

## RESEARCH PAPER

# Female advantage in gynodioecious plants: A meta-analysis focused on seed quality

S. Varga 

School of Life Sciences, University of Lincoln, Joseph Banks Laboratories, Lincoln, LN6 7TS, UK

**Keywords**

female advantage; gynodioecy; seed germination; seedling performance.

**Correspondence**Sandra Varga, School of Life Sciences, University of Lincoln, Joseph Banks Laboratories, Lincoln LN6 7TS, UK.  
E-mail: svarga@lincoln.ac.uk or sandravarga30@hotmail.com**Editor**

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**ABSTRACT**

- In gynodioecious systems, female plants must counteract the selective disadvantage of not passing genes *via* pollen production, as hermaphrodites can. Theory predicts that females must produce more or better-quality seeds than hermaphrodites in order to be maintained within the same population. This female advantage has been widely measured and reported for seed number, but whether female advantage is gained through the production of better seeds remains relatively under-studied.
- Here, a meta-analysis approach was used to investigate whether females in gynodioecious species produce seeds of better quality than hermaphrodites (measured as seed mass, seed nutrient content, seed germinability and seedling survival and performance) in addition to achieving a larger seed production. In total, 50 studies were included, reporting traits for 34 gynodioecious species in 17 different families.
- Female advantage was significant for seed number and seed germination, but was not detected for seed mass, seed nutrient content or seedling performance.
- A female advantage in seed number was corroborated in this meta-analysis, which together with better seed germination, may explain maintenance of female plants within gynodioecious populations.

**INTRODUCTION**

Gynodioecy is a breeding system where populations are comprised of female individuals as well as hermaphrodite individuals. Even though gynodioecy is regarded as a relatively uncommon breeding system in plants (Renner, 2014), this system is the focus of much debate among evolutionary biologists trying to understand how gynodioecy may have evolved from hermaphroditism in several distinct plant lineages (Charlesworth, 2002; Henry *et al.*, 2018), and most importantly, how female plants are maintained with hermaphrodites (*e.g.* Dorken & Pannell, 2008; Yamauchi *et al.*, 2019). Since females do not father offspring as hermaphrodites do, theoretical models predict that female persistence within hermaphroditic populations can only occur when there is a female advantage over hermaphrodites that allows female plants to have higher fecundity than hermaphrodites by producing larger amounts of seeds and/or higher quality seeds (Charlesworth & Charlesworth, 1978; Shykoff *et al.*, 2003; Dufaj & Billard, 2012).

The level of reproductive advantage needed for female plants to be maintained within a hermaphroditic population has two main components. The first component relates to the genetic basis of sex determination and how genes are transmitted in the species (Lewis, 1941; Charlesworth & Charlesworth, 1978). In some gynodioecious species, male sterility genes are only under nuclear control and thus are inherited by both parents. In most species, however, male sterility is under a nuclear–cytoplasmic control, where in addition to the biparental inherited nuclear restorer genes, there are also cytoplasmic genes containing male sterility factors, which are primarily inherited from the plants mothering the seeds (see *e.g.* Bailey & Delph,

2007 for a review and a list of species). In species with a nuclear inheritance of male sterility, female plants need a two-fold reproductive advantage, whereas in species with cytoplasmic male sterility, the female reproductive advantage needed is less pronounced (Lewis, 1941; Lloyd, 1974). Moreover, different systems may have different costs associated with restoring male fertility, which may also contribute to differences found in the reproductive advantage reported in different populations (Bailey *et al.* 2003).

The second component determining the level of reproductive advantage needed in females relates to the ecology of the plant species and involves three, mutually non-exclusive factors: whether the species suffers from and/or has mechanisms to avoid inbreeding depression (see *e.g.* Ashman, 1992), whether females are able to reallocate resources saved from male reproductive structures such as pollen (see *e.g.* Obeso, 2002) and whether the two genders are differentially affected by less detrimental interactions with pathogens and herbivores (see *e.g.* Ashman, 2002) or more beneficial interactions with plant fungal mutualists (see *e.g.* Varga *et al.* 2009). All three factors can contribute to explain the hypothesized higher or better seed production in females.

