THE ROLE OF DIVERSIFICATION IN CAUSING THE CORRELATES OF DIOECY

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Abstract.—Dioecy is reported to be correlated with a number of ecological traits, including tropical distribution, woody growth form, plain flowers, and fleshy fruits. Previous analyses have concentrated on determining whether dioecy is more likely to evolve in lineages possessing these traits, rather than considering the speciation and extinction rates of dioecious lineages with certain combinations of traits. To address the association between species richness in dioecious lineages as a function of the ecological traits, we compared the evolutionary success (i.e., relative species richness) of dioecious focal lineages with that of their nondioecious sister groups. This test was repeated for the evolutionary success of randomly chosen nondioecious lineages (control lineages) compared with their nondioecious sister groups. If the possession of certain ecological traits enhances the evolutionary success of dioecious lineages, we predict an association between the presence of these traits and relative species richness in the former, but not latter, set of sister-group comparisons. Dioecious focal lineages with a higher number of these traits experienced higher evolutionary success in sister-group comparisons, whereas no trend was found for the control focal lineages. The increase in evolutionary success was especially true for dioecious focal lineages that had a tropical distribution or fleshy fruit. We discuss how these results provide strong support for differential evolutionary success theories for the correlations between dioecy and the ecological traits considered.

Key words.—Angiosperms, breeding system, dioecy, ecological correlations, extinction, phylogeny, sister-group comparison, speciation.

Dioecy, in which separate individuals perform male and female functions, is a rare breeding system (~ 6%) among the angiosperms (Bawa 1980; Givnish 1980; Thomson and Brunet 1990; Renner and Ricklefs 1995). Despite being distributed widely across taxonomic groups (Heilbuth 2000), dioecy is frequently reported to be correlated with several ecologically important traits (Vamosi et al. 2003). These ecological traits include a tropical distribution (Carlquist 1974; Bawa 1980; Givnish 1980), woody growth form (Freeman et al. 1980; Fox 1985; van Dulmen 2001), small, white (hereafter, ''plain'') flowers (Bawa and Opler 1975; Bawa 1980), and fleshy fruits (Givnish 1980; Muenchow 1987). Determining the cause of these ecological correlations can contribute greatly to our understanding of why dioecy evolves and/or what allows dioecy to persist.

A number of theories have suggested that correlations between dioecy and tropical distribution, woodiness, plain flowers, and fleshy fruits exist because dioecy evolves more often in lineages with these ecological traits (Bawa and Opler 1975; Bawa 1980; Givnish 1980; Beach 1981; Lloyd 1982; Charlesworth 1993; Renner and Ricklefs 1995; Sakai and Weller 1999). Plain flowers, for example, may promote the evolution of dioecy because female individuals of plain-flowered species are less likely to be discriminated against by pollinators (Bierzychudek 1987; Charlesworth 1993). Fleshy fruit, which may be dispersed farther and more frequently by specialized frugivores, may select for individuals that devote more energy to female reproduction (Bawa 1980; Givnish 1980). Large plants such as trees and shrubs are thought to experience higher geitonogamous (within-plant) selfing than herbs due to increased numbers of flowers, which may produce

increased selection pressure for outcrossing via dioecy (Freeman et al. 1980).

A recent large-scale analysis of transition rates to dioecy in angiosperms found little support overall for the hypotheses that dioecy is more prone to evolve in lineages that have a tropical distribution, woody growth form, plain flowers, or fleshy fruits than in those lacking them (Vamosi et al. 2003). These findings do not rule out that dioecy may be selected for in certain lineages in response to the above factors (e.g., increased selfing in a genus composed of arboreal representatives) but suggest that other factors may be involved in most lineages. An alternative, yet little studied, process that would lead to correlations between dioecy and ecological traits is differential diversification (i.e., speciation minus extinction) of dioecious lineages as a function of the number of traits associated with each lineage. We illustrate the difference between the two theories using the ecological trait of fleshy fruit (Fig. 1). In the scenario envisioned in previous theories, dioecy arises more often in clades that are associated with the trait (Fig. 1A). Differential diversification may, if common, also produce a correlation between dioecy and fleshy fruits (Fig. 1B). Here, the order in which the traits of dioecy and fleshy fruits arise is irrelevant. What is important is that when dioecy and fleshy fruits both arise in a lineage, the subsequent proliferation of the clade is greater than in clades lacking the combination of dioecy and fleshy fruit (Fig. 1B). Indeed, there is some evidence among nonangiosperm plants that lineages with the combination of dioecy and fleshy propagules have higher species richness than sister groups lacking this combination of traits (Donoghue 1989). Dioecious clades may experience even higher relative diversification if in combination with more than one of the correlated traits. Diversification of dioecious lineages with fleshy fruits, for example, may be especially pronounced when in com-

