

# Present day risk of extinction may exacerbate the lower species richness of dioecious clades

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## ABSTRACT

Dioecious clades have been observed to have lower species richness than their non-dioecious sister groups indicating that dioecious species experience higher extinction rates and (or) lower speciation rates. To determine whether current threats to biodiversity may exacerbate this pattern, we examined the threat to exclusively dioecious families of angiosperms among the 13,013 species of threatened plants included in the IUCN Red List of Threatened Species. When examined phylogenetically, dioecious families had proportionally more species listed than their sister groups. We then examined whether ecological traits correlated with dioecy, namely tropical distribution, woody growth form, and fleshy fruits, are associated with having higher proportions of threatened species. Ignoring breeding system, woody growth form was the only trait that was associated with a greater than expected proportion of threatened species per family. Red-Listed dioecious families were more likely to have a woody growth form than non-dioecious families. Woody growth habit is likely contributing to the higher incidence of dioecious species being at risk of extinction but is not solely responsible for the pattern because higher risk within dioecious groups was also apparent in a comparison of exclusively woody sister-group pairs. Our results indicate that dioecious plants may warrant special attention in conservation practices.

## Keywords

Angiosperms, biodiversity, dioecy, evolutionary history, extinction, sister-group comparisons, species richness.

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## INTRODUCTION

The world is facing an extinction crisis (Koopowitz & Kaye, 1990; McKinney, 1999; von Euler, 2001). Without question, some species will be more at risk than others (Bennett & Owens, 1997; Russell *et al.*, 1998; Purvis *et al.*, 2000; Cardillo & Bromham, 2001). Thus, it is imperative that we begin to assess which species are more at risk than others and the most likely causes of extinction in order to formulate plans for preserving biodiversity and evolutionary history (Nee & May, 1997; Heard & Mooers, 2000). The IUCN Red List of Threatened Species™ (IUCN, 2003; hereafter referred to as 'Red List'), the most recent worldwide list of endangered and threatened species available, allows us to perform comparative tests to infer whether species with certain distributions, life histories, or breeding systems are more at risk than others. This is a potentially fruitful avenue for research (see Cardillo & Bromham, 2001), but one where plants have been particularly neglected. Considering how the loss of evolutionary history is greatly magnified when extinction is concentrated on certain branches of a phylogeny over others (Heard & Mooers, 2000), performing these studies is of great importance. Based on

empirical studies of local flora (Gillespie, 1999; Somanathan & Borges, 2000) and phylogenetic analyses of species richness (Heilbuth, 2000), various authors have hypothesized that angiosperms with a dioecious breeding system may be more prone to extinction. Here we examine how breeding systems, especially dioecy, may affect the risk of extinction in angiosperm families on a global scale.

Dioecy, the breeding system whereby there are separate male and female individuals, is thought to evolve frequently within angiosperms due to short-term benefits accrued in terms of reduced inbreeding depression and/or more efficient allocation of resources (reviewed by Charlesworth, 1999). However, despite the potential benefits of separating sexual functions, dioecy is found in only a very small proportion of flowering plants (*c.* 6%; Renner & Ricklefs, 1995), partially because dioecious clades have lower species richness than their non-dioecious sister groups (Heilbuth, 2000; Vamosi & Vamosi, 2004). It is unknown, at present, whether the cause of this pattern is due to higher extinction rates or lower speciation rates or both. Several hypotheses have been proposed as to why dioecious plants may be at a severe disadvantage compared to non-dioecious plants, including

reduced mate assurance (Pannell & Barrett, 1998), a 'seed-shadow handicap' (Heilbuth *et al.*, 2001), and a reliance on large pollinator pools (Vamosi & Otto, 2002). First, the founding of new subpopulations may be hampered by the need for at least one individual of each sex to be present. Second, the seed-shadow handicap, which exists because only females produce seeds, further slows the spread of dioecious populations and also makes them more vulnerable to invasion by non-dioecious species (Heilbuth *et al.*, 2001; Wilson & Harder, 2003). Finally, reliance on pollinators, which may experience rather dramatic fluctuations in their population abundance over time (Herrera, 1989; Eckhart, 1992; Kevan & Phillips, 2001; Roubik, 2001), may increase the likelihood of extinction in dioecious populations (Vamosi & Otto, 2002). Acting alone or in concert, these mechanisms may increase the probability of extinction in dioecious lineages or limit their potential for speciation.

