

Lower Species Richness in Dioecious Clades

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ABSTRACT: Despite the extensive research on the potential benefits of dioecy to individuals, little is known about the long-term success of dioecious lineages in relation to their hermaphroditic or monoecious relatives. This study reports on the evolutionary success of worldwide dioecious flora in light of recent phylogenetic work by performing sister-group comparisons of species richness between clades of angiosperms with different breeding systems. Whether this analysis is performed at the family or genus level, species richness is generally far lower in dioecious taxa when compared to their hermaphroditic or monoecious sister taxa. Despite the advantages of avoiding inbreeding depression and of allocating resources separately to male and female function, dioecy in angiosperms does not appear to be a key innovation promoting evolutionary radiation. A potential explanation for the low representation of dioecious lineages is that dioecious plants may have lower colonization rates. Baker's Law states that self-compatible lineages will have higher rates of successful long-range dispersal since they do not require a mate; consequently, self-compatible lineages may have higher rates of allopatric speciation. However, identical analyses performed with hermaphroditic self-incompatible angiosperms did not produce similar results, suggesting that Baker's law is not the reason for the poor representation of dioecy among angiosperm species.

Keywords: Baker's law, dioecy, extinction, sister-group comparison, speciation.

Dioecy, the separation of male and female function into separate individuals, is taxonomically distributed among most of the major orders of angiosperms, both primitive and advanced (Thomson and Barrett 1981). Although there has been considerable discussion regarding the evolutionary forces leading to dioecy in plants (e.g., Carlquist 1966, 1974; Bawa 1980; Thomson and Brunet 1990), little work has been done to determine whether dioecy is a beneficial evolutionary strategy. Dioecy is hypothesized to

have evolved as a mechanism to reduce inbreeding (Baker 1959; Carlquist 1966, 1974; Charlesworth and Charlesworth 1978) and/or to improve resource allocation (Bawa 1980; Givnish 1980). Various authors (Baker 1959; Williams 1975) have argued that dioecy is an easier route to outbreeding, both genetically and physiologically, and empirical evidence suggests that it is a more efficient means of avoiding inbreeding than gametophytic self-incompatibility (Anderson and Stebbins 1984). As well, theoretical studies show that plants carrying a mutation conferring male or female sterility can be favored in a hermaphroditic population (Charnov 1982) when a division of labor into males and females allows each individual to fulfill its roles more efficiently.

Despite the many possible advantages of dioecy, dioecious flora comprise only ~6% of the world's angiosperms (Renner and Ricklefs 1995). The low representation of dioecy is consequently a puzzle and might be caused by dioecious species experiencing a higher extinction rate, lower speciation rate, high reversion rates back to the monomorphic state (Richards 1997), or low origination rates. A possible explanation for the low representation of dioecy might be that a recent environmental shift has favored the evolution of dioecy so that dioecious groups are fairly young but not necessarily speciating or going extinct at different rates. This explanation would agree with the commonly held belief that dioecy occurs mostly on the tips of phylogenetic trees as they "are usually more closely related to hermaphrodite species within their own genus or family than they are to each other" (Lebel-Hardenack and Grant 1997, p. 130.). This study is the first to examine whether the infrequent occurrence of dioecy among angiosperms is due to a series of recent adaptations that arise on the tips of trees. Using phylogenetic evidence, I performed sister-group comparisons of species richness using clades that are entirely or mostly dimorphic (those with dioecious, polygamodioecious, gynodioecious, or subdioecious breeding systems; see table 1 for terms) as the focal group and monomorphic lineages (those with bisexual, monoecious, andromonoecious, gynomonoecious, or polygamomonoecious breeding systems) as the sister group to identify whether dioecious clades are more or less species rich than their hermaphroditic sister taxa. A

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sister-group comparison (fig. 1) uses a phylogeny to determine the difference in number of species between a focal group (in this case, a dimorphic clade) and its sister group (a monomorphic clade). If dioecy is a recent adaptation, then both the dimorphic and the monomorphic clades in the sister-group comparison should be small but equally species rich. These sister-group comparisons were performed at the family and generic levels and, at both levels of analysis, dioecious clades were found to be far less species rich than their nondioecious sister groups, indicating that dioecious lineages have lower speciation rates and/or higher extinction rates.

The possibility that dioecious lineages experience lowered speciation rates is consistent with Baker's law (Baker 1953), which states that a self-compatible hermaphrodite will be a better colonizer than a dioecious plant owing to the fact that it does not need a mate. Long-range dispersers can found new populations that may diverge and form new species allopatrically. If dioecious populations accomplish this long-range dispersal less often than hermaphroditic populations, it could potentially lead to a lower speciation rate among dioecious clades. To examine this possibility, I have again used the sister-group comparison approach, this time using self-incompatible taxa as the focal group against self-compatible sister taxa. Self-incompatibility is achieved in approximately half of the non-dioecious angiosperms through a variety of morphological (e.g., heterostyly) and molecular (e.g., gametophytic and sporophytic self-incompatibility) means. Self-incompatible species are subject to the same difficulties as dioecious ones when dispersing to a new area where mates may be either nonexistent or in short supply. If Baker's law plays a large role in determining diversification rates, these incompatible groups should also show lowered species richness than dioecious clades do when examined phylogenetically using the same methods. However, this study found no evidence for this as the self-incompatible lineages

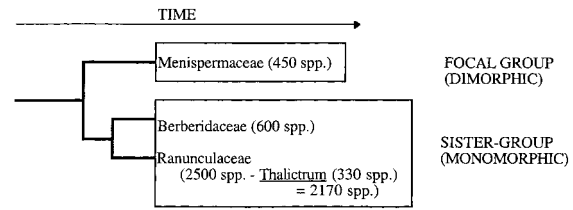


Figure 1: A sister-group comparison. Focal group and sister group have existed for the same amount of time (i.e., since their divergence from a common ancestor) and, hence, should have equal numbers of species on average unless the trait in question (here, dimorphic breeding system) has a direct or indirect effect on speciation and/or extinction rates.

were as species rich as their sister groups, implying that Baker's law is not a large factor in determining divergence rates.

The evidence gained in this study agrees with studies done on local flora, such as that on the Hawaiian flora (Sakai et al. 1995a), which suggest that Baker's law does not reduce the amount of dioecious colonizers. In fact, Sakai et al. (1995b) found that the high proportion of dioecious flora in Hawaii is due in part to a disproportionately high (~10%) percentage of dioecious colonizers. However, our results do differ from those of Sakai et al. (1995b) in that their comparisons of lineage size in the Hawaiian Islands show no trend for higher extinction rates or lower speciation rates: dimorphic genera are as species rich as monomorphic genera. Several factors may contribute to dioecy being relatively more successful on the Hawaiian Islands. The prevalence of dioecy has been shown to be correlated with tropical environments (Renner and Ricklefs 1995), a correlation that may result from dioecious species having higher speciation rates or lower extinction rates in tropical environments. Furthermore, the numbers of dimorphic and monomorphic species on

Table 1: Quick reference for breeding systems in angiosperms

Breeding system	Definition
Dimorphism:	
Dioecy	Male and female plants
Gynodioecy	Hermaphroditic and female plants
Androdioecy	Hermaphroditic and male plants
Subdioecy	Hermaphroditic, male, and female plants
Polygamodioecy	Synonymous with subdioecy
Monomorphism:	
Hermaphroditism	Bisexual flowers
Monoecy	Male and female flowers on each plant
Andromonoecy	Male and bisexual flowers on each plant
Gynomonoecy	Female and bisexual flowers on each plant
Polygamomonoecy	Male and/or female and bisexual flowers on each plant
Polygamous	Polygamomonoecious and/or polygamodioecious

Hawaii may not reflect long-term expectations given the relatively recent (maximum 5.7 MYA; MacDonald et al. 1983) nature of the present-day islands. For example, dioecious plants may be more successful in species-poor habitats. As well, Sakai et al. (1995b) did not employ the sister-group comparison approach and, therefore, did not control for the ages of the lineages compared.