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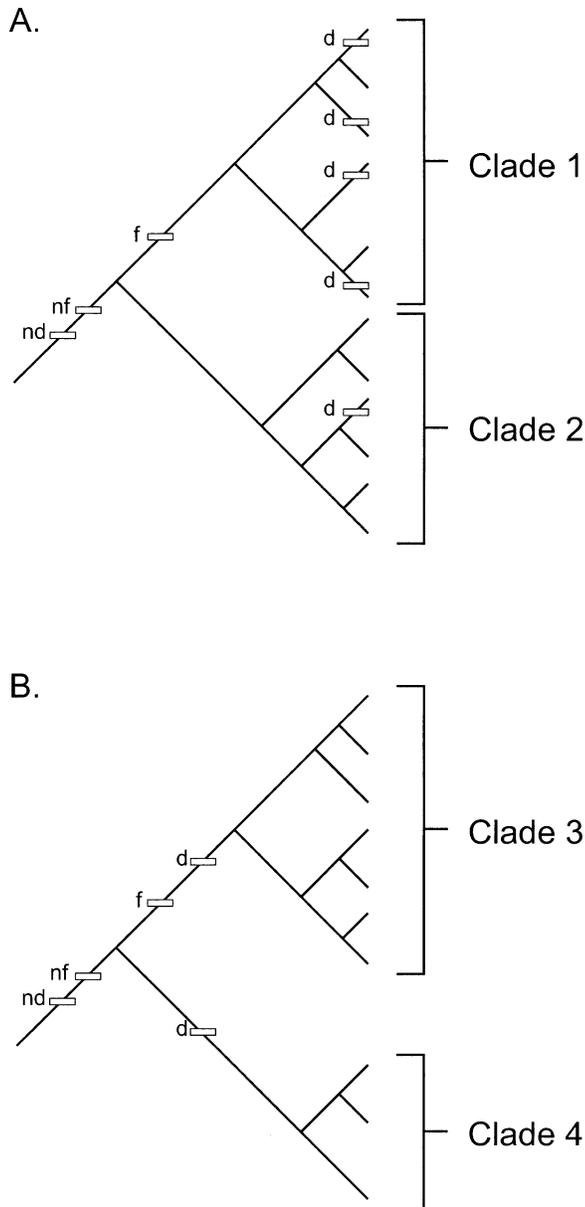
A.

B.

FIG. 1. Hypothetical phylogenies to illustrate the differential orig-
ination (A) and differential diversification (B) hypotheses for the
origin of correlations between dioecy and ecological traits (e.g.,
fleshy fruits). The lineages considered initially have dry fruits (nf)
and are not dioecious (nd). Furthermore, the state of fleshy fruits
(f) evolves once in both cases (lineage leading to clade 1 in A or
clade 3 in B). In the differential origination scenario (A), dioecy
(d) is favored when in combination with fleshy fruits, originating
more often in clade 1 (four transitions) than in clade 2 (one tran-
sition). In the differential diversification scenario (B), dioecy
evolves twice (once in lineage leading to clade 3 and once in lineage
leading to clade 4). Clade 3 (seven species) subsequently experi-
ences greater diversification than clade 4 (three species) because
of the combination of dioecy and fleshy fruits in the former clade.

bination with a tropical distribution and a woody growth
form.

Whether diversification is a key factor in causing the cor-
relations between dioecy and the ecological traits is com-
plicated by the finding that the species richness of dioecious

lineages is lower than that of non-dioecious lineages (Heil-
buth 2000). Dioecious lineages, thus, appear to have higher
extinction rates and (or) lower speciation rates. Theories that
consider how fleshy fruits, plain flowers, and woody growth
increase diversification rates in dioecious lineages tend to
focus on how they could reduce the higher extinction prob-
ability that is potentially associated with a dioecious breeding
system. For example, dioecious species likely suffer from a
''seed shadow handicap'' whereby seed dispersal is compro-
mised because only females disperse seeds (Heilbuth et al.
2001; Wilson and Harder 2003). The seed dispersal disad-
vantage may be alleviated in species that have fleshy fruits,
where a higher number of seeds disperse far distances away
from the maternal plant. An analysis of the evolution of
showy floral traits suggests that dioecious species tend to
become sexually dimorphic for floral display, with males
attracting the majority of pollinator visits. This may result
in inefficient pollen delivery and a higher risk of extinction
for showy dioecious lineages (Vamosi and Otto 2002). Thus,
dioecious lineages may experience greater evolutionary suc-
cess if they adopt abiotic pollination or are pollinated by
generalists, pollination syndromes that are usually associated
with having plain flowers. Finally, work on mate assurance
predicts that woody (perennial) dioecious plants may be at
a lower risk of extinction because there is a reduced prob-
ability of dying without reproducing (Baker 1954; Carlquist
1974; Bawa 1980; Pannell and Barrett 1998). Additionally,
traits such as fleshy fruits, plain flowers and long life span
could increase speciation rates of dioecious lineages. Fleshy
fruits, which may be transported long distances by birds and
other vertebrates, may disperse both male and female seeds
to the same location, which is necessary for colonization and
subsequent speciation of dioecious lineages in new habitats,
such as islands (Carlquist 1974).

Here, we examine whether differential diversification of
dioecious lineages associated with certain ecological traits
may be driving the observed correlations between dioecy and
these traits. We do this by comparing the relative species
richness of dioecious lineages with that of their nondioecious
sister groups when certain ecological traits are present (ab-
sent) in the dioecious lineage. We use a method based on
that introduced by Slowinski and Guyer (1993) whereby the
evolutionary success of a lineage is defined in terms of its
relative representation in a sister-group pair (Fig. 2), the
members of which are, by definition, equally old (Cracraft
1981; Felsenstein 1985). We use data on species richness and
ecological traits of a large number of sister-group pairs in-
volving dioecious lineages to address three questions: (1)
What is the effect of each of the four traits (tropical distri-
bution, woody growth habit, plain flowers, and fleshy fruits)
on evolutionary success? (2) How do different combinations
of the four traits affect evolutionary success? (3) Does evo-
lutionary success of dioecious lineages increase with number
of these traits associated with the focal lineage?

MATERIALS AND METHODS

Datasets and Data Coding

We investigated patterns of evolutionary success of an-
giosperm lineages, with respect to their ecological traits, us-

A.