Other attributes of dioecy may make them particularly susceptible to anthropogenic disturbances. Dioecy is correlated with a number of ecological traits (Vamosi *et al.*, 2003; Vamosi & Vamosi, 2004) including having a tropical distribution (Carlquist, 1974; Bawa, 1980; Givnish, 1980), woody growth form (Freeman *et al.*, 1980; Fox, 1985; van Dulmen, 2001), and fleshy fruits (Givnish, 1980; Muenchow, 1987; Renner & Ricklefs, 1995). Weak economies, rapid population expansion, and practices such as clear cutting and slash-and-burn agriculture are potential sources of threat to all plants in the tropics (Koopowitz & Kaye, 1990). Woody plants are especially vulnerable, given their economic value as timber and their long regeneration times (Martinez-Garza & Howe, 2003). Habitat disturbances may impact population densities of native birds and mammals that disperse fleshy fruits over long distances, reducing the ability of fleshy-fruited dioecious species to colonize cleared habitats (Gillespie, 1999). Furthermore, introduced species may forage on fruits without providing the benefits of seed dispersal (Merrett *et al.*, 2002). For these reasons, dioecious species may be more threatened than non-dioecious species more because of the complex of traits that they are associated with rather than because of their breeding system. We utilize a sister-group comparison approach to determine whether breeding system affects risk of extinction in angiosperms. We compared the number of threatened species in all exclusively dioecious families (whether or not they were listed on the Red List) with that of their sister groups. In this approach, shared evolutionary history is explicitly accounted for (Felsenstein, 1985), thus reducing the number of traits other than dioecy that could influence extinction risk. To further explore the conditions that are conducive to increased threat, we assessed whether: (1) any of the three ecological traits (i.e. tropical distribution, woody growth form, and fleshy fruits) were associated with increased threat irrespective of breeding system, and (2) these ecological traits also tended to be over-represented in threatened exclusively dioecious families.

## METHODS

We gathered information on the presence and abundance of dioecy and number of threatened species in each of the 455 families

of angiosperms represented by the Brummitt (1992) classification system, which conforms most closely to the Red List scheme (IUCN, 2003). Only a portion of the taxa represented in the 1997 Red List have had their status re-classified according to new guidelines of the 2003 Red List. We followed the suggestion on the 2003 Red List web site and combined the data on threat status from the 1997 (Walter & Gillett, 1998) and 2003 (IUCN, 2003) versions. When a family was listed in both versions, we recorded the number of threatened species that was higher. Furthermore, when families were not found in either version of the Red List, we assumed that they do not contain any threatened species, even though their absence may be the result of inadequate information. The representation of dioecy in each angiosperm family was determined using a large database from Renner & Ricklefs (1995). We classified any taxa listed in the Renner & Ricklefs (1995) database in families that are not recognized by Brummitt (1992) to conform to the Brummitt system. Sister groups of dioecious families were determined by consulting family level phylogenies (e.g. Soltis *et al.*, 2000; Stevens, 2001; see Table 1), using the most current information when sources differed.

To adequately test the hypothesis of whether dioecious families are more at risk of extinction in a phylogenetic manner, we need to include those families that are not present on the Red List. We identified 47 families that are entirely dioecious according to the Brummitt (1992) system of classification. In the sister-group comparisons including Araliaceae, Cymodoceaceae, Griseliniaceae, Misodendraceae, Phellinaceae, Physenaceae, and Trochodendraceae and their respective sister groups, neither the dioecious family nor its sister group had a single member on the Red List. Because this scenario results in an uninformative 'tie' of zero between the proportions of species threatened in the two groups, these groups were excluded from the analysis. We also excluded Lomandraceae, Pandaceae, Scyphostegiaceae, and Salicaceae because recent phylogenetic analysis (APG, 2003) has revealed that the positions of these families are extremely uncertain at present, making it unclear which clade(s) should be used as the sister group. If a dioecious family was the sister group to another dioecious family then they were combined to form a dioecious clade (e.g. Aucubaceae + Eucommiaceae + Garryaceae). We should note that Aquifoliaceae, although having only *c.* 92% of its species dioecious, was included as an entirely dioecious family due to its being the sister group of the entirely dioecious Helwingiaceae. Casuarinaceae and Anarthriaceae were excluded because they constitute outgroups to sister-group pairs already included in the analysis. These procedures of pruning comparisons, which are analogous to those performed by other sister-group analyses (e.g. Farrell *et al.*, 1991; Heilbuth, 2000; Sargent, 2004), leave us with 32 sister-group pairs containing a dioecious clade and at least one threatened species, either in the dioecious clade or its non-dioecious sister group (Table 1).

