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THE DISTRIBUTION OF PLANT MATING SYSTEMS: STUDY BIAS AGAINST OBLIGATELY OUTCROSSING SPECIES

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Abstract.—Early models of plant mating-system evolution argued that predominant outcrossing and selfing are alternative stable states. At least for animal-pollinated species, recent summaries of empirical studies have suggested the opposite—that outcrossing rates do not show the expected bimodal distribution. However, it is generally accepted that several potential biases can affect conclusions from surveys of published outcrossing rates. Here, we examine one potential bias and find that published studies of outcrossing rates contain far fewer obligate outcrossers than expected. We approximate the magnitude of this study bias and present the distribution of outcrossing rates after compensating for it. Because this study examines only one potential bias, and finds it to be large, conclusions regarding either the frequency of mixed mating or the shape of the distribution of outcrossing rates in nature are premature.

Key words.—Breeding system, dioecy, mating system, outcrossing, self-incompatibility, selfing.

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Lande and Schemske (1985) and Schemske and Lande (1985) sparked interest in the empirical distribution of outcrossing rates in plants with their landmark companion papers. They produced a theoretical model that allowed for an interaction between outcrossing rate and inbreeding depression. The model predicted that selfing and outcrossing were alternative evolutionary optima, and that mixed mating systems were not evolutionarily stable. In the accompanying meta-analysis, they collected estimated outcrossing rates from the literature and found that the resulting frequency distribution supported their model predictions. Species in their sample were predominantly highly outcrossed or highly selfed with relatively few species practicing mixed mating.

These papers instigated a wave of critical assessment, both on theoretical (e.g., Uyenoyama 1986, Waller 1986, Holsinger 1988, 1991; Porcher and Lande 2005) and empirical grounds (Aide 1986; Barrett and Eckert 1990; Vogler and Kalisz 2001; for reviews, see Barrett 2003 and Goodwillie et al. 2005). Several theoretical models found conditions under which mixed mating is optimal. For example, stable intermediate outcrossing rates are possible when pollen and seed discounting and/or associations between loci controlling genetic load and those controlling the mating system are considered (Holsinger 1988, 1991; Uyenoyama and Waller 1991a,b; Uyenoyama et al. 1993; Johnston 1998; Porcher and Lande 2005; Goodwillie et al. 2005). However, it is unclear how often the model assumptions or the parameter values that favor mixed mating are met in nature. It is also uncertain whether mixed mating systems are optimal when intermediate outcrossing rates are found. In many cases, intermediate outcrossing rates may reflect the inability of self-compatible plants with large floral displays to avoid geitonogamy (intraplant, interfloral pollen transfer).

Further empirical work on the distribution of outcrossing

rates focused on increasing the sample size and assessing potential biases. The potential taxonomic biases in the sample, and the effect of wind versus animal pollination on the distribution of observed outcrossing rates have been the primary concerns. Aide (1986) pointed out that Schemske and Lande's (1985) original data showed strong bimodality in wind but not animal-pollinated species. That point was expounded more recently by Vogler and Kalisz (2001). They found that 49% of animal-pollinated species had outcrossing rates between 0.2 and 0.8. They also plotted the cumulative distribution of outcrossing rates for wind and animal-pollinated species. The linear appearance of the cumulative distribution of outcrossing rates for animal-pollinated species prompted Barrett (2003, p. 993) to conclude that "the distribution of outcrossing rates is continuous with no hint of the bimodality predicted by most genetic models of mating-system evolution."

Any assessment of the fit of the distribution of observed outcrossing rates to that predicted by theory depends on the degree to which the sample is representative of the true distribution of outcrossing rates among species. As has been noted by others (e.g., Schemske and Lande 1987; Barrett and Eckert 1990; Goodwillie et al. 2005), there is potential for large biases that may cause overrepresentation of mixed mating in the sample. Taxa with extreme outcrossing rates could be underrepresented if obligately outcrossing or selfing taxa are understudied. This could occur either because such species are assumed to be 100% or 0% outcrossing, and thus their outcrossing rates are seldom measured, or because investigators specifically interested in mixed mating avoid them. Here, we examine the extent of one of these potential biases. We show that dioecious and self-incompatible species are severely underrepresented in studies of outcrossing rates.