Collospermum (2 spp.)   Focal dioecious lineage

Blandfordia (4 spp.)   Nondioecious
Milligania (5 spp.)   sister group

ES value = 2/((2+9)-1)
= 0.2

B.

Leitneria (1 sp.)   Focal dioecious lineage

Simaba (14 spp.)   Nondioecious sister group

ES value = 1/((1+14)-1)
= 0.07

C.

Calamus (370 spp.)   Focal dioecious lineage

Metroxylon (5 spp.)   Nondioecious sister group
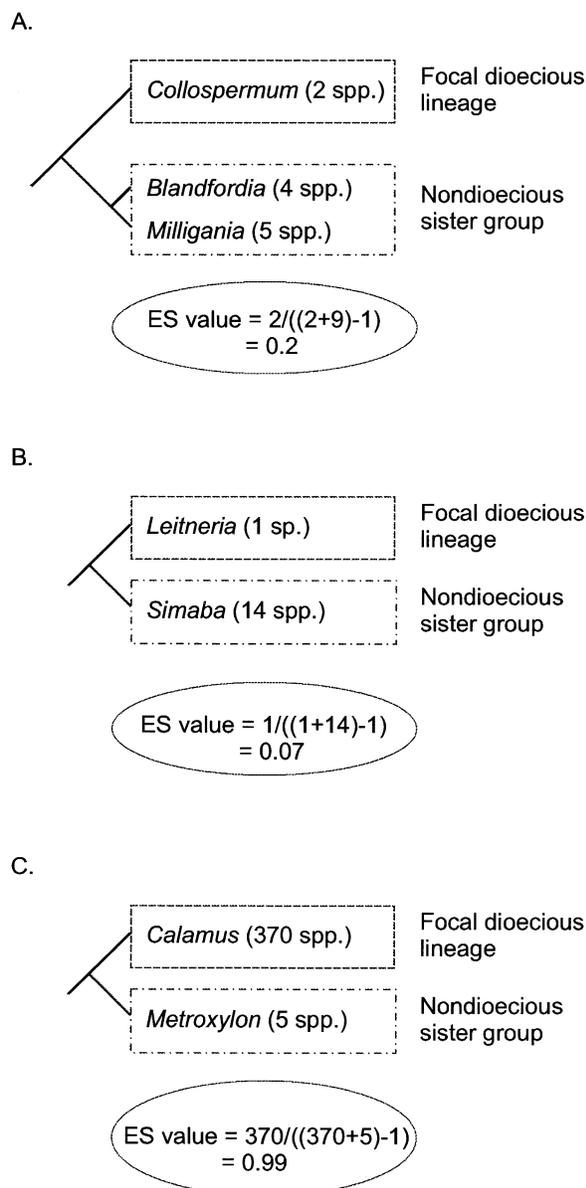
ES value = 370/((370+5)-1)
= 0.99

FIG. 2. Examples of sister-group comparisons and calculations of corresponding evolutionary success (ES) values. Shown are sister-group pairs in which: (A) both the dioecious focal lineage and its nondioecious sister group possess the same, single ecological trait (fleshy fruits); (B) both groups possess three traits, with two traits being the same (tropical distribution, woody growth form) and the third trait being different (*Leitneria*: plain flowers; *Simaba*: fleshy fruits); and (C) both groups possess all four traits, which, by definition, are all the same. Sister-group comparison (A) further illustrates a situation in which the sister group is composed of two lineages; in such cases, the number of species used for the sister group is simply the sum of the species-richness values for all the nondioecious lineages (e.g., 4 + 5 = 9 species). Sister-group pairs (A) and (C) would appear in sets 1 and 2, whereas (B) would appear in set 1 only (see Table 1). With reference to the analysis of the trait distribution in Table 3, (A) would be included as a sister-group pair where both groups had a temperate distribution and (B) and (C) would be included as sister-group pairs where both groups had a tropical distribution. With reference to Figure 3 (filled bars), sister-group pair (A) is the sole datapoint in the left side of panel C; (B) is one of the datapoints in the right side of panel F; and (C) is one of the datapoints in the right side of panel H. In sister-group pairs (A) and (B), there are fewer species in the dioecious focal

ing a large dataset composed of all the sister-group pairs containing a dioecious genus considered by Soltis et al. (1999) and Heilbuth (2000). Dioecious lineages were considered only once; in cases where a dioecious genus appeared in both sources, we used the sister-group pair as found in Heilbuth (2000). Estimates of species richness of lineages were obtained from Mabberley (1997). Breeding system status of genera was determined from Mabberley (1997), Takhtajan (1997), and the database, generously provided by S. Renner, used in Renner and Ricklefs (1995). We checked all the information within Heilbuth (2000) and updated where necessary. Changes were made to reflect the following new breeding system designations: *Acer*, *Carpodiptera*, *Christiana*, *Dodonaea*, *Osteomeles*, and *Viscum* (mostly nondioecious) and *Commiphora* and *Trichilia* (dioecious).

We determined distribution, growth form, flower size and showiness, and type of fruit for each genus by consulting literature sources (Bentham and Hooker 1880; Hutchinson 1964; Mabberley 1997; Takhtajan 1997), various sites on the World Wide Web, and (or) experts on a particular genus (list of sources available from authors). Genera with tropical or subtropical distributions were coded as tropical. Trees, shrubs, and lianas were coded as woody. Flowers with a corolla judged to be white or yellow-green and less than 10 mm in length were scored as plain, even though these plain flowers may group together into showy inflorescences. Genera reported to have showy bracts were coded as showy. When information regarding showiness of flower could not be found, then the status of the trait was decided by examining photographs and illustrations of representatives of the genus. Because dioecy has been correlated specifically with fleshy fruit, we scored genera not on the basis of their mode of dispersal (i.e., abiotic vs. biotic), as has been done in some studies of diversification in angiosperms (Tiffney and Mazer 1995), but on their fruit type (as in Herrera 1989). When sources did not report the presence of either fleshy or dry fruits, then fruit types such as drupes and berries were coded as fleshy fruits, while fruit types such as capsules and samaras were coded as dry.