Determining whether dioecious families were more threatened than their sister groups entailed controlling for the large discrepancy in clade size that was common among the sister-group pairs (Table 1; see also Heilbuth, 2000). We did this by calculating the proportion of threatened species in the sister-group pair that are in the dioecious group and subtracting the

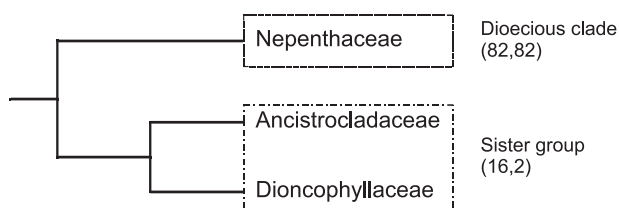
**Table 1** Number of species (No.) and number of listed species (Threat.) for exclusively dioecious angiosperm families represented in the Red List and their sister clades. To determine whether the dioecious clade is more threatened than its sister group, the test statistic (*T*) is calculated as the proportion of threatened species in the entire sister-group pair minus the proportion of total species in dioecious clade. For example, for the sister-group pair, Aextoxicaceae + *Berberidopsis*, Aextoxicaceae has 100% of the threatened species and  $1/(1 + 3) = 25\%$  of the species richness, giving *T* a value of  $(1.00 - 0.25) = 0.75$ . Sister-group pairs where both the dioecious group and its sister groups are composed of all woody members are marked with an asterisk

Dioecious Clade	No.	Threat.	Sister Clade	No.	Threat	T	Ref‡
*Aextoxicaceae	1	1	<i>Berberidopsis</i>	3	0	0.75	1
Achatocarpaceae	6	0	Amaranthaceae + Chenopodiaceae	2250	132	-0.0027	2
Amborellaceae	1	0	All angiosperms	232871	33086	-0.000004	1
*Aquifoliaceae + Helwingiaceae	375	72	<i>Phyllonoma</i>	8	0	0.02	1
Asteliaceae	34	9	Hypoxidaceae	142	6	0.41	1
Aucubaceae + Eucommiaceae + Garryaceae	15	1	Gentianales + Solanales + Lamiales	32759	4617	-0.0002	3
*Balanopaceae	9	1	Chrysobalanaceae + Dichapetalaceae + Trigoniaceae	714	287	-0.009	1
Barbeyaceae	1	0	Eleagnaceae + Rhamnaceae + <i>Dirachma</i>	952	182	-0.001	1
Cercidiphyllaceae	2	1	Haloragaceae + Crassulaceae + Saxifragaceae + Grossulariaceae	1768	372	0.002	4
Daphniphyllaceae	10	2	Paeoniaceae	30	11	-0.10	4
Datisceae	4	2	Begoniaceae	1020	64	0.03	1
*Didieraceae	11	3	<i>Calyptrorhiza</i>	2	0	0.15	5
*Didymelaceae	2	0	Buxaceae	70	21	-0.03	1
Dioscoreaceae	650	72	Taccaceae	10	0	0.01	6
*Ebenaceae	450	99	Lissocarpaceae	4	0	0.01	5
Hanguanaceae	6	0	Commelinaceae	700	29	-0.01	1
Lactoridaceae	1	0	Aristolchiaceae	475	35	-0.002	1
*Leitneriaceae	1	1	Simaroubaceae	50	13	0.05	1
Lepidobotryaceae	2	0	Parnassiaceae + Celastraceae	816	96	-0.002	1
Menispermaceae	400	38	Berberidaceae + Ranunculaceae	2650	337	-0.04	1
Montiniaceae	3	1	<i>Hydrolea</i> + <i>Sphenoclea</i>	13	0	0.81	3
*Myristicaceae	300	225	Annonaceae + Degeneriaceae + Eupomatiaceae + Himantandraceae + Magnoliaceae	2527	278	0.32	1
Myrothamnaceae	2	0	Gunneraceae	50	5	-0.04	1
Nepenthaceae	82	82	Ancistrocladaceae + Dioncophyllaceae	16	2	0.14	1
Pandanaceae	777	41	Cyclanthaceae	180	6	0.06	1
Restionaceae	320	58	Centrolepidaceae	36	6	0.01	1
*Ruscaceae	8	4	Asparagaceae	55	13	0.11	1
*Sargentodoxaceae	1	0	Lardizabalaceae	30	5	-0.03	1
Simmondsiaceae	1	0	Caryophyllales	7125	1426	-0.0001	5
Smilacaceae	311	11	Rhipogonaceae	6	0	0.02	1
*Sphenostemonaceae	7	1	Paracryphyaceae	1	0	0.13	7
*Ticodendraceae	1	1	Betulaceae	15	8	0.06	1