The distribution of the dioecious families included in this study spanned all 15 of the major subclasses of angiosperms (Takhtajan 1997) with the exception of Triurididae, which has no dimorphic family representatives. The analysis at the genus level also spans 10 of the 15 subclasses. The subclasses Triurididae, Alismatidae, Lamiidae, Ranunculidae, and Magnoliidae either have no dioecious genera or have dioecious representatives that could not be found on any published phylogeny. This survey of worldwide lineages gives us a better idea of when and where dioecy is a successful breeding system strategy. Using the sister-group comparison approach controls for the age of the lineages since sister groups are, by definition, the same age, and the trait in question (i.e., dioecy) is assumed to have evolved only once. As a final control for the possibility that the lower species richness found in dioecious clades may be an artifact of the methods used in this study or other taxonomic biases, the results of an additional set of sister-group comparisons using clades of angiosperms with monoecious breeding systems as the focal group were performed. Sister-group comparisons at the genus level with only monoecious focal groups revealed no trend for lowered species richness. Monoecy, where male and female organs are separated on different flowers on the same plant, is represented in ~5% of angiosperms and is an adaptation thought to reduce inbreeding (Richards 1997). As monoecy is as unique and morphologically distinct as dioecy, these sister-group comparisons can be used to assess the bias that may occur in systematic studies, which may bestow unique family or genus status to a group that shares an unusual breeding system. The results of the monoecious sister-group comparisons also clarify the causes of the low representation of dioecy, as monoecy and dioecy share some of the same ecological correlates as well as other features involved in having unisexual flowers. I conclude that the low species richness observed in dioecious clades is likely caused by factors that are unique to dioecy alone and not factors shared by both monoecious and dioecious species.

Methods

Family-Level Data Collection

Families in which the breeding system was defined as “mostly” or “completely” monoecious or dioecious were

found by referring to Takhtajan (1997). When this source was ambiguous, other sources were found, usually that given on the DELTA Web site (Watson and Dallwitz 1992) or in Judd et al. (1999). In the dioecious sister-group comparison, bisexual, monoecious, polygamomonoecious, and gynomonoecious were considered equivalent monomorphic species while dioecious, polygamodioecious, gynodioecious, and subdioecious species were considered dimorphic species following the system developed by Lloyd (1980). Species described as polygamous were omitted. For the self-incompatible (SI) comparisons, information regarding the outbreeding status of a plant species is not as readily available as its sexual status (i.e., dioecious, monoecious, or hermaphrodite) because outbreeding status can depend on chemical as well as morphological attributes. Finding families in which all or most of the members have some form of self-incompatibility (be it from gametophytic or sporophytic self-incompatibility, dichogamy, or heterostyly) was accomplished by referring to Judd et al. (1999). Monoecious families that were reported to be non-selfing due to dichogamy were also included in this analysis as not enough of them were found to warrant a separate sister-group comparison at the family level. Because Judd et al. (1999) covers only the major families of angiosperms, other reviews on self-incompatibility (Fryxell 1957; Charlesworth 1985) and heterostyly (Ganders 1979) were checked so as not to bias the comparisons in favor of large, major angiosperm families. These extra sources of information revealed Eupomatiaceae, Plumbaginaceae, Hypericaceae, Resedaceae, and Valerianaceae as additional SI focal groups.

The majority of families used in the analysis were found on the new multigene phylogeny created by Soltis et al. (1999). The dioecious families Physenaceae (Morton et al. 1997), Achatocarpaceae (Brown and Varadarjan 1985), Gyrostemonaceae (Rodman et al. 1996), Nolinaceae, and Didieraceae (Rice et al. 1997), which were not included in the phylogeny of Soltis et al. (1999), were found on other existing phylogenies to guard against any biases that might arise from their exclusion. Sister-group comparisons entailed comparing the number of species in the focal clade (e.g., dimorphic groups) to the number of species in the sister group (fig. 1). When the number of species in a family was given as a range, the average between the lowest possible number of species and highest number of species was used.

Commonly, the sister groups of the dimorphic families were families that included some dimorphic members. When this problem was encountered, I used a protocol similar to that of Farrell et al. (1991); the number of species reported for the sister group was the total number of species minus the number of dimorphic species within that family. Because the sister groups to dimorphic clades

tended to be more species rich, this procedure led to a conservative estimate of the number of species in the sister group. For example, the family Ranunculaceae is in the sister-group comparison for the dioecious family Menispermaceae. Ranunculaceae has 2,500 species, all of which are hermaphroditic, with the exception of a few in the genus *Thalictrum* (which has 330 species). Therefore, 2,170 [2,500 – 330 = 2,170] was the number of species reported for the family Ranunculaceae. The reciprocal procedure (subtracting monomorphic species from dimorphic clades) was not performed on the focal group since this would have increased the significance of the results. In the SI sister-group comparison, however, it became clear that the self-incompatible groups were more often larger than their sister groups, and hence the conservative approach was the opposite, with any known self-compatible genera being subtracted from the largely self-incompatible focal groups.

Further complications arose as a result of unresolved relationships and paraphyletic groupings on the consensus tree of Soltis et al. (1999). The protocol for unresolved relationships was to only include the family if any sister-group comparison made between the focal group and any other member of the polytomy resulted in the same sign (e.g., Phellinaceae, table 2). In the few cases where paraphyly was indicated for the sister group, the group reported as sister to the focal group consisted only of those genera listed in the phylogeny (e.g., Salicaceae, table 2).

Genus-Level Data Collection

In most respects, the genus-level analysis was identical to the family-level analysis with the addition of monoecious genera (including genera that are andromonoecious, gynomonocious, and polygamomonocious) as the focal groups in a new set of sister-group comparisons (see appendix). Phylogenies that used molecular, morphological, or a mixture of both types of data were collected from the literature. If the literature article contained a number of different types of phylogenies, all showing slight differences in the relationships of its members, the strict consensus cladogram was preferred. Phylogenies for all three sets of sister-group comparisons (i.e., dioecious, SI, and monoecious) were found through independent literature searches, but some phylogenies are used in more than one set of sister-group comparisons.

The breeding system status of genera was found by referring to Yampolsky and Yampolsky (1922), Hutchinson (1964), and Heywood (1981). Care was taken to confirm the breeding system status of genera by referring to more recent sources, such as Uhl and Dransfield (1987; for Araceae), a database used by Weller et al. (1995), Jarvie and Ermayanti (1996), and Mabberley (1997). These efforts

resulted in >90% of the genera (and 100% of the dioecious focal genera) used in this study being confirmed in regards to their breeding system by very recent sources. Self-incompatible genera were identified from the compilations in Fryxell (1957), Ganders (1979), Charlesworth (1985), Watson and Dallwitz (1992; for Poaceae only), and Weller's database (Weller et al. 1995). The number of species reported in each genera were taken from Mabberley (1997) unless more up-to-date information could be found in Judd et al. (1999).

Phylogenies were accepted or rejected for sister-group analysis based on their completeness for the genus in question and its relatives. Phylogenies that are absolutely complete for all the genera in a family are rare. Therefore, all the sister groups reported in this study may not reflect the true relationships among the genera. Phylogenetic inaccuracies should tend to randomize the size of the sister group in comparison to the focal group. Nevertheless, there might be biases such that focal groups tend to be smaller in size than their sister groups as a result of the methods employed. The analyses with self-incompatible and monoecious plants as focal groups suggest that such biases are not strong. To minimize such inaccuracies, phylogenies were used only if they reported sister groups that were in the same taxonomic order. Exceptions were made to this rule, however, when the sister-group comparison involved an order that consisted of only one genus. In this case, the sister group to this genus is inevitably a member of another order. Similarly, there are many families of angiosperms that contain only one genus. If this was the case, then the sister-group comparison was made with the nearest clade, which would consist of another family. As the family-level analysis would also include these families (or orders) with only one genus, the family- and genus-level analyses should not be considered as completely independent. The family- and genus-level analyses were kept separate, instead of combined, to show that the pattern of lowered species richness can be seen at more than one taxonomic level.

Occasionally, a genus could be found on more than one phylogeny. If this was the case, the phylogeny that was most complete for the family to which that genus belonged was used. If both phylogenies were equally complete and gave opposite results as to whether the sister group was larger or smaller, then both sister-group comparisons were listed. If the two phylogenies gave the same result, then only one was listed. In a few rare cases, the genus was listed in more than two phylogenies with different sister groups in each, giving a mix of positive and negative results. When this was the case, the relationships of the genus were deemed too undefined for analysis, and the group was omitted from the data set.