Determining Evolutionary Success

We use four sets of sister-groups for our analyses (summarized in Table 1). The procedures detailed above resulted in 93 sister-group pairs (set 1 in Table 1). The 93 dioecious focal lineages represent 126 dioecious genera (see Appendix online at http://dx.doi.org/10.1554/03-312.1.s1), which is approximately 19% of the estimated 670 angiosperm genera that are mostly or entirely dioecious (Renner and Ricklefs 1995). Of these 93 sister-group pairs, 33 were composed of dioecious lineages with sister groups that were identical in terms of the four ecological traits they possessed (e.g., both groups had a tropical distribution, woody growth form, showy

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lineage than in its sister-group, thus, ES values are < 0.5. The dioecious focal lineage in (C) has more species than its sister group, with an ES value > 0.5. The latter comparison illustrates how ES values approach unity when the focal lineage has a far higher number of species than its sister group.

TABLE 1. Summary of sets of sister-group pairs used. Entries under the different headings refer to breeding system of the group (focal lineage and sister group), number of sister-group pairs (*N*), and whether ecological traits potentially differ or are identical between the two members of each sister-group pair (ecological traits). To be scored as identical, the focal lineage and its sister-group must have the same trait combination (e.g., both clades have tropical distribution, woody growth form, showy flowers, and dry fruits). Note that set 2 is a subset of set 1 and set 4 is a subset of set 3. Sets 3 and 4 are the control lineages chosen randomly to ensure that any patterns seen in sets 1 and 2 are unique to dioecious lineages.

Set	Focal lineage	Sister-group	*N*	Ecological traits
1	dioecious	nondioecious	93	potentially differ
2	dioecious	nondioecious	33	identical
3	nondioecious	nondioecious	93	potentially differ
4	nondioecious	nondioecious	32	identical

flowers, and dry fruits; set 2 in Table 1). Direct comparisons between dioecious sister-group pairs with and without a particular ecological trait are not feasible at the present time due to the paucity of phylogenies of purely dioecious families and orders. Therefore, the evolutionary success of dioecious focal lineages was compared to that of their nondioecious sister groups. In comparing two sister groups, there is no information on whether the dioecious focal lineage or the nondioecious sister group is displaying the ancestral condition for diversification (Sanderson and Donoghue 1994). If we assume, however, that dioecy is the derived condition, the ancestor of the sister-group pair was more likely similar to the nondioecious sister-group in diversification, and thus we interpret any change in diversification to have occurred along the dioecious branch.

The method of sister-group comparisons is illustrated in Figure 2. The species richness of the focal lineage (i.e., lineage of interest) is compared to that of its sister group, where the focal lineage and the sister group compose a single sister-group pair. Two or more dioecious genera were rarely sister groups (e.g., *Aciphylla* + *Anisotome*; see Appendix). In such cases, the two genera were combined into one lineage and analyzed together. In contrast, the sister group of the dioecious focal lineage was often a combination of a number of nondioecious genera (e.g., Fig. 2A). For each of the 93 sister-group pairs, we determined whether the dioecious focal lineage had lower (fewer species), equivalent (equal number of species), or higher (more species) evolutionary success than its sister group, using the method introduced by Slowinski and Guyer (1993). If a sister-group pair has *n* species, to determine if dioecy is associated with lower evolutionary success, one calculates the probability that $n - r$ species will belong to the focal lineage, while *r* species will belong to the sister group, calculated as:

$$P = (n - r)/(n - 1). \tag{1}$$

This probability approaches zero (one) if the focal lineage has far fewer (greater) species than its sister group and 0.5 if species are distributed equally between the two groups, especially as *n* increases. Sample calculations for three sister-group pairs are shown in Figure 2. The Slowinski-Guyer probabilities (hereafter, evolutionary success, or ES, values)

give a measure of the evolutionary success of focal lineages possessing a given trait (Slowinski and Guyer 1993). ES values were arcsine transformed prior to analyses.

Statistical Analyses

Species richness.—We can test the validity of the finding that dioecious lineages have lower species richness, on average, than their sister groups (Heilbuth 2000) with the 33 sister-group pairs in which all the traits except breeding system are the same (set 2). A significant number of the sister-group pairs used by Heilbuth (2000) did not possess the same traits (e.g., dioecious focal lineages with a temperate distribution and woody growth form were compared with nondioecious sister groups with a tropical distribution and herbaceous growth form). We used the Slowinski-Guyer test, which involves a Fisher's combined probability test of the independent ES values from all sister-group pairs (Slowinski and Guyer 1993).

Effects of individual traits.—To determine if any one of the four ecological traits is associated with increased diversification of dioecious lineages, we chose sister-group pairs from set 1 (Table 1), where the focal lineages and their sister groups possessed the same state of a particular trait. For example, we identified 52 sister-group pairs in which both the dioecious focal lineage and its nondioecious sister group had a tropical distribution. An additional 16 pairs were identified as having both groups with a temperate distribution. Invoking parsimony, we assume that it is most likely that dioecy evolved within a lineage with a tropical distribution in the former sister-group pair and within a lineage with a temperate distribution in the latter case. To determine whether dioecy has higher evolutionary success when it evolves in lineages possessing a particular ecological trait, we compared the ES values from sister-group pairs with the trait correlated with dioecy (e.g., tropical distribution) with those from sister-group pairs that did not possess the trait (e.g., temperate distribution). These comparisons were conducted for each trait using two-sample *t*-tests.