METHODS

To estimate the proportion of obligate outcrossing species in nature, we conducted a literature search for studies that estimated the proportion of obligate outcrossers (self-incom-

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TABLE 1. Frequency of self-incompatibility and dioecy (obligate outcrossing; SI + D) in different plant communities. Studies are considered to be tropical if they were performed between the tropics of Cancer and Capricorn, temperate if not. Of the Island studies, only that of McMullen is tropical by this criterion. Habitat: woody, only woody plants examined; herb, only herbaceous; mixed, both growth forms examined.

Flora	<i>n</i>	SI + D	Habitat	Study
Mainland				
Temperate				
Canadian forest herbs	12	41.7%	herb	Barrett and Helenum 1987
Canadian salt marsh	17	29.4%	herb	Pojar 1974
Canadian bog	28	32.1%	herb	Pojar 1974
Canadian subalpine meadow	37	48.6%	herb	Pojar 1974
New England shrubs	12	41.7%	woody	Rathcke 1988
North Carolina forest wildflowers	11	27.3%	herb	Motten 1986
U.S. and Argentine deserts	26 ^a	76.9%	woody	Neff et al. 1977
Patagonian alpine flora	124 ^b	34.1%	herb ^c	Arroyo and Squeo 1990
Chilean temperate dry forest	37 ^b	43.5%	mixed	Arroyo and Uslar 1993
Chilean valdivian forest	39 ^b	46.4%	mixed	Riveros et al. 1996
Argentine chaco forest	15 ^a	60.0%	mixed	Aizen and Feinsinger 1994
Argentine chaco forest	32 ^a	43.8%	mixed	Morales and Galetto 2003
Argentine chaco understory	7 ^a	85.7%	woody	Bianchi et al. 2000
Tropical				
Mexican deciduous forest	33 ^b	79.1%	woody	Bullock 1985
Costa Rican dry forest	34 ^b	84.0%	woody	Bawa 1974
Costa Rican Lowland Forest	64 ^b	61.3%	mixed	Kress and Beach 1994
Brazilian savanna, near Brasilia	30 ^b	81.0%	woody	Oliveira and Gibbs 2000
Venezuelan tropical dry forest	49 ^b	55.2%	mixed	Jaimes and Ramirez 1999
Venezuelan palm swamp	25 ^b	22.5%	mixed	Ramirez and Brito 1990
Venezuelan cloud forest	25 ^b	53.0%	mixed	Sobrevilla and Arroyo 1982
Islands				
Chiloe Island, Chile	20	60.0%	woody ^e	Smith-Ramirez et al. 2005
Galapagos Islands, Ecuador	51 ^{b,c}	5.0%	mixed	McMullen 1990
Juan Fernandez Islands, Chile	22	40.9%	mixed	Anderson et al. 2001
Montane rainforest, Jamaica	8 ^b	30.9%	woody	Tanner 1982
New Zealand	47 ^{b,d}	32.7%	mixed	Newstrom and Robertson 2005
Total:	805	48.7%		

^a These studies did not estimate the proportion of the flora that is dioecious.

^b Sample size listed is only for tests of self-compatibility in hermaphrodites. Dioecy was estimated separately from a larger dataset.

^c The estimate for dioecy is from Baker and Cox (1984).

^d The estimate for dioecy is from Carlquist (1966).

^e One or two species in sample have the alternative growth form.

patible or dioecious species) in different plant communities. In each of these community studies (Table 1), a sample of species were examined for breeding system characteristics. In most studies, a sample of species was assayed for the fraction that were dioecious and then hermaphrodite species were hand pollinated to provide an estimate of the proportion of species that were obligate outcrossers (self-incompatible plus dioecious). In some studies, as noted in Table 1, the proportion of dioecious species was estimated from a larger survey, and was followed with crosses conducted on a sample of hermaphrodites for estimation of the self-incompatible proportion. Studies tended to sample plants that flowered during the particular season in which the research was conducted, and vary in the proportion of woody and herbaceous species examined. We found 25 such studies. Twenty included data on the presence of both self-incompatibility and dioecy, the remaining five sampled only hermaphrodite species. The 25 studies used here include 805 species from more than 100 plant families and provide the best available estimates of the frequency of self-incompatibility and dioecy (i.e., obligate outcrossing) in natural communities.