As in the family-level sister-group comparison, careful

Table 2: Sister-group comparisons for dimorphic families

Dioecious clade	No.	Nondioecious clade	No.	+/-
Aextoxicaceae	1	Berberidopsidaceae	7,000	-
Amborellaceae	1	Eumagonliids (>5,000) + Nymphaeaceae (70) + Austrobaileyaceae(1) + Schisandraceae (50)	>5,000	-
Anacardiaceae (600) + Burseraceae (550)	1,150	Sapindaceae (2,139) + Simaroubaceae (26) + Meliaceae (896) + Rutaceae (1,555)	4,616	-
Balanopaceae	9	Chrysobalanaceae (495) + Dichapetalaceae (180) + Trigoniaceae (26)	701	-
Barbeyaceae	1	Elaeagnaceae	44	-
Cannabaceae	4	<i>Trema</i> (12) or <i>Celtis</i> (100) of Celtidaceae	≥12	-
Didiereaceae	11	Portulacaceae	450	-
Didymelaceae	2	Buxaceae	70	-
Dioscoreaceae	650	Taccaceae	13	+
Garryaceae (13) + Aucubaceae (1) + Eucommiaceae (1)	15	<i>Icacina</i> of Icacinaceae	6	+
Griselinaceae	6	Melanophyllaceae (<i>Melanophylla</i> alone [8]) or Apiaceae (3,048) + Araliaceae (1,089) + Pittosporaceae (246)	≥8	-
Gyrostemonaceae	17	Resedaceae	80	-
Helwingiaceae (5) + Aquifoliaceae (400)	405	Phyllonomaceae	4	+
Heteropyxidaceae	3	Vochysiaceae	200	-
Menispermaceae	450	Berberidaceae (600) + Ranunculaceae (2,170)	2,770	-
Montiniaceae	4	Hydroleaceae (<i>Hydrolea</i> alone)	11	-
Myricaceae	50	Juglandaceae	53	-
Myristicaceae	370	Annonaceae (2,395) + Eupomatiaceae (2) + Magnoliaceae (238) + Himantandraceae (2) + Degeneriaceae(2)	2,639	-
Myrothamnaceae	2	Gunneraceae	40	-
Nolinaceae	50	Ruscaceae	6	+
Nyssaceae ^{a,b}	7	Cornaceae (47) or Loasaceae (300)	≥47	-
Pandanaceae	700	Cyclanthaceae	235	+
Phellinaceae	10	Alseuosmiaceae (12) or Argophyllaceae (11) or Menyanthaceae (60) or Calyceraceae (50) + Goodeniaceae (420) or Asteraceae (23,000)	≥11	-
Physenaceae	2	Asteropeiaceae	5	-
Restionaceae	400	Poaceae	5,772	-
Salicaceae	400	<i>Flacourtia</i> (60) + <i>Abatia</i> (12) of Flacourtiaceae	72	+
Simmondsiaceae	1	Asteropeiaceae (5) + Caryophyllaceae (1,478) + Amaranthaceae (813) + Molluginaceae (120) + Portulacaceae (424) + Cactaceae (500) + Nyctaginaceae (359) + Phytolaccaceae (30) + Aizoaceae (2,414)	6,143	-
Tetramelaceae	2	Cucurbitaceae (391) or Begoniaceae (950) or Coriariaceae (18) + Corynocarpaceae (13)	≥31	-

Note: The number given for the nondioecious families in the sister clade have been corrected against bias by subtracting the number of dioecious members in the family from the total (detailed information regarding these calculations can be obtained from the author). All the focal groups here are entirely or mostly dioecious with the exception of Nyssaceae. The final column states the outcome of the sister-group comparison; + indicates the dimorphic clade had more species; - indicates the monomorphic clade had more species.

^a Dioecious.

^b Some polygamodioecious members.

attention was paid to ensure that the number of species reported for the sister group was not artificially inflated because of the inclusion of dimorphic members. If the sister group contained dimorphic members, the number of dimorphic species was determined and subtracted from the total number of species reported for the sister group. To be conservative, monomorphic species were not excluded from the focal group. Occasionally, a sister-group comparison engulfed a smaller sister group within it. In these cases, both the species contained within the focal group and the sister group of the smaller sister-group comparison were removed from the analysis of the larger sister-group comparison.

Statistical Analysis

All species richness values were tabulated for the focal dimorphic groups and their corresponding sister groups (see tables 2, 3; appendix). Two-tailed sign tests were performed to see whether the proportion of dimorphic groups that have higher species richness values were significantly

different from one half as one would expect if equivalent processes were governing species richness values in the focal and sister groups. The sign test was chosen over other statistical tests available for analyzing key innovations (i.e., signed-ranks test [Wiegmann et al. 1993], randomization test for matched pairs [Barraclough et al. 1995], and the Slowinski-Guyer test [Slowinski and Guyer 1993]) both because its lack of power makes it the most conservative test available (see De Queiroz 1998 for discussion) and because the other tests require more exact information on the numbers of species in each group. As well, Fisher's exact tests were performed to determine whether the proportion of self-incompatible or monoecious clades having higher species diversity values was significantly different from that obtained in the sister-group comparisons using dimorphic clades.

Results

Family-Level Analysis

The results of all the sister-group comparisons and statistical analyses are presented in table 4. Dimorphic clades

Table 3: Obligate outbreeders and their sister taxa

Self-incompatible family	No.	Self-compatible clade	No.	+/-
Betulaceae	85	Casuarinaceae	96	-
Cactaceae	1,300	Portulacaceae	950	+
Caryophyllaceae	1,527	Amaranthaceae	1,000	+
Cyperaceae	5,168	Juncaceae	355	+
Eupomatiaceae	2	Annonaceae	2,400	-
Gentianaceae	1,176	Loganiaceae	15	+
Geraniaceae	450	Vivianiaceae (6) or Greyiaceae (3) + Francoaceae (2) + Melianthaceae (14)	≤19	+
Hypericaceae	550	Podostemaceae	275	+
Illiciaceae	42	Schisandraceae	50	-
Juglandaceae	60	Myricaceae	50	+
Lythraceae	600	Onagraceae	680	-
Malvaceae	1,205	Sarcolaenaceae (62) + Dipterocarpaceae (700) + Cistaceae (200) + Tiliaceae (450) or Thymelaeaceae (700) or Bixaceae (4) or Neuradaceae (10)	≤962	+
Myrsinaceae	1,000	Primulaceae (1,000) + Theophrastaceae (110)	1,110	-
Orchidaceae	18,457	Blandfordiaceae (4) or Anthericaceae (575) or Asteliaceae (35) or Hypoxidaceae (220) or Asparagales (families totaling ~5,216 spp.)	≤5,216	+
Oxalidaceae	700	Cunoniaceae (250) + Elaeocarpaceae (325) + Tremandraceae (43)	618	+
Passifloraceae	600	Malesherbiaceae (35) + Turneraceae (150)	185	+
Plumbaginaceae	650	Polygonaceae	1,100	-
Platanaceae	10	Proteaceae	1,050	-
Resedaceae	80	Brassicaceae	3,200	-
Rutaceae	1,366	Meliaceae (1,300) or Simaroubaceae (100)	≤1,300	+
Valerianaceae	400	Linnaeaceae (250) + Caprifoliaceae (260) + Dipsacaceae (300)	810	-
Winteraceae	80	Canellaceae	16	+

Note: The number of species given for the self-incompatible families in the focal group have been corrected against bias by subtracting the number of self-compatible members in the family from the total (detailed information regarding these calculations can be obtained from the author). For a description of +/-, see table 2.

Table 4: Summary of the different sister-group comparisons performed and their results

	Family level			Genus level		
	Results	Different from half (<i>P</i> value)	Different from DSGC (<i>P</i> value)	Result	Different from half (<i>P</i> value)	Different from DSGC (<i>P</i> value)
Consensus tree:						
Dioecious (DSGC)	6/28	.007	...	22/66	.009	...
Monoecious	27/50	.672	.037
Self-incompatible	13/22	.524	.009	29/56	.894	.045
Shortest tree:						
Dioecious	7/36	.0003
Monoecious	9/16	.804	.020
Self-incompatible	17/32	.860	.005

Note: The results show the proportion of times that the focal group in question was more species rich than its sister group. The result is analyzed with respect to how different it is from the one-half expected due to random processes using a binomial test (see "Methods") and how different the result is from the dioecious sister-group comparison (DSGC) using the Fisher-exact test (where applicable).

were far less species rich than their sister taxa. Of the 28 families included within molecular phylogenies (table 2), only six were more species rich than their sister taxa ($P = .0071$; two-tailed sign test); this fraction is much less than the half expected if there was no difference in speciation or extinction rates between dimorphic and monomorphic lineages. If the shortest tree of Soltis et al. (1999) is used instead of the consensus tree, several more relationships are resolved and the results become even more convincing, with only seven out of 36 sister-group comparisons showing larger lineage size in the dimorphic clade (data not shown).