Effects of trait combinations.—We examined the evolutionary success of focal lineages with different ecological trait combinations because dioecious lineages were often associated with more than one trait. To determine whether the effects of trait combinations are unique to dioecious lineages, we explored trends in a set of 93 randomly chosen sister-group pairs in which neither the focal lineage nor its sister group are dioecious (Table 1, set 3). In an attempt to clarify which nondioecious groups we are referring to in a given analysis, we hereafter drop the breeding system designation (i.e., nondioecious) of the members of these sister-group pairs and refer to them simply as ''control focal lineages'' and ''sister groups,'' respectively. The control focal lineages were generated by randomly sampling taxa that had not been used in the previous analysis from the phylogeny of Soltis et al. (1999; list available from authors on request). Once a control focal lineage was thus selected, we were able to determine the lineage(s) that composed its sister group. Because the members of each sister-group pair share the same breeding system, the designation of focal lineage is arbitrary. We feel that results obtained from comparisons with the control
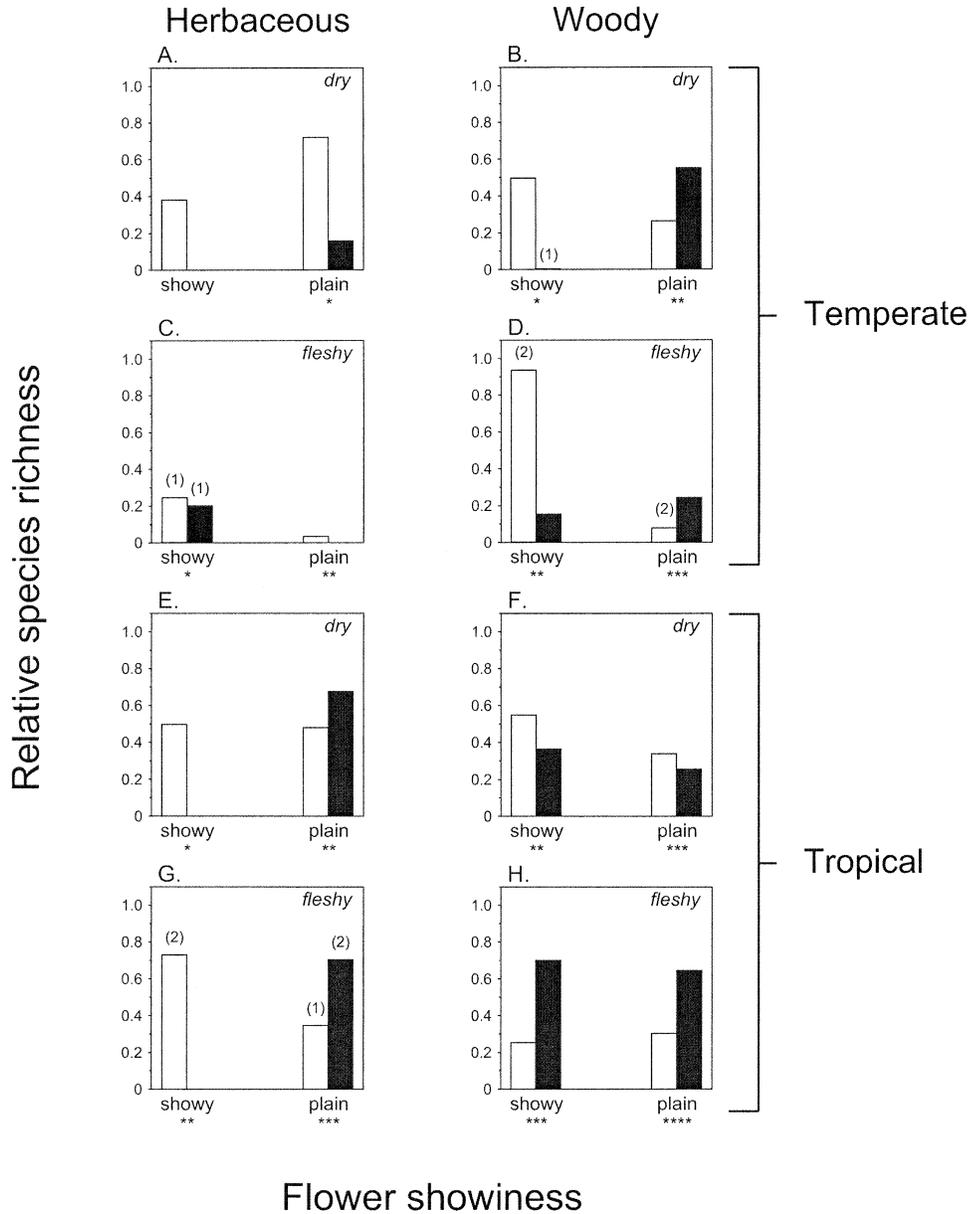
FIG. 3. Evolutionary success of dioecious (filled) and control (open) focal lineages as a function of trait combinations observed in the focal group. Asterisks below each label refer to the number of ecological traits represented by each trait combination. In panel (A), for example, are shown lineages with a temperate distribution, herbaceous growth form, showy flowers, and dry fruits (i.e., no correlated traits) and lineages with a temperate distribution, herbaceous growth form, plain flowers, and dry fruits (i.e., one correlated trait).

sample are likely to be robust for two reasons. First, the mean species richness of the 93 control focal lineages did not differ significantly from that of the 360 nondioecious lineages available for sampling from the Soltis phylogeny ($t_{451} = 0.31$, $P = 0.86$). Furthermore, the proportion of lineages possessing the ecological traits did not differ between the 93 control focal lineages and the 360 nondioecious lineages (contingency tests, all $P > 0.05$). Second, analyses with a different sample of control focal lineages produced qualitatively the same results (Heilbuth 2001).