We calculated the fraction of self-incompatible species in these community studies by designating species as self-in-

compatible if their index of self-incompatibility [ISI = (proportion of fruit set after selfing)/(proportion of fruit set after outcrossing)] was <0.2 , a widely used standard for classification (e.g., Bawa 1974, Ruiz and Arroyo 1978, Bullock 1985). Most self-incompatible species had ISI values at or close to 0. The fraction of obligately outcrossing species calculated in this way should be regarded as a rough approximation.

To estimate the proportion of obligately outcrossing taxa in the outcrossing rate literature we used the database of Barrett and Eckert (1990) and expanded it by searching the Web of Science for recent estimates of outcrossing rates. When multiple reports of outcrossing rates (t) were found for a particular species or subspecies, we averaged the reported values. Estimates of $t > 1$ were collapsed to 1 because disassortative mating for the marker loci on which outcrossing rate estimates are based is unlikely. We also recorded whether each species in the updated database of outcrossing rates was reported as hermaphrodite or dioecious, and if hermaphrodite, whether they are self-compatible or self-incompatible using author determinations or, if available, ISI values.

Next, we compared the fraction of obligately outcrossing taxa in the community-wide surveys (Table 1) to that in the

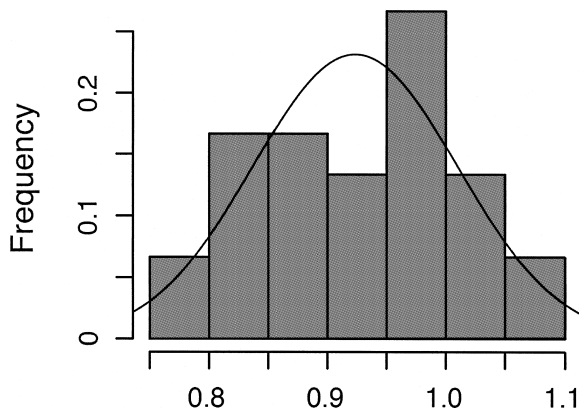


FIG. 1. The distribution of estimated outcrossing rates for obligately outcrossing plant species ($n = 30$). The normal curve fitted to the distribution is shown ($\mu = 0.932$, $\sigma = 0.087$).

updated outcrossing rate database for species where presence or absence of particular obligate outcrossing mechanisms (self-incompatibility and dioecy) is known. To compensate for any detected bias, we simply added the estimated number of missing t -values by sampling from the normal distribution

fitted to the distribution of estimated t -values of obligately outcrossing taxa. Because the estimated t -values of the obligately outcrossing taxa are uniformly high (Fig. 1), as is the number of resampled taxa, repeated resampling from the underlying distribution produces little variation in the resulting adjusted distribution. We therefore show the results of a single resampling to simplify the presentation.

RESULTS

The updated outcrossing rate dataset consists of 329 taxa. Of these, 28 are self-incompatible, two dioecious, and 197 self-compatible. For the remaining 102 taxa, we did not find data on the presence or absence of self-incompatibility or dioecy. The distribution of outcrossing rates among taxa that were “known” ($n = 227$) to have or lack incompatibility or dioecy did not differ significantly from those among “unknown” ($n = 102$) taxa, for which these character states were unreported (Fig. 2a; Kolmogorov-Smirnov $D = 0.143$, $P = 0.11$). We use the distribution of outcrossing rates among “known” taxa for the subsequent calculations.

Our survey of community-wide estimates of the fraction of plants that are obligate outcrossers indicates that approximately one half of plant species are either self-incompatible