By contrast, obligate outbreeders did not have significantly different species richness values than their selfing sister groups overall. Of the 22 sister-group comparisons performed, the self-incompatible group was more species rich than its self-compatible sister group in 13 cases ($P = .524$; two-tailed sign test), which is not significantly different from the expectation of no difference in speciation or extinction rates between self-incompatible and self-compatible flora. The number of self-incompatible families with higher species diversity values was, however, significantly greater than the proportion of dioecious families with higher species richness ($P = .009$; two-tailed Fisher's exact test). If the shortest tree of Soltis et al. (1999) is used instead of the consensus tree, the results are much the same, with 17 out of 32 comparisons showing the self-incompatible group to be more species rich, which is again not significantly different from one-half ($P = .860$; two-tailed sign test) but is significantly different from the number of dioecious families that have higher species richness ($P = .005$; two-tailed Fisher's exact test). The shortest tree also resolved a few additional monoecious families, which enabled a separate sister-group comparison to be performed. Nine out of 16 comparisons (data not shown) showed the monoecious focal group to be more species

rich than its sister group, which is not significantly different from one-half ($P = .804$; two-tailed sign test) and is significantly different from that found in the dioecious sister-group comparison ($P = .020$; two-tailed Fisher's exact test). Although these results are dependent on the accuracy of the phylogeny, I feel our results are robust, as a similar test using a different phylogeny (i.e., Chase et al. 1993) gave similar results.

Genus-Level Analysis

The lowered species richness of dioecious clades is also reflected at the genus level. Out of 66 sister-group comparisons (appendix), only 22 showed the dimorphic clade to be more species rich than its sister group, which is significantly less than expected ($P = .009$; two-tailed sign test). As can be seen in table 2 and the appendix, the conditions of gynodioecy, androdioecy, polygamodioecy, and subdioecy are relatively rare so this result mainly reflects attributes of dioecious clades. In contrast to the results of the sister-group comparison with dimorphic genera, the self-incompatible genera seem to be as species rich as their self-compatible sister groups on average. In 56 sister-group comparisons, 29 showed the self-incompatible group to have greater species richness ($P = .894$; two-tailed sign test). As in the family-level analysis, this is significantly different from the proportion of dimorphic genera found to have more species than their sister groups ($P = .045$; Fisher's two-tailed exact test).

The uniqueness of the low species richness associated with dioecy is further demonstrated by a sister-group comparison done using monoecious genera. The nonmonoecious genera used as the sister groups were predominantly hermaphroditic although some comparisons were between monoecious and dioecious genera. Out of the 50 sister-group comparisons between monoecious and nonmon-

oecious genera, 27 showed the monoecious sister group to be more species rich ($P = .672$; two-tailed sign test), which is not different from what is expected. This was again significantly different from what was found in the dimorphic genera sister-group comparison (.037; Fisher's two-tailed exact test). Even if only the comparisons with hermaphroditic sister groups are used in the analysis, the results are much the same, with 21 out of 41 comparisons showing the monoecious clade to be larger than its sister group ($P = .875$; two-tailed sign test), which results in a marginally significant difference from the dioecious sister-group comparison ($P = .067$; Fisher's two-tailed exact test).

Discussion

Key innovations are expected to correlate with a radiation in the number and variety of species (Farrell et al. 1991; Hodges and Arnold 1994). Although there is some evidence that the combination of dioecy and animal-dispersed seeds leads to increased species diversity in non-angiosperms (Donoghue 1989), this does not seem to be the case with dioecy in angiosperms. Our results demonstrate that dioecious groups are less species rich than their sister groups and, therefore, must have higher rates of extinction and/or lower rates of speciation due to particular constraints involved with the dioecious condition. Among the 28 family sister-group comparisons, 22 showed the dimorphic lineage to have a lower species richness. This was further exemplified at the genus level, where 44 of the 66 sister-group comparisons showed the dimorphic lineage to have a lower species richness.

One potential cause of the difference in lineage size between dimorphic and monomorphic clades could be due to different colonization abilities of dimorphic and monomorphic plants. According to Baker's law (Baker 1953), self-compatible hermaphroditic plants are better colonizers because of the fact that a single propagule can found a population. If this population receives little to no gene flow from the ancestral population, a new species may form allopatrically. It is not known how often new allopatric populations are founded by single individuals in nature or to what extent dioecious populations have evolved compensatory mechanisms in order to accomplish an equivalent amount of long-range dispersal (e.g., animal-dispersed fruit containing seeds of both sexes or "leaky" dioecious systems that allow for selfing under certain environmental conditions (Baker and Cox 1984). Furthermore, approximately half (Thomson and Barrett 1981) of the nondioecious angiosperms are unable to self owing to a number of self-incompatibility mechanisms (gametophytic self-incompatibility in Solanaceae, Legumaceae, Liliaceae, and Poaceae; sporophytic self-incompatibility in

Brassicaceae and Asteraceae; protoandry or protogyny in Juglandaceae and Araceae; and heterostyly in Rubiaceae). Self-incompatible species ought to be at a similar disadvantage when colonizing as dioecious species as they too need an individual of the opposite mating type.

The existence of self-incompatible taxa provides a way to test the extent to which Baker's law explains the disparity in lineage size between dimorphic and monomorphic lineages. Sister-group comparisons using focal groups that are predominantly self-incompatible did not show any tendency to be either larger or smaller than their sister groups and produced results that were significantly different from the results with the dimorphic focal groups at both the family ($P = .009$; two-tailed Fisher's exact test) and genus level ($P = .045$; two-tailed Fisher's exact test). The fact that the pattern of low species richness is not continued with other groups that experience the same difficulties in regards to colonization (i.e., needing a mate) indicates that the difference seen between dimorphic and monomorphic lineage size cannot simply be explained by the fact that dimorphic lineages are unable to self.

If Baker's law is not the reason why dioecy is correlated with small lineage size, the question of why dioecious lineages are so poorly represented remains a mystery. The possibility that these results could be due to the more readily bestowed assignment of separate genus or family status to plants with different breeding systems has been ruled out by the sister-group comparisons performed using monoecious focal groups (which were more species rich than their sister groups in 27 out of the 50 comparisons). This observation is useful as it forces us to look for factors that are unique to dioecy alone for clues as to what may cause the decreased species richness of dioecious clades. Renner and Ricklefs (1995) examined the worldwide distribution of dioecy and found correlations between dioecy and climbing growth form, biotic dispersal, abiotic pollination, and tropical distribution, which were also ecological correlates of monoecious species with the exception of tropical distribution. Interestingly, tropical climate has putatively been named as the cause of high diversity values of many angiosperm taxa (e.g., Qian and Ricklefs 1999), so one might think that the correlation of dioecy and tropical climate would result in higher species richness values for dioecious clades. It may be that dioecious angiosperms may go extinct at a faster rate in both temperate and tropical environments but that this process occurs less rapidly in tropical environments, which would explain both the low overall representation of dioecy and its higher prevalence in the Tropics. Understanding the relative speciation and extinction rates of dioecious groups in and out of the Tropics requires further investigation but may illuminate what environmental factors are necessary for a dioecious clade to persist and/or speciate.

Several other factors are unique to dioecy alone and provide avenues for future investigations into why the pattern of decreased speciation/increased extinction exists in dioecious clades. Extinction may be more common in dioecious clades since only half the population (the females) sets seed, and females may not be able to compensate for the loss. The amount by which a dioecious species suffers from this “cost of males” is only beginning to be understood (Lloyd and Webb 1977; Lloyd 1982; Pannell 1997; Richards 1997 and references therein). Furthermore, demes of dioecious plants may go extinct more often if they are segregated into small populations in which there are no members of the opposite sex (Pannell and Barrett 1998). The likelihood of this problem may increase when differences exist between the sexes in ecological tolerances (Meagher 1984, references therein). Investigations into resource allocation and demographic stochasticity questions like these have always been framed with regard to how they might contribute to the evolution of a dioecious breeding system. A change in the focus of studies to how they might affect a dioecious system that has already evolved may reveal how these factors could influence speciation and extinction rates. Recent work by Weller and Sakai (1999) and Weiblen et al. (2000) elucidates the strengths of phylogenetic approaches in providing new insights in both the evolution of, and causes of ecological correlations with, different breeding systems in angiosperms. It seems clear that phylogenetic approaches will be of use in studying how speciation and extinction rates are correlated with changes in breeding system as well.