Evolutionary success values were calculated for each combination of traits (e.g., temperate herbs with plain flowers and fleshy fruits) for both sets of 93 sister-group pairs. We compared mean ES values of dioecious focal lineages with that of control focal lineages for combinations where both groups had three or more representatives using two-sample t-tests.

Effects of number of traits.—We also regressed ES values against number of ecological traits (i.e., 0–4) associated with the focal lineage in both sets 1 and 3 because low sample sizes in the trait combination analysis resulted in nine trait combinations being excluded (Fig. 3). The two regression slopes obtained were then compared using an analysis of covariance to determine whether the relationship between relative species richness and number of traits differs between the dioecious and control focal groups.

TABLE 2. Species-level analysis of 93 dioecious focal lineages and their nondioecious sister groups. Contingency tests of correlations between number of species for all four traits and dioecy were highly significant at the species level.

Trait	State	Dioecious	Nondioecious	P
Distribution	tropical	4925	8607	<0.0001
	temperate	764	3857	
Growth form	woody	5467	6669	<0.0001
	herbaceous	222	5789	
Flowers	plain	5128	6733	<0.0001
	showy	561	5728	
Fruit	fleshy	3466	5872	<0.0001
	dry	2223	6586	

In the previous analyses, the focal lineage may have a different number of ecological traits than its sister group (see Appendix for set 1). Thus, we calculated the regression slopes obtained with only those sister-group pairs in each dataset in which the focal lineage and its sister group had identical states for all four traits. The subset with dioecious focal lineages was composed of 33 sister-group pairs (set 2) and the subset with control focal lineages had 32 sister-group pairs (set 4). Because the latter set of sister-group pairs is composed of two lineages that are identical in all four ecological traits and breeding system, any asymmetry in species richness should be simply due to chance. In other words, the control focal lineage should be larger than its sister group in approximately half the comparisons and smaller in the other half, regardless of the number of traits associated with the sister-group pair. Such a pattern predicts a relationship with a slope equal to zero and an intercept of 0.5. If the null hypothesis is not rejected in the subset with control focal lineages and a positive relationship is observed between ES values and number of ecological traits in the subset with dioecious focal lineages, this result would strongly suggest that these traits offset the decreased diversification experienced by lineages with a dioecious breeding system.

RESULTS

A list of the species richness and ecological traits of the 93 dioecious focal lineages and their nondioecious sister groups considered in our study can be found in the Appendix. There are highly significant correlations between dioecy and all four traits if one tallies the number of species with and without the four traits in dioecious focal lineages and their sister groups, as done in traditional species-level analyses (contingency tests, $P < 0.0001$; Table 2). Furthermore, most dioecious focal lineages are associated with a number of the traits. All lineages were associated with at least one of the traits and 63 of 93 (68%) with three or four traits. Woody growth form was the most prevalent trait, found in 78 of 93 (84%) dioecious focal lineages, followed by plain flowers (83%), tropical distribution (69%), and fleshy fruits (56%).

Species Richness

Restricting our attention to the 33 sister-group pairs in which the dioecious focal lineages and their sister groups possess the same combination of the four traits (see Appendix), dioecious lineages still have lower species richness than

TABLE 3. Evolutionary success (ES) values for sister-group comparisons in which the dioecious focal lineage and its nondioecious sister group have the same ecological trait. We chose sister-group pairs from set 1 (Table 1) where the focal group and sister group shared the same state of the ecological trait being analyzed. We determined whether evolutionary success was higher in dioecious focal lineages associated with an ecological trait (e.g., tropical distribution) than in those lacking the trait (e.g., temperate distribution) with two-sample t-tests.

Trait	State	N	Mean ES value	P
Distribution	tropical	52	0.546	0.03
	temperate	16	0.233	
Growth form	woody	60	0.533	0.54
	herbaceous	12	0.434	
Flowers	plain	52	0.464	0.36
	showy	12	0.318	
Fruit	fleshy	40	0.563	0.03
	dry	32	0.311	

their sister groups ($P = 0.024$). Thus, the low representation of dioecy among angiosperms can be partially attributed to the lower evolutionary success, on average, of lineages with a dioecious breeding system.

Individual Traits

Our analyses of sister-group pairs with dioecious focal lineages having the same status of an ecological trait as their sister group revealed that ES values of dioecious focal lineages were significantly higher when both groups had a tropical distribution ($t_{66} = 2.21$, $P = 0.03$) and fleshy fruits ($t_{70} = 2.16$, $P = 0.03$) than when they did not. The evolutionary success of dioecious focal lineages also increased, albeit not significantly, when the sister-group pairs were associated with woody growth form and plain flowers (Table 3). In light of previous conclusions about the evolutionary success of dioecious lineages (Heilbuth 2000), it is worth noting that the presence of the ecological traits results in dioecious focal lineages having ES values not significantly higher than 0.5 (two-sample t-tests, all $P > 0.25$). In other words, although possessing an ecological trait tended to reduce the disparity in species richness between dioecious lineages and their nondioecious sister groups, it did not result, on average, in dioecy being a more evolutionary successful trait than cosexuality (i.e., possessing a nondioecious breeding system).