\*‡References used for phylogeny are numbered as follows: (1) Stevens (2001 onwards); (2) Kadereit *et al.*, 2003; (3) Bremer *et al.*, 2002; (4) Soltis *et al.*, (2000); (5) APG (2003); (6) Caddick *et al.*, 2002; (7) Cameron, 2003.

proportion of total species in the sister-group pair that are dioecious (Fig. 1). With a null hypothesis that there should be no difference in extinction risk between the dioecious and non-dioecious sister-group pair, the number of threatened species in the dioecious group should be in proportion to its relative species richness within the sister-group pair. This approach leaves us with a test statistic that should be significantly higher than zero if the

dioecious families have, on average, more species listed on the Red List than expected compared to the sister group. We should note here that this procedure is conservative in that the inclusion of small dioecious clades that have no listed species (e.g. the monotypic family Barbeyaceae; Table 1) will reduce the significance of the test because the null hypothesis predicts a very low probability of small clades having even a single threatened species. Our



**Figure 1** A sister-group comparison illustrating the asymmetry of species richness and proportion threatened among the members of a sister-group pair. Numbers in parentheses refer to: (number of species in clade, number of species threatened). This sister-group pair contains 98 species, of which 82 (83.7%) are found in the dioecious clade. Eighty-four of the 98 species are threatened, 82 (97.6%) of which are dioecious. Thus, in this case, more of the threatened species are found in the dioecious clade than expected (i.e. % threatened species that are dioecious — % species that are dioecious > 0).

approach to calculating the test statistic is based on the methods developed by Barraclough *et al.* (1995).

We sought to determine whether patterns of threat were associated with the state of three ecological trait(s): distribution, fruit type and growth form. We assigned traits to all of the angiosperm families in terms of their distribution (subtropical/tropical, temperate or both), growth form (woody, herbaceous or both) and fruit type (fleshy, dry or both) by consulting the DELTA database (Watson & Dallwitz, 1992). As discussed earlier, dioecious taxa tend to be associated with tropical distributions, woody growth form, and fleshy fruits. We utilized a non-phylogenetic analysis to obtain a preliminary assessment whether these traits were associated with increased threat. The percentage of species at risk in each family was subject to the modified arcsine transformation recommended by Zar (1996) for data sets with small and large proportions:

$$p' = [\arcsin\sqrt{X/(n+1)} + \arcsin\sqrt{(X+1)/(n+1)}] \quad (1)$$

We analysed the effect of each ecological trait with one-way ANOVAS; differences among means were assessed with the Tukey HSD test. We then determined whether the proportions of listed dioecious families with these ecological traits differed from that of listed non-dioecious families with a Fisher exact test. Finally, to determine if dioecy is associated with higher risk even when the presence of other traits associated with risk are controlled for, we repeated our phylogenetic test for differences in proportion of threatened species using the subset of the sister-group comparisons where both clades had similar ecological traits (e.g. both the dioecious family and its sister group had a woody growth form). If dioecious families tend to have a greater proportion of their species threatened in this analysis, it suggests that something unique to dioecy is responsible for the levels of threat observed.

## RESULTS

Results from the 32 sister-group comparisons revealed that the number of threatened species in the dioecious group was greater

than expected in 18 sister-group comparisons, and less than expected in 14 sister-group comparisons. On average, the proportion of threatened species in the dioecious group was significantly higher than the proportion of total number of species in the dioecious group (Table 1,  $P = 0.016$ , Wilcoxon signed rank test). Our results indicate that, even for closely related groups that have a number of traits in common, a difference in breeding system can have an effect on extinction risk.