This study gives evidence that dimorphic clades have fewer species on average than their monomorphic relatives

even when origination and reversion rates are controlled for. This analysis was performed on a wide range of angiosperm taxa and seems to be robust at both the family and genus levels. However, I am unable to determine whether dimorphic lineages go extinct at a more rapid pace or speciate at a slower one than their monomorphic relatives. There are many consequences to having a dioecious breeding system that may contribute to its lack of success, such as a possible decrease in seed set or different ecological tolerances between the sexes. Although the ability to self and the possibility of taxonomic bias have been shown to be less likely explanations for why the pattern of lowered species richness in dioecious clades may exist, further study using more complete phylogenies as they arise, along with more detailed studies within specific families, should illuminate where and when dioecy is a successful breeding system and, in doing so, clarify why dioecy is commonly an evolutionary dead end.

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APPENDIX

Table A1: Genus-level differences in species diversity

Order/genera	No.	Sister group	No.	+/-	Reference ^a
Dioecious:					
Apiales:					
<i>Aciphylla</i> (39) + <i>Anisotome</i> (15)	54	<i>Ligusticum</i> (45) + <i>Lecokia</i> (1) + <i>Smyrniium</i> (7)	53	+	34
<i>Meryta</i>	30	<i>Munroidendron</i> (1) + <i>Tetraplasandra</i> (6)	7	+	6
Arecales:					
<i>Chamaerops</i>	1	<i>Cocos</i>	1	=	9
<i>Hyphaene</i> (10) + <i>Bismarkia</i> (1) + <i>Latania</i> (3) + <i>Lodoicea</i> (1) + <i>Borassodendron</i> (2) + <i>Bor-</i> <i>assus</i> (11)	28	<i>Nannorrhops</i>	1	+	26
<i>Kerridoxa</i>	1	<i>Chuniophoenix</i>	3	-	26
<i>Mauritiella</i>	14	<i>Nypa</i>	1	+	9
<i>Phoenix</i>	17	<i>Sabal</i> (16) + <i>Chelyocarpus</i> (4) + <i>Itaya</i> (1) + <i>Schippia</i> (1) + <i>Coccothrinax</i> (47) + <i>Zombia</i> (1)	70	-	26
<i>Phytelephas</i> (4) + <i>Ammandra</i> (2) + <i>Ravenea</i> (17) + <i>Oran-</i> <i>iopsis</i> (1) + <i>Ceroxylon</i> (15) + <i>Juania</i> (1)	40	<i>Wallichia</i> (7) + <i>Iriartea</i> (1) + <i>Manicaria</i> (4) + <i>Butia</i> (8) + <i>Allagoptera</i> (5) + <i>Euterpe</i> (30) + <i>Kentiopsis</i> (1) + <i>Podococcus</i> (1) + <i>Synechan-</i> <i>thus</i> (2) + <i>Gaussia</i> (4) + <i>Hyophorbe</i> (5) or <i>Colpotherinax</i> (2) + <i>Pritchardia</i> (25) + <i>Cop-</i> <i>ernicia</i> (25) + <i>Livistona</i> (28) + <i>Pholidocar-</i> <i>pus</i> (6) + <i>Johannesteijsmannia</i> (4) + <i>Licuala</i> (108) + <i>Brahea</i> (12) + <i>Washingtonia</i> (2) + <i>Acoelorrhaphe</i> (1) + <i>Corypha</i> (6) + <i>Chunio-</i> <i>phoenix</i> (3)	≥68	-	26
<i>Plectocomia</i> (16) + <i>Mauritia</i> (3)	19	Outgroup to all other Arecaceae on this phylogeny	≥68	-	26
<i>Trachycarpus</i>	4	<i>Trithrinax</i>	5	-	9
<i>Wendlandiella</i> (3) + <i>Chamaedo-</i> <i>rea</i> (100)	103	<i>Hyophorbe</i> (5) or <i>Gaussia</i> (4) or <i>Synechanthus</i> (2)	≤5	+	26
Asparagales:					
<i>Lomandra</i>	50	<i>Sowerbaea</i>	5	+	22
<i>Nolina</i> (30) ^{b,c} + <i>Calibanus</i> (1) + <i>Dasyilirion</i> (15) + <i>Beaucarnea</i> (1) ^{b,c}	47	<i>Dracaena</i> (60) + <i>Sansevieria</i> (100) + <i>Liriope</i> (5) + <i>Maianthemum</i> (27) + <i>Aspidistra</i> (16) + <i>Polygonatum</i> (55)	263	-	31
<i>Ruscus</i>	6	<i>Asparagus</i>	135	-	37
Asterales:					
<i>Antennaria</i>	71	<i>Gnaphalium</i> ^d	50	+	11
Begoniales:					
<i>Datisca</i> ^e	2	<i>Symbegonia</i> (14) + <i>Begonia</i> (900) + <i>Hillebran-</i> <i>dia</i> (1)	915	-	2
Butomales:					
<i>Vallisneria</i>	6	<i>Butomus</i>	1	+	22

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
Buxales:					
<i>Didymeles</i>	2	<i>Buxus</i> (50) + <i>Pachysandra</i> (3)	53	-	25
Capparales:					
<i>Carica</i> (23) + <i>Batis</i> (2)	25	<i>Floerkea</i> (1) + <i>Limnanthes</i> (7) + <i>Tovaria</i> (2) + <i>Capparis</i> (250) + <i>Reseda</i> (60) + <i>Brassica</i> (35)	355	-	43
<i>Hirschfeldia</i> ^f	2	<i>Erucastrum virgatum</i>	1	+	4
Caryophyllales:					
<i>Didierea</i> (2) + <i>Alluaudia</i> (6)	8	<i>Anredera</i> (12) or <i>Claytonia</i> (24)	≥12	-	32
<i>Spinacia</i>	4	<i>Chenopodium</i>	100	-	32
Cercidiphyllales:					
<i>Cercidiphyllum</i>	2	<i>Heuchera</i>	55	-	6
Coryales:					
<i>Ticodendron</i> ^{b,c}	1	<i>Betula</i> (35) + <i>Corylus</i> (10)	45	-	1
Cornales/Eucommiales:					
<i>Aralidium</i>	1	<i>Melanophylla</i>	8	-	6
<i>Garrya</i> (13) + <i>Aucuba</i> (14) + <i>Eucommia</i> (1)	28	<i>Nicotiana</i> (67) + <i>Borago</i> (3) + <i>Antirrhinum</i> (20) + <i>Gentiana</i> (361) + <i>Apocynum</i> (12) + <i>Gelsemium</i> (2)	465	-	6
<i>Nyssa</i> ^e	8	<i>Davidia</i> ^d	1	+	6
Cucurbitales:					
<i>Abobra</i>	1	<i>Corallocarpus</i> (13) or <i>Luffa</i> (6) or <i>Marah</i> (7)	≥6	-	2
Dioscoreales:					
<i>Dioscorea</i>	850	<i>Tacca</i>	10	+	22
Ericales:					
<i>Diospyros</i>	475	<i>Symplocos</i>	250	+	6
Euphorbiales:					
<i>Cheilosa</i> (1) + <i>Pimelodendron</i> (7)	8	<i>Falconeria</i> (1) + <i>Stillingia</i> (30) + <i>Sapium</i> (100) + <i>Gymnanthes</i> (15) + <i>Shirakia</i> (8) + <i>Triadica</i> (2) + <i>Excoecaria</i> (40) + <i>Sebastiania</i> (100) + <i>Microstacys</i> (17) + <i>Omalanthus</i> (35)	348	-	27
<i>Wetria</i> (1) + <i>Homonoia</i> (2)	3	<i>Lasiococca</i> (3) + <i>Spathiostemon</i> (3)	6	-	3
Griselinales:					
<i>Griselinia</i>	7	<i>Pittosporum</i>	150	-	7
Juncales:					
<i>Distichia</i> (3) + <i>Oxychloe</i> (7)	10	<i>Marsippospermum</i> (3) + <i>Rostkovia</i> (2)	5	+	21
Lardizabalales:					
<i>Sargentodoxa</i>	1	<i>Akebia</i>	2	-	24
Liliales:					
<i>Chamaelirium</i>	1	<i>Heloniopsis</i>	4	-	22
<i>Collospermum</i>	2	<i>Blandfordia</i> (4) + <i>Milligania</i> (5)	9	-	22
<i>Smilax</i>	300	<i>Ripogonum</i>	8	+	22
Malvales:					
<i>Byttneria</i>	132	<i>Kleinhovia</i>	1	+	42
<i>Carpodiptera</i>	8	<i>Berrya</i>	4	+	42
<i>Christiana</i>	2	<i>Berrya</i>	4	-	38
<i>Heliocarpus</i>	10	<i>Triumfetta</i>	70	-	42