Trait Combinations

Evolutionary success of dioecious and control focal lineages tended to respond differently to the various trait combinations (Fig. 3). For example, herbaceous dioecious focal lineages (Fig. 3A, C, E, G) tended to be rare and/or have low ES values unless they had a tropical distribution and plain flowers, whereas herbaceous control focal lineages were relatively common and had ES values close to 0.5 unless in combination with fleshy fruits (Fig. 3C, G). Of the seven combinations that were tested, only one yielded a marginally significant difference: the control focal lineages tended to have higher ES values than dioecious focal lineages when associated with a temperate distribution, herbaceous growth form, plain flowers, and dry fruits ($t_{10} = 2.01$, $P = 0.07$;
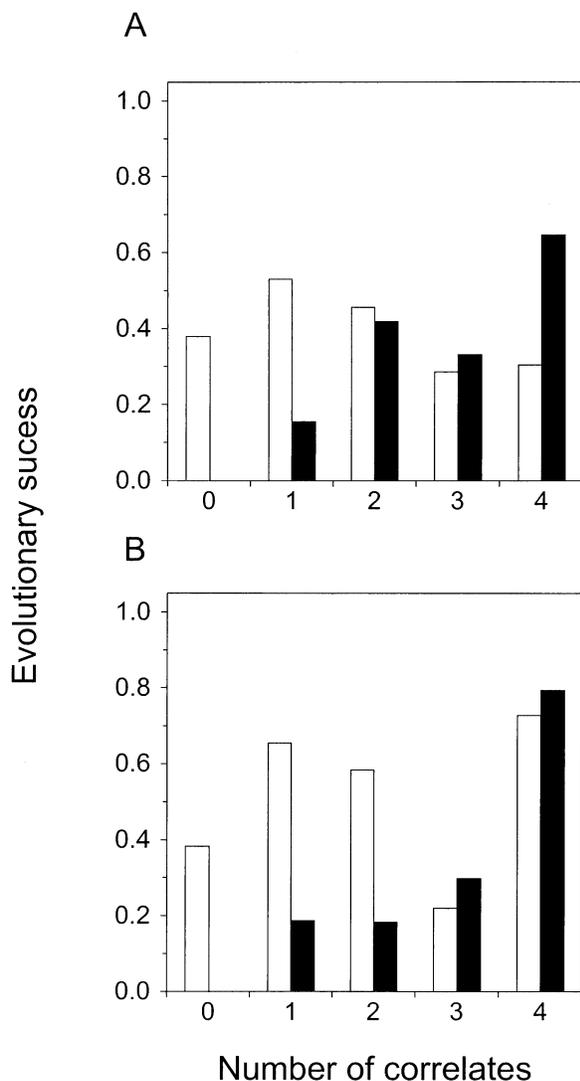
A

B

Number of correlates

FIG. 4. Evolutionary success of dioecious (filled) and control (open) focal lineages as a function of number of ecological traits observed in the focal group, for the entire dataset (A) or when considering only those sister-group pairs with the same combination of traits (B). Relative evolutionary success increases with number of ecological traits for dioecious, but not control, focal lineages.

Fig. 2A). This combination, which involved only a single ecological trait (i.e., plain flowers), may confer higher evolutionary success to lineages with a cosexual breeding system.

Number of Traits

Dioecious focal lineages with more of the ecological traits were not only more common but tended to have higher evolutionary success than those with few traits. Using all 93 sister-group pairs (i.e., sets 1 and 3), ES values of dioecious focal lineages showed a highly significant increase with the number of correlates ($F_{1,91} = 6.83$, $P = 0.01$), whereas ES values tended to decrease with number of traits possessed by the control focal lineages ($F_{1,91} = 1.780$, $P = 0.18$; Fig. 4A). Furthermore, the slopes of these relationships were significantly different ($F_{1,182} = 7.74$, $P = 0.006$). Analyses of sets

2 and 4 (i.e., both members of a sister-group pair are associated with the same number of traits) produced a similar pattern, with ES values increasing significantly with number of traits possessed by dioecious focal lineages ($F_{1,31} = 9.03$, $P = 0.005$. Fig. 4B). The hypothesized null distribution of ES values as a function of number of traits was upheld, with the analysis of 32 control focal lineages producing a slope not significantly different from zero ($F_{1,30} = 0.004$, $P = 0.95$) and an intercept not significantly different from 0.5 ($t_{30} = 0.53$, $P = 0.60$). Overall, dioecious focal lineages associated with more of the ecological traits are shown to have higher evolutionary success, a pattern not found with control focal lineages, which may contribute to the correlations between dioecy and the individual traits.

DISCUSSION

In addition to confirming that dioecy is associated with low species diversity compared with their nondioecious sister groups (Heilbuth 2000), our analyses show that the relative species richness of dioecious lineages is dependent on their association with ecological traits. The observation that dioecy is commonly associated with certain ecological and life-history traits, such as tropical distribution, woody growth form, plain flowers, and fleshy fruits has typically been attributed to dioecy evolving more often in lineages with these traits (Fig. 1A; also see Bawa 1980; Givnish 1980; Charlesworth 1993). Our results provide strong support for the hypothesis that differential evolutionary success of lineages that possess one or more of the ecological traits may contribute to the observed correlations (Fig. 1B). We found that an increase in the number of traits possessed by dioecious focal lineages was associated with increased relative evolutionary success compared to their nondioecious sister groups. Furthermore, the effects of these four traits appear to depend on breeding system, because a similar analysis conducted with control (i.e., nondioecious) focal lineages did not reveal the same pattern. In addition to an effect of number of traits, certain combinations of these traits appear to be more successful than others. Tropical distribution and fleshy fruits were found to be the most important traits for increasing the evolutionary success of dioecious lineages.