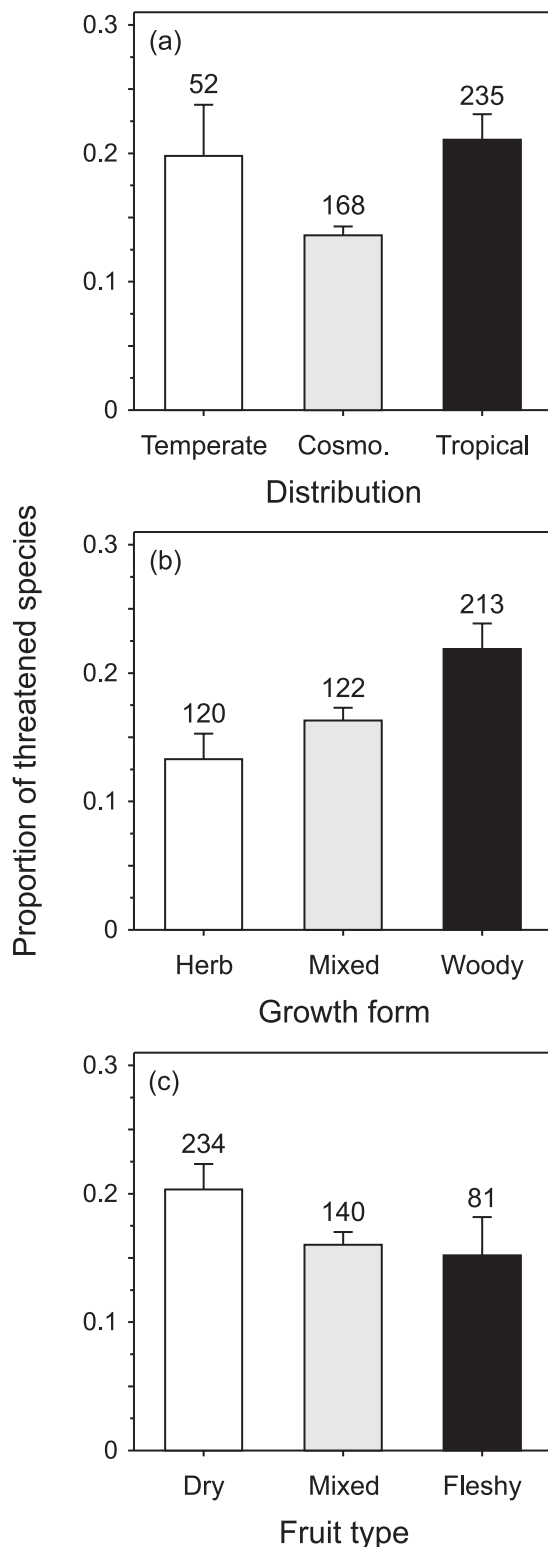
Examining the level of risk of angiosperms in terms of distribution, growth form, and fruit type, independent of breeding system, indicates that all three traits showed some patterns in terms of extinction risk. By examining all 455 families of angiosperms we found distribution to have a significant effect on threat ( $F_{2,455} = 7.44$ ,  $P = 0.0007$ ), with threat being significantly higher in families with subtropical/tropical or temperate distributions than in families with representatives in both regions (Fig. 2a). Growth form also had a significant effect on threat ( $F_{2,455} = 7.47$ ,  $P = 0.0006$ ), with woody families having significantly higher proportion of species threatened than families with herbaceous growth forms (Fig. 2b). Finally, fruit type also had a significant effect on threat ( $F_{2,455} = 4.51$ ,  $P = 0.012$ ), with families possessing only dry fruit having a higher proportion of their species threatened than families with mixed fruit types.

Twenty-five of 329 angiosperm families represented in the Red List were exclusively dioecious (Table 1) and 187 families were exclusively non-dioecious. Among listed families, a significant association was observed only between dioecy and growth form (Table 2). Eighteen of the 25 (72%) dioecious families represented on the Red List were characterized as having woody or shrubby growth forms, whereas this was true for only 73 of 187 (39%) non-dioecious families (Fisher exact test,  $P = 0.002$ ). Proportions of listed species having only dry fruits or distributions restricted to temperate or tropical regions were equivalent between breeding system classes (Table 2).