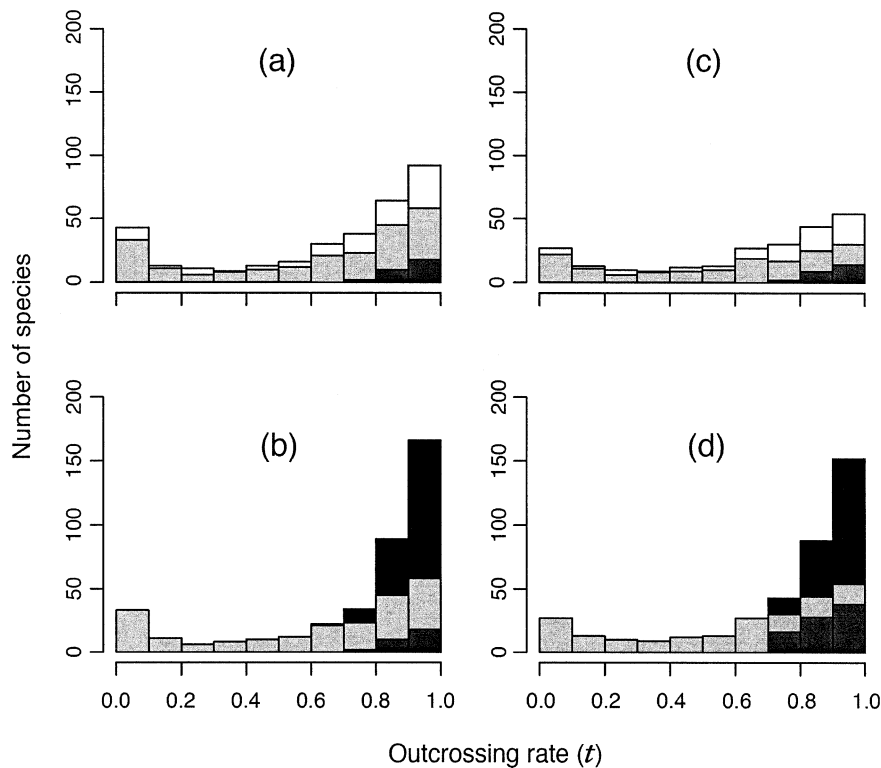


FIG. 2. Outcrossing rate distributions from published data from all plant species (a) and animal-pollinated species (c) and these distributions with our estimates of undersampled obligately outcrossing taxa added (b and d). (a) The distribution of published outcrossing rates for all plant species ($n = 329$). Shading denotes the proportion of taxa whose breeding systems are obligately outcrossing (dark gray; $n = 30$), self-compatible (light gray; $n = 197$), and unknown (white; $n = 102$). (b) Distribution of outcrossing rates of all species with the addition of 267 species (black) estimated to be missing from published data due to undersampling of obligate outcrossers (other shading as in (a)). See text for estimation details. (c) The distribution of published outcrossing rates of animal-pollinated species (shading as in (a)). (d) The distribution of outcrossing rates of animal-pollinated species with the addition of 155 species (black) estimated to be missing from the published data due to undersampling of obligate outcrossers (other shading as in (a)). See text for estimation details. The outcrossing rates added to the distributions in (b) and (d) were sampled from the normal distribution fitted to the data shown in Figure 1.

or dioecious (Table 1). In contrast, this fraction is only 13% in outcrossing rate studies for which such data are available (Fig. 2b). This represents a near four-fold difference, indicating a strong study bias against obligate outcrossers. The mean estimated outcrossing rate for species classified as obligate outcrossers was 0.93 (SE = 0.016) and the distribution of estimated outcrossing rates was not different from normal (Fig. 1; $n = 30$, Shapiro-Wilk's $W = 0.97$, $P > 0.53$; $\mu = 0.932$, $\sigma = 0.087$). We accounted for the study bias against obligate outcrossers by adding values drawn from this distribution to the "known" dataset until 48.7% of values in the adjusted dataset came from either known obligate outcrossers, or from these added values (Fig. 2b). This provides an estimate of the distribution of outcrossing rates when study bias against obligate outcrossing taxa is taken into account.

Much of the discussion concerning the frequency of mixed mating in nature has focused on animal-pollinated species (Aide 1986; Vogler and Kalisz 2001). We plotted the distribution of outcrossing rates among animal-pollinated species (Fig. 2c). In this case the distribution of outcrossing rates differed between animal-pollinated taxa that were "known" to have or lack obligate outcrossing mechanisms ($n = 157$) and those for which no information on the presence or absence of incompatibility or dioecy could be found ($n = 82$; Fig. 2c; Kolmogorov-Smirnov $D = 0.24$, $P = 0.003$). The difference stems primarily from the high rate of reporting of self-compatibility in highly selfing taxa, likely because no crosses are necessary to infer self-compatibility when plants are partially or wholly autogamous. Because of this difference in distributions, we used a more conservative method to compensate for undersampled obligately outcrossing species in the animal-pollinated dataset. We assumed that all "unknown" species with $t \geq 0.7$ were obligate outcrossers, and all those with $t < 0.7$ were not. This is conservative because no "known" obligate outcrossing taxa have an estimated $t < 0.75$ (Fig. 1), but many taxa known to be self-compatible have $t \geq 0.7$ (Fig. 2a). Thus, we add fewer obligately outcrossing taxa when adjusting the distribution by this method. Combining the "known" taxa with the "unknown" taxa classified in this manner, we then again sampled from the distribution of outcrossing rates of obligately outcrossing taxa (Fig. 1) until the total frequency of outcrossing taxa reached 48.7% (Fig. 2d).