Attributes commonly correlated with dioecy, thus, appear to have allowed dioecious lineages to have higher degrees of evolutionary success. The observation that dioecious lineages have higher evolutionary success when in combination with certain ecological traits has rarely been discussed (but see Donoghue 1989), yet our findings are consistent with previous work on dioecy. First, dioecious lineages with showy flowers may develop extreme sexual dimorphism, which can lead to higher extinction rates when pollinators become rare and neglect to visit the females (Vamosi and Otto 2002). Such a mechanism would lead to a preponderance of dioecious lineages with plain flowers even with equal transition rates to dioecy in showy- and plain-flowered lineages. Second, fleshy fruits are often dispersed by birds, which are thought by some to disperse fruit farther (Bawa 1980; Givnish 1980). Greater seed dispersal could be an important determinant of success in dioecious species that have twice the amount of sib-competition because seeds disperse around

only the females in a population with separate sexes (Heilbuth et al. 2001; Wilson and Harder 2003). Finally, the correlation with woody habit may exist because long-lived dioecious species are less likely to go extinct because individuals have a higher probability of finding a mate (Pannell and Barrett 1998).

We found evidence for increased diversification in dioecious focal lineages with tropical distributions and also in lineages with fleshy fruits. The most established theory regarding the prevalence of dioecy in the tropics has proposed that it is an indirect result of the high incidence of woody lineages within the tropics bearing fleshy fruits (Bawa 1980; Sakai and Weller 1999). A recent phylogenetic analysis revealed that lineages with fleshy fruits are indeed more common in the tropics (Vamosi et al. 2003) and, thus, the greater evolutionary success of dioecy in tropical lineages compared with temperate lineages may simply be due to the high incidence of fleshy fruits. However, controlling for the presence of the other traits reveals that dioecious focal lineages evolving in tropical dry-fruited lineages have a mean ES value of 0.34, whereas dioecious focal lineages evolving in temperate fleshy-fruited lineages have a mean ES value of 0.31. Both of these values are approximately half of the mean ES value (0.64) for dioecious focal lineages associated with both traits, indicating that both of these traits contribute relatively equally to the increase in evolutionary success of dioecious focal lineages (Fig. 3). These findings imply that there is something unique about the tropical climate that is critical for the success of dioecious lineages notwithstanding the high proportions of fleshy-fruited, woody species found in the tropics. One factor that warrants closer attention as a possible cause of the increased success of dioecious lineages in the tropics is selection for greater seed size due to high predation pressures within the tropics (Janzen 1971; Coley and Barone 1996; Harms and Dalling 1997). Another factor worth investigating is the lack of seasonality in the tropics, which may allow for increased asynchrony of flowering and fruiting, thereby potentially decreasing competition for pollinators and dispersers with nondioecious species.

Perhaps surprisingly, the traits that appear to result in higher evolutionary success in dioecious lineages are typically thought to reduce diversification rates in angiosperms. Short life spans in angiosperms have repeatedly been found to be associated with an increase in diversification (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Dodd et al. 1999; Verdú 2002). Angiosperm lineages bearing dry fruit have higher species richness, on average, than those with fleshy fruits (Tiffney and Mazer 1995), whereas we found that bearing fleshy fruits was associated with higher species richness in dioecious lineages. Biotic pollination may result in larger lineages than abiotic pollination (which is strongly correlated with flowers that are plain) as a result of the coevolutionary dynamics of plants with their pollinators (West-Eberhard 1983; Kiester et al. 1984). Together, these factors may be partially responsible for the observed trend in control focal groups for evolutionary success to decrease when in combination with higher numbers of the traits correlated with dioecy (especially woody growth form, plain flowers, and fleshy fruit). We speculate that dioecious lineages experience reduced extinction rates when associated with woody growth form, plain flowers and fleshy fruits, but still suffer from reduced speciation rates for the reasons discussed above for nondioecious lineages. This interplay between speciation and extinction rates would result in the correlations between dioecy and these ecological traits and reduced prevalence of dioecy amongst angiosperms, because dioecy appears to have increased evolutionary success in lineages that, generally, do not experience high rates of diversification.

Factors associated with variation in diversification rates in angiosperms have received considerable attention in recent studies (e.g., Eriksson and Bremer 1992; Ricklefs and Renner 1994; Tiffney and Mazer 1995; Dodd et al. 1999; Heilbuth 2000; Verdú 2002; Sims and McConway 2003). We suggest that future large-scale studies of species richness should account for breeding system status of lineages to better understand these differing patterns of diversification. Furthermore, we found that the correlations between dioecy and tropical distribution, woody growth, plain flowers, and fleshy fruits are caused, at least in part, by the increased evolutionary success experienced by dioecious lineages that possess these traits. This finding may explain why previous transition rate analyses have been able to confirm the presence of the correlations but unable to rule out any of the theories about the sequence of acquisition of traits that form the correlations with dioecy (Donoghue 1989; Sakai et al. 1997; Vamosi et al. 2003). Acknowledging that two processes instead of one are causing the correlations between dioecy and various ecological traits represents a significant step forward in our understanding of the connections between ecology and adaptation.

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