The former set of results suggests that the increased proportion of threatened species in dioecious groups may be due to a correlation between dioecy and woody growth form, with woodiness being the causative factor rather than dioecy. Restricting our attention to the 12 sister-group comparisons where both the

**Table 2** Proportions of character states for exclusively dioecious and exclusively non-dioecious angiosperm families found in the Red List. Significance levels based on Fisher's exact tests

Trait	+	–	<i>P</i>
<i>Distribution</i>	Temperate or Tropical	Cosmopolitan	
Dioecious	19	6	0.22
Non-dioecious	123	64	
<i>Growth form</i>	Woody	Herbaceous/Mixed	
Dioecious	18	7	0.002
Non-dioecious	73	114	
<i>Fruit</i>	Fleshy/Mixed	Dry	
Dioecious	12	13	0.26
Non-dioecious	73	114	



**Figure 2** Mean (+ standard error) proportion of threatened species, regardless of breeding system, as a function of distribution (a), growth form (b), and fruit type (c). Bars in black designate the characteristic dioecious condition (i.e. subtropical or tropical distribution, woody growth form, and fleshy fruits). Numbers above the bars designate the number of families in each category.

dioecious family and its sister group had a woody growth form, we found that the proportion of threatened species in the dioecious clade was still higher than expected ( $P = 0.013$ , one-tailed Wilcoxon signed rank test). This finding reinforces the notion that something unique to exclusively dioecious families is associated with increased threat.

## DISCUSSION

Dioecy is a plant breeding system that has been associated with reduced speciation rates and (or) extinction rates (Baker, 1959; Heilbut, 2000). Extinction rates may be elevated because only female individuals bear seed and, hence, suffer half the number of seed shadows, which may reduce their spread compared to non-dioecious lineages (Heilbut *et al.*, 2001). Dioecious lineages may also be more prone to extinction through the interplay between selection for increased showiness of male flowers and fluctuations in densities of pollinators (Vamosi & Otto, 2002). In this paper we evaluated whether dioecious angiosperm families are currently more vulnerable to extinction than non-dioecious lineages by examining their representation in the Red List (IUCN, 2003).

The proportion of species threatened in exclusively dioecious families was found to be significantly higher than expected when compared to non-dioecious sister-groups. We are unable to discern the ultimate cause for the increased risk to dioecious families. A possible artifact may be that dioecious species are investigated more often because of their relatively unique breeding system or because they tend to be found in small clades. However, we feel that recording bias is an unlikely ultimate cause of the patterns reported here because dioecious species are rarely showy; indeed, dioecy is correlated with white, inconspicuous flowers (Bawa, 1980). Thus, they are likely to be undervalued and/or overlooked by all but the most dedicated researchers and amateur naturalists. Potential causes of a real increased risk for dioecious species include the harvesting of woody species for their timber or to make way for agriculture and the relatively slow recovery of woody species following such disturbances (Martinez-Garza & Howe, 2003). Thus, increased threat to dioecious taxa may become apparent solely because of an underlying correlation between woodiness and dioecy. Indeed, the major threats listed in the record for the dioecious katsura tree (*Cercidiphyllum japonicum*) in China and Japan, for example, were both harvesting and poor regeneration, with the latter being cited as the main threat (Walter & Gillett, 1998). However, the finding that the majority of sister-group comparisons consisted of comparisons between exclusively woody dioecious families and their woody sister groups strongly suggests the association with woody growth form alone cannot account for the increased threat to dioecious species.

This study gathers evidence that anthropogenic disturbances differentially affect dioecious species on a global scale, likely by further reducing mate assurance (Pannell & Barrett, 1998). Females of dioecious populations require visits from pollinators that have recently received pollen from a male individual. All else being equal, this probability is lower than that for an individual

in a hermaphroditic population (Vamosi & Otto, 2002). Selective logging and (or) habitat fragmentation is likely to have cascading effects: individuals become more isolated → altered behaviour of pollinators/dispersers → reduced number of cross-pollination events → reduced seed set (Mack, 1997; Gillespie, 1999; Somanathan & Borges, 2000; Ghazoul & McLeish, 2001). Furthermore, the negative impacts of this cascade are likely to be exacerbated by decreases in pollinator abundances. Gillespie (1999) found that the abundance of dioecious species in Central America decreased with decreasing forest cover and fragment size and posited that a reduction in pollinator visits was the cause. Females of the dioecious canopy tree *Aglaia flavida* that were situated greater than 200 m from a male produced significantly smaller crop sizes (Mack, 1997). Clearly, more information is needed about the specific threats to dioecious species. Future examination of whether animal-pollinated species are more at risk of extinction than wind-pollinated species could potentially indicate whether pollination is the most prevalent cause of increased extinction to dioecious species.

