
	Lecythidaceae	<i>Grias</i>	<i>neuberthii</i>	H	Tree	31.00
	Chrysobalanaceae	<i>Licania</i>	<i>longipedicellata</i>	H	Tree	29.21
	Arecaceae	<i>Astrocaryum</i>	<i>chambira</i>	M	Tree	26.98
	Humiriaceae	<i>Vantanea</i>	<i>guianensis</i>	H	Tree	25.05
	Myrtaceae	<i>Eugenia</i>	<i>granvariable</i>	H	Tree	20.05
	Arecaceae	<i>Phytelephas</i>	<i>temicaulis</i>	D	Tree	16.86
	Myristicaceae	<i>Compsoeura</i>	<i>capitellata</i>	D	Tree	16.61
	Arecaceae	<i>Astrocaryum</i>	<i>murumuru</i>	M	Tree	16.07
	Olacaceae	<i>Aptandra</i>	<i>tubicina</i>	H	Tree	15.22
	Fabaceae	<i>Swartzia</i>	<i>benthamiana</i>	H	Tree	13.50
	Fabaceae	<i>Brownea</i>	<i>lore</i>	H	Tree	13.23
	Arecaceae	<i>Mauritia</i>	<i>flexuosa</i>	D	Tree	13.06
	Fabaceae	<i>Zygia</i>	<i>schultzeona</i>	H	Tree	12.44
	Fabaceae	<i>Zygia</i>	<i>heteroneura</i>	H	Tree	11.52
Tambopata, Peru						Volume (mm ³)
	Icacinaceae	<i>Casimirella</i>	<i>ampla</i>	H	Liana	61 645.5
	Icacinaceae	<i>Calatola</i>	<i>venezuelana</i>	D	Tree	53 074.4
	Chrysobalanaceae	<i>Licania</i>	<i>unguiculata</i>	H	Tree	39 169.6
	Cucurbitaceae	<i>Fevillea</i>	<i>pedatifolia</i>	D	Liana	30 453.4
	Fabaceae	<i>Centrolobium</i>	sp.	H	Tree	30 411.7
	Arecaceae	<i>Phytelephas</i>	<i>macrocarpa</i>	D	Tree	23 888.7
	Caryocaraceae	<i>Caryocar</i>	<i>amygdaliforme</i>	H	Tree	19 671.9
	Euphorbiaceae	<i>Omphalea</i>	<i>diandra</i>	M	Liana	18 281.7
	Fabaceae	<i>Dipteryx</i>	<i>alata</i>	H	Tree	17 301.8
	Lecythidaceae	<i>Bertholletia</i>	<i>excelsa</i>	H	Tree	14 227.8
	Fabaceae	<i>Mucuna</i>	sp.	H	Liana	12 836.4
	Celastraceae	<i>Salacia</i>	<i>caloneura</i>	H	Liana	12 484.5
	Celastraceae	<i>Salacia</i>	<i>spectabilis</i>	H	Tree	11 977.4
	Anacardiaceae	<i>Poupartia</i>	<i>amazonica</i>	D	Tree	9132.8
	Fabaceae	<i>Dioclea</i>	<i>glabra</i>	H	Liana	8237.4

all of which are dioecious and have seeds < 0.005 g. There are no *Cecropia* species among the sampled species from Tambopata. Conversely, monoecious figs contribute 15 species to the Tambopata data, and have seeds < 1.6 mm³, whereas there is only one *Ficus* present in the Yasuni data.

OTHER POTENTIAL COMPENSATORY FITNESS ADVANTAGES OF DIOECIOUS SPECIES

Although we found limited evidence of an increase in seed size associated with an evolutionary divergence between cosexuality and dioecy, the amount of variation in seed mass explained by breeding system, growth form and WSG was low ($R^2 < 0.10$ in most models, Tables 2 and 4), hence other mechanisms are likely to confer fitness advantages and enable dioecious species to persist in the face of competition with cosexual species. These mechanisms may include higher fecundity, higher rates of offspring recruitment, more frequent reproduction or higher quality offspring (with higher rates of survivorship). In most cases, such advantages are assumptions in models investigating the evolutionary ecology of dioecious lineages (e.g. Charlesworth & Charlesworth 1978; Heilbut *et al.* 2001; Barot & Gignoux 2004; Vamosi *et al.* 2007). It is likely that, in most cases, a combination of traits will be involved. This prediction is based on two large-scale patterns reported for dioecious lineages. First, despite the relative rarity of dioecy among angiosperms, there are well-documented associations between dioecy and a number of ecological/life-history traits (reviewed by Renner & Ricklefs 1995), including a tropical distribution (Bawa 1980; Vamosi *et al.* 2003), fleshy fruits (Givnish 1980), plain flowers (Bawa 1980) and woody and climbing growth forms (Freeman *et al.* 1980; Vamosi *et al.* 2008). Secondly, focusing on the evolutionary success (i.e. relative species richness, scaled to that of its non-dioecious sister group) of dioecious lineages, Vamosi & Vamosi (2004) demonstrated that lineages that possessed three or four of the aforementioned correlates were more common and tended to have higher evolutionary success than those with two or fewer traits. Furthermore, particular combinations of traits (e.g. woody lineages with plain flowers but dry fruits) had higher evolutionary success than lineages with the same number of correlated traits, but in different combinations (e.g. woody lineages with fleshy fruits but showy flowers). Therefore, it is plausible that, for example, large seed size (and/or some associated but unstudied trait[s]) may compensate for some of the disadvantages of dioecy in certain forests (e.g. Carpenter *et al.* 2003; Vamosi *et al.* 2008), but not in other forests (e.g. the current study). Although there is evidence that differences in ecological traits do aid in the co-existence of many hundreds of species (Engelbrecht *et al.* 2007; John *et al.* 2007; Kraft *et al.* 2008), frequency-dependence (Queenborough *et al.* 2007b; Comita & Hubbell 2009), neutral population dynamics and dispersal limitation (Hubbell 2001) suggest that these differences are not necessarily essential.

In conclusion we have found no evidence of greater seed mass in dioecious species compared to their cosexual counterparts in the forest at Yasuni. Because trees and shrubs are

longer-lived than herbs and therefore have more reproductive episodes over which to maximize fecundity, and due to physical and physiological constraints of the environment, an evolutionary increase in seed size associated with a change in breeding system may be less likely to occur in woody species (Vamosi *et al.* 2008). Other fitness advantages, such as lower rates of inbreeding, increased seed production, greater dispersal distances (Vamosi *et al.* 2007) and elevated seedling survival (e.g. through the production of better-defended seeds) may represent alternative life-history adaptations that enable dioecious tropical tree populations to persist.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Weighted mean seed size for Yasuní species.

Fig. S2. Mean abundance of Yasuní species by breeding system.

Table S1. Seed mass by growth form and breeding system in Yasuní species.

Table S2. Effect of seed mass on abundance in Yasuní species.

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