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
Myrothamnales: <i>Myrothamnus</i>	2	<i>Gunnera</i>	40	—	25
Nepenthales: <i>Nepenthes</i>	82	<i>Dionaea</i> (1) + <i>Drosera</i> (110) + <i>Drosophyllum</i> (1) + <i>Triphyophyllum</i> (1) + <i>Ancistrocladus</i> (12)	125	—	33
Physenales: <i>Physena</i>	2	<i>Krameria</i> (15) + <i>Guaiacum</i> (6) + <i>Tribulus</i> (25)	46	—	40
Poales: <i>Distichlis</i>	5	<i>Eragrostis</i>	300	—	15
<i>Gynerium</i>	1	<i>Pennisetum</i> ^g (130) + <i>Cenchrus</i> (30) + <i>Neurachne</i> (6) + <i>Zea</i> (4) + <i>Sorghum</i> (24) + <i>Hyparrhenia</i> (55) + <i>Tristachya</i> (22)	271	—	17
Polygonales: <i>Triplaris</i>	18	<i>Eriogonum</i>	240	—	33
Primulales: <i>Clavija</i> ^{c,e,f}	50	<i>Theophrasta</i>	2	+	36
<i>Embelia</i> (100) + <i>Grenacheria</i> (10)	110	<i>Conomorpha</i> (124) + <i>Grammadenia</i> (11)	135	—	35
<i>Myrsine</i> (5) + <i>Rapanea</i> (136) + <i>Suttonia</i> (9)	150	<i>Pleioimeris</i>	1	+	35
<i>Wallenia</i> (25) + <i>Stylogyne</i> (60)	85	<i>Ardisia</i> (250) + <i>Parathesis</i> (84) + <i>Labisia</i> (6) + <i>Tapeinosperma</i> (4) + <i>Conandrium</i> (2) + <i>Solonia</i> (1)	347	—	35
Rosales: <i>Osteomeles</i>	3	<i>Cotoneaster</i> (261) + <i>Pyrus</i> (25) + <i>Malus</i> (55) + <i>Heteromeles</i> (1) + <i>Photinia</i> (65) + <i>Chaenomeles</i> (4) + <i>Sorbus</i> (193) + <i>Mespilus</i> (2) + <i>Crataegus</i> (186) + <i>Malacomeles</i> (3) + <i>Peraphyllum</i> (1) + <i>Amelanchier</i> (33)	829	—	19
Salvadorales: <i>Azima</i>	4	<i>Salvadora</i>	5	—	28
Santalales <i>Viscum</i> (65) + <i>Osyris</i> (7)	72	<i>Opilia</i>	2	+	24
Sapindales: <i>Bursera</i> ^f	50	<i>Commiphora</i>	190	—	8
<i>Dodonaea</i> (68) ^{c,e} + <i>Acer</i> (111) ^{c,e}	179	<i>Aesculus</i>	7	+	8
<i>Guarea</i>	40	<i>Trichilia</i> (84) + <i>Cipadessa</i> (1)	85	—	8
<i>Leitneria</i>	1	<i>Simaba</i>	14	—	8
<i>Ptaeroxylon</i> ^f	1	<i>Cneorum</i>	2	—	8
<i>Simarouba</i>	6	<i>Quassia</i> (40) + <i>Brucea</i> (8)	48	—	8
<i>Toxicodendron</i> (30) + <i>Schinus</i> (30)	60	<i>Mangifera</i> (30) ^h	30	+	8
<i>Zanthoxylum</i>	250	<i>Flindersia</i> (15) + <i>Acronychia</i> (43)	58	+	8
Saxifragales: <i>Ribes</i> ^{b,i}	150	<i>Saxifraga</i> (440) + <i>Peltoboykinia</i> (1) + <i>Chrysosplenium</i> (60) + <i>Mitella</i> (20) + <i>Elmera</i> (1) + <i>Heuchera</i> (55) + <i>Tolmiea</i> (1) + <i>Lithophragma</i> (9) + <i>Bensoniella</i> (1) + <i>Orestitrophe</i> (1) + <i>Mukdenia</i> (2) + <i>Bergenia</i> (7) + <i>Rodgersia</i> (6) + <i>Darmera</i> (1) + <i>Astilboides</i> (1) + <i>Sullivantia</i> (6)	637	—	29

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
		+ <i>Suksdorfia</i> (3) + <i>Boykinia</i> (8) + <i>Bolandra</i> (2) + <i>Astilbe</i> (12)			
<i>Tanakaea</i>	1	<i>Leptarrhena</i>	1	=	29
Simmondsiales:					
<i>Simmondsia</i>	1	<i>Dianthus</i> (300) + <i>Stegnospermum</i> (4) + <i>Phytolacca</i> (25) + <i>Basella</i> (5) + <i>Schlumbergera</i> (6)	340	-	33
Trochodendrales:					
<i>Trochodendron</i> ^c (1) + <i>Tetracentron</i> ^c (1)	2	<i>Hydrangea</i> (23) + <i>Berzelia</i> (12) + <i>Hedera</i> (8) + <i>Coriaria</i> (5) + <i>Eucryphia</i> (6) + <i>Francoa</i> (1) + <i>Geranium</i> (300) + <i>Hibbertia</i> (115) + <i>Dillenia</i> (60) + <i>Schumacheria</i> (3)	533	-	25
Winterales:					
<i>Tasmannia</i>	5	<i>Drimys</i>	6	-	25
Self-incompatible:					
Apiales:					
<i>Daucus</i>	22	<i>Pseudorlaya</i>	2	+	34
Arales:					
<i>Symplocarpus</i>	1	<i>Lysichiton</i>	1	=	39
Asparagales:					
<i>Agave</i>	100	<i>Bravoa</i>	2	+	22
<i>Allium</i>	690	<i>Ipheton</i>	20	+	22
<i>Aloe</i>	365	<i>Bulbine</i>	50	+	22
<i>Asparagus</i>	135	<i>Hemiphylacus</i>	1	+	22
<i>Curculigo</i>	10	<i>Spiloxene</i>	30	-	22
<i>Cordyline</i>	15	<i>Chamaescilla</i>	2	+	22
<i>Hemerocallis</i>	15	<i>Dianella</i>	20	-	22
<i>Hypoxis</i>	150	<i>Rhodohypoxis</i>	6	+	22
<i>Iris</i>	210	<i>Orthrosanthus</i>	9	+	22
Asterales:					
<i>Liatris</i>	43	<i>Chromolaena</i>	165	-	12
<i>Helianthus</i>	50	<i>Wyethia</i>	14	+	12
<i>Solidago</i>	80	<i>Bellis</i>	8	+	11
<i>Sonchrus</i>	62	<i>Lactuca</i>	75	-	11
<i>Tagetes</i>	50	<i>Pectis</i>	100	-	11
Austrobaileyales:					
<i>Austrobaileya</i>	1	<i>Illicium</i> (42) + <i>Schisandra</i> (25) or outgroup to all basal eudicots on the phylogeny (>2,000 spp.)	≥67	-	25
Berberidales:					
<i>Epimedium</i>	44	<i>Vancouveria</i>	3	+	43
<i>Podophyllum</i>	5	<i>Dysosma</i>	7	-	43
Butomales:					
<i>Butomus</i>	1	<i>Vallisneria</i>	6	-	22
Capparales:					
<i>Brassica</i>	35	<i>Cleome</i> (150) or <i>Arabidopsis</i> (18)	150 or 18	+/-	28/24
<i>Crambe</i>	20	<i>Muricaria</i> (1) + <i>Coincya</i> (6) + <i>Erucastrum</i> (20) + <i>Hemicrambe</i> (2) + <i>Sinapis</i> (7) + <i>Raffenaldia</i> (2) + <i>Rapistrum</i> (2) + <i>Ceratocnemum</i> (1) + <i>Guiraoa</i> (1) + <i>Otocarpus</i> (1) + <i>Cordylocarpus</i> (1) + <i>Kremeriella</i> (1)	45	-	4