The correlation of dioecy with other traits, such as fleshy fruits and tropical distribution, do not appear to be factors associated with increased vulnerability of dioecious clades in our analysis. Our results are consistent with that of Gillespie (1999) who found that, although mammal-dispersed species may be more at risk of extinction in Central America, species dispersed by other animals were not. While this may be the general pattern, poor fruit dispersal has been cited as the likely factor influencing the risk of extinction of the dioecious *Gardenia actinocarpa* (Osunkoya, 2003). Although families with a tropical distribution tended to have a relatively high proportion of species threatened there was, somewhat surprisingly, no correlation between threatened dioecious families and tropical distribution. This pattern is consistent with the observation that dioecious clades were no more likely to be at risk of extinction than hermaphroditic clades in the Hawaiian Islands (Sakai *et al.*, 2002). Dioecious clades have been observed to be more evolutionarily successful in the tropics than in temperate environments (Vamosi & Vamosi, 2004) and therefore may be better able to resist the effects of anthropogenic changes in tropical environments. The reasons for the increased evolutionary success of dioecious lineages in the tropics may be simply due to the correlation between tropical environments and fleshy fruit (Bawa, 1980; Vamosi *et al.*, 2003) or due to some as yet unidentified factor such as reduced predation or shade tolerance (Vamosi & Vamosi, 2004).

The already low species richness of dioecious families (Heilbuth, 2000) is likely to be an important factor in the present day risk to dioecious species: five of the 25 (20%) exclusively dioecious families represented in the Red List are monotypic compared to 14 of the 187 (7%) nondioecious families. Russell *et al.* (1998) documented that, in birds and mammals, species in small genera tended to have higher probabilities of extinction. Furthermore, the lower species richness of dioecious clades makes the patterns in terms of higher contemporary risk of extinction for dioecious families all the more worrisome. If dioecious families do go extinct, the potential loss of evolutionary history

may be quite severe. These results suggest that dioecious lineages may warrant special attention for conserving evolutionary history.

Heard & Mooers (2000), extending the findings of Nee and May (1997), found that loss of evolutionary history will considerably increase if: (1) extinction rates vary among lineages, and (2) extinction is concentrated in lineages that have lower speciation rates. We have shown that the former is almost certainly true for angiosperm lineages and that this variation depends, at least partially, on breeding system. Whether speciation rates of dioecious clades are, in fact, lower than those of nondioecious clades has yet to be assessed. Dioecious clades are not likely to experience higher speciation rates, at the very least, given the low relative species richness of dioecious clades (Heilbuth, 2000) and the high amounts of gene flow estimated for outcrossing species (Hamrick & Godt, 1996; Loveless *et al.*, 1998). Therefore, based on the results of this study and previous work which identified their already low species richness (Heilbuth, 2000), we advocate that strategies aimed at preserving evolutionary history in angiosperms should include special consideration of dioecious lineages.

Identifying groups of organisms that may be particularly vulnerable to extinction promises to be a fruitful first step in attempts to preserve biodiversity and evolutionary history. Analyses to date have focused mostly on the effects of body size on risk of extinction in birds and mammals (Russell *et al.*, 1998; Cardillo & Bromham, 2001). Our study of angiosperms indicates that breeding system is a factor associated with higher risk of extinction. The next logical step is to assess the causes of non-random patterns in the risk of extinction and to determine whether they are the same causes that predisposed these lineages to low diversification (i.e. speciation–extinction) rates in the past. For example, how exactly do pollination dynamics increase the risk of extinction of dioecious species, and did such dynamics have the same effect on extinction rates of dioecious lineages in the past? To begin to answer such questions, future efforts in this area will involve investigating the angiosperm fossil record to determine whether patterns of extinction in dioecious families in the past reflect current patterns of risk (J. Vamosi, unpublished data).

## ACKNOWLEDGEMENTS

We thank S. Otto for discussions about the consequences of dioecy for extinction and speciation in angiosperms, S. Renner for providing us with her database of dioecious angiosperms, P. Abrams, S. C. H. Barrett, and L. Rowe for providing logistic support, and two anonymous reviewers for insightful comments on the manuscript. This work was made possible by postdoctoral fellowships to both authors from the Natural Sciences and Engineering Research Council (Canada).

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