DISCUSSION

Our estimate of the frequency of obligate outcrossing in communities (48.7%; Table 1) is in good agreement with previous estimates for the fraction of self-incompatible species (50%; Darlington and Mather 1949; Brewbaker 1959) and dioecious or functionally dioecious species (~5%; Yampolsky and Yampolsky 1922; Bawa 1980; Renner and Ricklefs 1995). This estimate may itself contain biases, although their magnitude and direction are difficult to assess. First, the frequency of herbaceous versus woody taxa, growth forms that may differ in their frequency of obligate outcrossing (Barrett and Eckert 1990), could vary between our sample and the true distribution. Eight community studies examined exclusively or predominantly woody species, six others herbs, while eleven examined plants of both growth habits.

The extent of any bias is difficult to assess because we find no estimates of the proportion of species that have each growth form. However, even herbaceous species are likely to have frequencies of obligate outcrossing significantly higher than currently found in the database of outcrossing rate estimates. For instance, estimates for Solanaceae, a large family with many herbaceous species, show that nearly 40% of taxa are self-incompatible, and self-incompatibility is common in many of the largest, primarily herbaceous, plant families (e.g., Asteraceae, Orchidaceae, Poaceae; Iqic et al. 2004; B. Iqic, unpubl. data). Second, the majority of community studies have been performed in the temperate zones where obligate outcrossing may be less frequent (Bawa 1980; Baker et al. 1983), although two thirds of angiosperm species are thought to be tropical (World Conservation Monitoring Centre 1992). Therefore tropical species may, if anything, be underrepresented in these community studies, although the same may also be true of the outcrossing rates data. Overall, regardless of the exact frequency of obligate outcrossing in nature, the best available data indicate that there is a substantial bias against obligate outcrossers in the studies that estimate outcrossing rates.

The underrepresentation of obligate outcrossers in current mating system studies has two important consequences. Accounting for these missing taxa could alter our view of both the relative frequency of mixed mating and the shape of the distribution of outcrossing rates. For instance, Vogler and Kalisz (2001) used data from Barrett and Eckert (1990) to surmise that 33% of all taxa have intermediate outcrossing rates (rates between 0.2 and 0.8) and that among animal-pollinated taxa, this fraction increased to 49% (see also Kalisz et al. 2004). In our dataset of published outcrossing rates, these values remain similar, 35% and 42%, respectively (Figs. 2a,c). However, any statement concerning the frequency of mixed mating in nature is clearly premature. Even this simple study, which estimates and compensates for only one source bias, reduces these fractions to 23.9% for all taxa, and 32.8% for animal-pollinated species, despite the more conservative adjustment used for the latter group.

For animal-pollinated species, the fit of the distribution of outcrossing rates to bimodal expectations of Lande and Schemske (1985) has also been challenged (Vogler and Kalisz 2001; Barrett 2003). Although we are not aware of any statistically rigorous tests of bimodality, data for animal-pollinated species (Figs. 2c,d) show a higher representation of species in extreme ($0 \leq t < 0.1$ and $0.9 < t \leq 1$) than in intermediate ($0.1 \leq t \leq 0.9$) classes, consistent with the prediction. This is true even when the study bias against obligate outcrossers, as shown here, is not taken into account. Study bias against highly selfing taxa is also potentially large, but more difficult to assess. If highly selfing species are underrepresented in the studies of outcrossing rates, the frequency of intermediate outcrossers would further erode. Because there remain many potential biases in the present dataset, it is too soon to say whether the distribution of outcrossing rates deviates from that predicted (Barrett 2003).