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
Caryophyllales:					
<i>Beta</i>	12	<i>Chenopodium</i>	100	-	32
Cistales:					
<i>Cistus</i>	18	<i>Helianthemum</i>	110	-	23
Cornales:					
<i>Cornus</i>	65	<i>Alangium</i>	21	+	7
Ericales:					
<i>Kalmia</i>	7	<i>Leiophyllum</i>	1	+	41
Geraniales:					
<i>Pelargonium</i>	280	<i>Geranium</i> (300) + <i>Monsonia</i> (25)	325	-	8
Liliales:					
<i>Colchicum</i>	65	<i>Androcymbium</i>	12	+	22
<i>Lilium</i>	100	<i>Fritillaria</i> (100) + <i>Nomocharis</i> (7)	107	-	22
Malvales:					
<i>Abutilon</i>	100	<i>Malope</i> (5) or <i>Gossypium</i> (39) + <i>Hampea</i> (21) + <i>Thespesia</i> (17)	≤77	+	42
<i>Waltheria</i>	40	<i>Hannafordia</i>	4	+	42
Myrtales:					
<i>Cuphea</i>	260	<i>Duabanga</i> (2) + <i>Lawsonia</i> (1) + <i>Nesaea</i> (56)	59	+	5
<i>Lythrum</i>	36	<i>Trapa</i>	15	+	5
<i>Oenothera</i>	124	<i>Clarkia</i>	41	+	5
Oleales:					
<i>Jasminum</i>	200	<i>Ligustrum</i>	40	-	7
Plumbaginales:					
<i>Acantholimon</i>	165	<i>Dictyolimon</i>	4	+	33
<i>Armeria</i>	100	<i>Psylliostachys</i>	10	+	33
Poales:					
<i>Agropyron</i>	15	<i>Eremopyrum</i>	4	+	13
<i>Calamagrostis</i>	250	<i>Ammophila</i> (2) or <i>Arrhenatherum</i> (6)	≤6	+	15
<i>Cymbopogon</i>	56	<i>Andropogon</i> (100) + <i>Schizachyrium</i> (60) + <i>Hyparrheria</i> (55) + <i>Zea</i> (4)	219	-	13
<i>Dactylis</i>	3	<i>Poa</i> (200) + <i>Sesleria</i> (27)	227	-	16
<i>Ehrharta</i>	35	Outgroup to all other Poaceae on the phylogeny (totaling 41 applicable genera)	2,072	-	15
<i>Molinia</i>	3	<i>Phragmites</i>	3	=	17
<i>Pennisetum</i>	130	<i>Panicum</i>	500	-	15
<i>Phalaris</i> (20) + <i>Agrostis</i> (220) + <i>Anthoxanthum</i> (18)	258	<i>Arrhenatherum</i>	6	+	15
<i>Psathyrostachys</i>	8	<i>Hordeum</i> (20) + <i>Peridictyon</i> (1)	21	-	13
<i>Pseudoroegneria</i>	16	<i>Dasypryrum</i> (2) + <i>Australopyrum</i> (3) + <i>Heteranthelium</i> (1) + <i>Henrardia</i> (2) + <i>Thinopyrum</i> (20) + <i>Secale</i> (3) + <i>Aegilops</i> (21) + <i>Triticum</i> (4)	60	-	13
<i>Sorghastrum</i>	17	<i>Dichanthium</i> (20) + <i>Capillipedium</i> (14) + <i>Bothriochloa</i> (35) + <i>Ischaemum</i> (65) + <i>Chrysopogon</i> (26) + <i>Heteropogon</i> (6) + <i>Sorghum</i> (24)	190	-	13

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
<i>Zoysia</i>	10	<i>Spartina</i>	17	-	15
Polygonales:					
<i>Rheum</i>	30	<i>Polygonum</i>	20	+	33
Pontederiales:					
<i>Ananas</i>	8	<i>Aechmea</i>	85	-	20
<i>Hedychium</i>	50	<i>Riedealea</i>	60	-	20
<i>Pontederia</i>	5	<i>Monochoria</i>	6	-	20
<i>Zingiber</i>	60	<i>Globba</i>	35	+	20
Primulales:					
<i>Cyclamen</i>	19	<i>Dodecatheon</i>	13	+	36
Rosales:					
<i>Eriobotrya</i>	26	<i>Rhaphiolepis</i> (9) + <i>Vauquelinia</i> (3)	12	+	19
<i>Geum</i>	40	<i>Spiraea</i> (90) + <i>Photinia</i> (65)	155	-	40
<i>Pyrus</i>	25	<i>Heteromeles</i> (1) + <i>Malus</i> (55) + <i>Photinia</i> (65) + <i>Chaenomeles</i> (4)	95	-	19
Solanales:					
<i>Atropa</i> (4) + <i>Lycium</i> 100)	104	<i>Nicandra</i> (1) or <i>Juanulloa</i> (8) + <i>Markea</i> (18) + <i>Solandra</i> (10) + <i>Schultesianthus</i> (5) + <i>Trianaea</i> (4)	≤45	+	30
Monoecious:					
Apiales:					
<i>Aralia</i>	36	<i>Scheffera</i>	650	-	6
<i>Centella</i> (40) + <i>Micropleura</i> (2)	42	<i>Delarbrea</i>	6	+	6
<i>Myrrhis</i> ^d (1) + <i>Osmorhiza</i> (10) + <i>Anthriscus</i> (11) + <i>Scandix</i> (18) + <i>Chaerophyl- lum</i> (35)	75	<i>Daucus</i> (22) + <i>Pseudorlaya</i> (2) + <i>Laserpitium</i> (35) + <i>Cuminum</i> (4)	63	+	34
Arales:					
<i>Philodendroideae</i> (600) + <i>Aroideae</i> (590)	1,190	<i>Calla</i>	1	+	39
Arecales:					
<i>Archontophoenix</i> (3) + <i>Howea</i> (2)	5	<i>Oraniopsis</i> ^b	1	+	9
<i>Arecinae</i> (238) + <i>Cocoeae</i> (966) + <i>Geonomeae</i> (91)	1,295	<i>Hyophorbeae</i> (11) + <i>Cyclospatheae</i> (4)	15	+	10
<i>Bactris</i> (239) + <i>Aiphanes</i> (38)	277	<i>Phoenix</i> ^b	17	+	9
<i>Cocos</i>	1	<i>Chamaerops</i> ^b	1	=	9
<i>Nypa</i> (1) + <i>Pseudophoenix</i> (4)	5	<i>Salacca</i> ^b (20) + <i>Chamaedorea</i> ^b (100)	132	-	9
<i>Serenoa</i>	1	<i>Phoenix reticula</i> ^b	1	=	9
<i>Thrinax</i>	7	<i>Trithrinax</i> (5) + <i>Trachycarpus</i> ^b (4)	9	-	9
Asterales:					
<i>Achillea</i> ^g	115	<i>Santolina</i>	18	+	11
<i>Ainsliaea</i>	40	<i>Stiffia</i>	5	+	11
<i>Cacosmia</i> ^g (3) + <i>Liabum</i> ^g (38)	41	<i>Vernonia</i> (500) + <i>Stokesia</i> (1) + <i>Piptocarpha</i> (45) + <i>Lychnophora</i> (26)	572	-	11
<i>Chromolaena</i> ^g	165	<i>Liatris</i>	43	+	11
<i>Cotula</i> ^g	55	<i>Ursinia</i>	38	+	11
<i>Galinsoga</i> ^g	13	<i>Stevia</i> (235) + <i>Eupatorium</i> (45)	280	-	11
<i>Gnaphalium</i> ^g	50	<i>Antennaria</i> ^b	71	-	11
<i>Haplocarpha</i> ^g (8) + <i>Arctotis</i> ^g (50)	58	<i>Gazania</i>	17	+	11
<i>Mutisia</i> ^g	59	<i>Gerbera</i>	35	+	12
<i>Palafoxia</i> ^g (12) + <i>Bahia</i> ^g (13)	25	<i>Marshallia</i>	7	+	11
<i>Perityle</i> ^g	64	<i>Geraea</i>	2	+	11
<i>Wyethia</i> ^g	14	<i>Helianthus</i>	50	-	11

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
Begoniales:					
<i>Symbegonia</i> (14) + <i>Begonia</i> (900) + <i>Hillebrandia</i> (1)	915	<i>Datisca</i> ^c (2) + <i>Octomeles</i> ^b (1) + <i>Tetrameles</i> ^b (1)	4	+	2
Buxales:					
<i>Buxus</i> (50) + <i>Pachysandra</i> (3) + <i>Styloceras</i> (5)	58	<i>Didymeles</i> ^b	2	+	25
Cornales:					
<i>Curtisia</i>	1	<i>Alangium</i> (21) + <i>Cornus</i> (65)	86	-	7
<i>Davidia</i>	1	<i>Nyssa</i> ^c	8	-	6
Corylales:					
<i>Betula</i> (35) + <i>Corylus</i> (15)	70	<i>Ticodendron</i> ^c	1	+	1
Cyperales:					
<i>Kyllinga</i> ^d	40	<i>Cyperus</i>	300	-	21
<i>Mapania</i> (73) + <i>Hypolytrum</i> (40) + <i>Scleria</i> (200) + <i>Carex</i> (2,000) + <i>Uncinia</i> (54)	2,367	<i>Rhynchospora</i>	250	+	21
Euphorbiales:					
<i>Lasiococca</i> (3) + <i>Spathiostemon</i> (3)	6	<i>Wetria</i> ^b (1) + <i>Homonoia</i> ^b (2)	3	+	3
Fagales:					
<i>Fagus</i> (10) + <i>Castanea</i> (10) + <i>Chrysolepis</i> (2) + <i>Quercus</i> (400) + <i>Trigonobalanus</i> (3)	425	<i>Davidsonia</i>	2	+	1
Gunnerales:					
<i>Gunnera</i>	40	<i>Myrothamnus</i> ^b	2	+	25
Juglandales:					
<i>Carya</i> (18) + <i>Juglans</i> (21) + <i>Alfaroa</i> (7)	46	<i>Rhoiptelea</i>	1	+	1
Juncales:					
<i>Marsippospermum</i> (3) + <i>Rostkovia</i> (2)	5	<i>Distichia</i> ^b (3) + <i>Oxychloe</i> ^b (7)	10	-	21
Malvales:					
<i>Akebia</i>	2	<i>Sargentodoxa</i> ^b	1	+	24
<i>Lactoris</i> ^g	1	<i>Saruma</i> (1) + <i>Asarum</i> (70) + <i>Aristolochia</i> (120)	191	-	24
<i>Sterculia</i>	150	<i>Fremontodendron</i> (3) + <i>Ochroma</i> (1) + <i>Quararibea</i> (35) + <i>Bombax</i> (20) + <i>Camptostemon</i> (2) + <i>Thespesia</i> (17) + <i>Gossypium</i> (39)	117	+	23
Musales:					
<i>Musa</i>	35	<i>Orchidantha</i>	7	+	20
Poales:					
<i>Arrhenatherum</i> ^d	6	<i>Anthoxanthum</i> (18) + <i>Phalaris</i> (20) + <i>Agrostis</i> (220)	258	-	15
<i>Coix</i>	6	<i>Bothriochloa</i> (35) + <i>Capillipedium</i> (14) + <i>Dichanthium</i> (20) + <i>Sorghastrum</i> (17)	86	-	13
<i>Hordeum</i> ^d	20	<i>Secale</i> (3) + <i>Thinopyrum</i> (20) + <i>Agropyron</i> (15) + <i>Eremopyrum</i> (4) + <i>Henrardia</i> (2) + <i>Australo-</i> <i>pyrum</i> (3) + <i>Dasypyrum</i> (2) + <i>Pseudoroegneria</i> (150) + <i>Peridicyon</i> (1)	200	-	13
<i>Ischaemum</i> ^d	65	<i>Cymbopogon</i> (56) + <i>Sorghum</i> (24) + <i>Heteropogon</i> (6) + <i>Chrysopogon</i> (26)	112	-	13
<i>Lithachne</i> (4) + <i>Olyra</i> (23)	27	<i>Chusquea</i> (120) + <i>Otatea</i> (2) + <i>Bambusa</i> (120)	242	-	15
<i>Pharus</i>	8	<i>Anomochloa</i> (1) + <i>Hakonechloa</i> (1) + <i>Danthoni-</i> <i>opsis</i> (20) or <i>Nardus</i> (1)	22 or 1	-/+	13/16

Table A1 (Continued)

Order/genera	No.	Sister group	No.	+/-	Reference ^a
<i>Phragmites</i> ^d	3	<i>Aristida</i>	330	—	14
<i>Triticum</i> ^d	4	<i>Aegilops</i>	21	—	13
<i>Zea</i>	4	<i>Hyparrhenia</i> (55) + <i>Schizachyrium</i> (60) + <i>Andropogon</i> (100)	215	—	13
<i>Zizania</i>	3	<i>Oryza</i> (18) + <i>Bambusa</i> (120)	138	—	17
Orchidales:					
<i>Catasetum</i>	100	<i>Clowesia</i>	6	+	18
<i>Mormodes</i> (60) + <i>Cycnoches</i> (23)	83	<i>Dressleria</i>	5	+	18
Sapindales:					
<i>Kirkia</i>	5	<i>Swietenia</i> (3) + <i>Schmardaea</i> (1) + <i>Trichilia</i> (84) + <i>Cipadessa</i> (1) + <i>Nymania</i> (1) + <i>Guarea</i> (40) + <i>Melia</i> (3) + <i>Quassia</i> (40) + <i>Brucea</i> (8) + <i>Leitneria</i> ^b (1) + <i>Harrisonia</i> (4) + <i>Cneorum</i> (2) + <i>Ptaeroxylon</i> (1) + <i>Acronychia</i> (43) + <i>Flindersia</i> (16) + <i>Murraya</i> (4) + <i>Ruta</i> (7) + <i>Buchanania</i> (25) + <i>Toxicodendron</i> (30) + <i>Schinus</i> ^d (30) + <i>Mangifera</i> ^h (30) + <i>Acer</i> ^{b,c} (111)	485	—	8
Typhales:					
<i>Typha</i> (11) + <i>Sparganium</i> (14)	25	<i>Prionium</i> (1) + <i>Tradescantia</i> (70) + <i>Pontederia</i> (5) + <i>Eichhornia</i> (7) + <i>Heteranthera</i> (12)	95	—	20

Note: Breeding systems other than true dioecy or monoecy are indicated in footnotes. For the monoecious focal groups, comparisons with dioecious sister groups are indicated. Where the outgroup conflicted on different trees the symbol +/- is used and both the + and - signs are used as separate data points.

^a Numbers in columns correspond to phylogenetic references as follows: (1) Manos and Steele 1997; (2) Swensen et al. 1998; (3) van Welzen et al. 1998; (4) Warwick and Black 1997; (5) Conti et al. 1997; (6) Plunkett et al. 1996; (7) Xiang et al. 1993; (8) Gadek et al. 1996; (9) Anzizar et al. 1998; (10) Hahn et al. 1995; (11) Watson et al. 1991; (12) Jansen et al. 1991; (13) Mason-Gamer et al. 1998; (14) Mathews and Sharrock 1996; (15) Soreng and Davis 1998; (16) Davis and Soreng 1993; (17) Linder et al. 1996; (18) Romero 1990; (19) Campbell et al. 1995; (20) Graham and Barrett 1995; (21) Simpson 1995; (22) Chase et al. 1995; (23) Alverson et al. 1998; (24) Soltis et al. 1997; (25) Hoot et al. 1999; (26) Uhl et al. 1995; (27) Esser et al. 1997; (28) Rodman et al. 1998; (29) Soltis et al. 1996; (30) Knapp et al. 1997; (31) Bogler and Simpson 1996; (32) Downie and Palmer 1994; (33) Lledo et al. 1998; (34) Downie et al. 1998; (35) Stahl 1996; (36) Anderberg and Stahl 1995; (37) Rudall and Cutler 1995; (38) Bayer et al. 1999; (39) French et al. 1995; (40) Crayn et al. 1995; (41) Kron 1997; (42) Alverson et al. 1999; (43) Kim and Jansen 1998.

^b Dioecy.

^c Polygamodioecy.

^d Andromonoecy.

^e Androdioecy.

^f Gynodioecy.

^g Gynomonoecy.

^h Polygamomonoecy.

ⁱ Subdioecy.

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