At least two general causes may explain the bias against obligate outcrossers in studies of outcrossing rates. First, as mentioned above, it is possible that the outcrossing rate data have a higher representation of herbaceous, temperate zone

species than the community studies. However, this cannot completely explain the disparity because the five estimates from studies of exclusively herbaceous, temperate zone species average 35.8% obligate outcrossing. This figure is nearly threefold higher than the 13% occurrence of obligate outcrossing species in the outcrossing rate database. Obligate outcrossers appear underrepresented even in temperate zone studies. Gymnosperm taxa, which do not display self-incompatibility, are overrepresented in the outcrossing rate dataset, but they generally have high estimated rates of outcrossing. The bias against obligate outcrossers most likely affects angiosperm taxa disproportionately. Second, there may be a consistent bias in the direction of intermediate outcrossers. Investigators are potentially more likely to choose self-compatible hermaphrodites either because they are specifically interested in mixed mating systems, or because it is frequently assumed that self-incompatible and dioecious species are invariably outcrossing (e.g., Silvertown et al. 2002). This is a reasonable assumption, as we find that these taxa have average population outcrossing rates of 0.93 (SE = 0.016). Although their means are significantly different from unity, the rates are consistently high (Fig. 1).

That mean outcrossing rates are smaller than unity in many obligately outcrossing taxa is not entirely unexpected, and there are at least three explanations for it. First, the trivial possibility is that self-incompatibility was ascribed to plants that are not self-incompatible. Second, "leaky" self-incompatibility (Vogler and Stephenson 2001) and inconstancy of sex expression (Bawa 1982) could lead to reduced values of t . It is unclear whether leaky self-incompatibility affects population outcrossing rates strongly or consistently, since no relevant experiments have been performed. Also, female plants in dioecious and gynodioecious species are often not variable in sex expression (Bawa 1982), but even they commonly exhibit estimated outcrossing rates <1 (mean $t = 0.934$; $n = 7$). Biparental inbreeding may commonly reduce measured outcrossing rates to values less than unity. Methods for inferring the level of biparental inbreeding, which rely on the difference in single and multilocus estimates of outcrossing rates, may consistently underestimate it (Leclerc-Potvin and Ritland 1994), as has been shown empirically (Griffin and Eckert 2003).

Even if the true distribution of outcrossing rates in nature fits the qualitative predictions of bimodality, as we argue it may, it remains a fact that there is a substantial number of species that practice mixed mating. The challenge is to ascertain how frequently mixed mating systems represent an optimal solution to some combination of genetic and ecological factors. Often, mixed mating may be suboptimal, representing either a transitional state or a constraint—unavoidable geitonogamy in self-compatible taxa with large floral displays, for example. The latter would imply that selfed offspring have low fitness and usurp ovules otherwise available for outcrossing (reviewed in Barrett 2003). With the possible exception of plants producing a mixture of cleistogamous and chasmogamous flowers (Lu 2002), there has been no convincing demonstration that a mixed-mating system observed in nature is optimal for that species. For instance, Kalisz et al. (2004) showed that higher rates of selfing in years of low pollinator availability benefit *Collinsia verna*,

but the generally high outcrossing rates in that species are difficult to explain given the low (<0.5) estimates of inbreeding depression. Convincing demonstrations of stabilizing selection acting on mixed mating systems in nature continue to elude biologists interested in this question.

If the true distribution of outcrossing rates in nature can be determined, the relative frequencies of highly outcrossed and highly selfed species will be of considerable interest. Microevolutionary mating system theories (e.g., Lande and Schemske 1985; Porcher and Lande 2005) make no predictions regarding the relative frequencies of predominant selfers and outcrossers. They predict only that these two states are stable within populations and species. Even if these theories are correct in positing that intermediate outcrossing rates are unlikely to be evolutionarily stable, the frequencies of highly outcrossed and highly selfed species need not be balanced. Likewise, the overall distribution of species' outcrossing rates need not be strongly bimodal. If selfing is a stable mating strategy within populations and species but also an evolutionary dead end (Stebbins 1957, 1974; reviewed in Takabayashi and Morrell 2001), a distribution of species' outcrossing rates that is skewed toward high outcrossing rates could result. The expected shape of this distribution would then vary with the speciation and extinction rates of selfers and outcrossers, as well as the rate of transition from outcrossers to selfers.

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