Regardless of the underlying genetic and ecological mechanisms explaining how females obtain their reproductive advantage, its existence is relatively well-established, especially for seed quantity (reviewed in Shykoff *et al.* 2003; Dufaj & Billard 2012). However, one may argue that seed quality is a better estimate of female reproductive advantage than seed quantity, as ultimately it is whether seeds are able to germinate and establish that genes will be transferred and fitness achieved. However, few studies have estimated whether female plants

have a reproductive advantage in seed quality (but see Shykoff *et al.* 2003) or whether this advantage is larger or smaller than the reproductive advantage gained from seed quantity.

Several parameters can be used to estimate seed quality. Here, I refer to seed quality as the potential performance of a seed to germinate and establish. Several important plant functional traits can therefore be used to describe seed quality within the context of plant communities. For example, not only germination rate but also germination speed may be an important trait conferring a competitive advantage when trying to establish within a plant community (Jimenez-Alfaro *et al.*, 2016), however, this trait is usually not reported. When analysing germination rate and/or speed, the amount of stored nutrients is crucial. Larger seeds will have an advantage over small seeds in total nutrient content; however, there is a trend for smaller seeds to have higher concentrations of mineral elements (Leishman *et al.*, 2000). One of the main functions of a seed is to provide the embryo with nutrients before the first photosynthetic tissue is produced. After germination, a larger relative growth rate (RGR), which is positively correlated with nutrient reserves, will usually be also positively related to competitive ability and thus survival (*e.g.* Walters & Reich, 2000; Soriano *et al.*, 2001). Moreover, a negative relationship between seedling RGR and seed size is usually reported: small-seeded species tend to have higher RGR (Jurado & Westoby, 1992). After an initial period when the large-seeded species will have an absolute size advantage, this will wear off as the faster-growing small-seeded species catches up (Kimenez-Alfaro *et al.*, 2016).

A previous meta-analysis by Shykoff *et al.* (2003) reported significant female advantage in seed quantity for 19 out of 43 species with available data, but no significant female advantage was reported for the same number of species. The authors suggested reallocation of resources saved from pollen production at the plant level as the proximal cause of this female advantage, but suggested also investigating pollen limitation and the effect of selfing avoidance. These two factors were later systematically reviewed by Dufaj & Billard (2012) in addition to measuring the magnitude of female advantage in 48 species and whether it varied among species, depending on the mode of gynodioecy determination, and among populations within species. Female advantage in seed quantity was indeed found in 40 out of the 48 studies included but the authors concluded that, for many species, reduced selfing was not necessarily the cause. Differences due to the mode of determination system (cytonuclear *versus* nuclear) were considered but were not statistically analysed due to the low sample size available (Dufaj & Billard, 2012). Indeed, regardless of the importance of knowing the genetics of the species, few species have been carefully examined.

These previous reviews (Shykoff *et al.* 2003; Dufaj & Billard, 2012) analysed female reproductive advantage related mainly to seed quantity, not quality, probably due to the lack of data regarding seed quality measurements even though in the meta-analysis by Shykoff *et al.* (2003), female advantage for seed size and seed germination were also included. At that time, data available for seed size and seed germination existed for 21 and 12 species, respectively, and female advantage was significant in 62% and 42% of the species included. The lower number of available studies regarding female advantage in seed quality is probably explained because counting the number of seeds

produced is relatively easy and straightforward (albeit time consuming), whereas measuring seed quality involves destroying the seeds or time-consuming controlled experiments to monitor seed germination and seedling establishment for relatively long periods of time.

In this study I conducted a meta-analysis on the available evidence for female reproductive advantage, based on seed quality for gynodioecious plants by including studies that reported at least one seed/seedling quality trait. Based on the previous evidence (reviewed by Shykoff *et al.*, 2003 and Dufaj & Billard, 2012), I tested the hypothesis that females in gynodioecious plants produce not only more seeds than hermaphrodites, but also better-quality seeds. For the first time, publication bias is statistically investigated to infer whether the available literature of female advantage in gynodioecious plants is unbiased. Publication bias can take many forms (*e.g.* Song *et al.* 2000), but the most important is probably when studies are published depending on the magnitude and/or direction of research findings, such as a tendency to publish towards statistically significant results.

## MATERIAL AND METHODS

### Literature search and data extraction

I used Web of Knowledge (<http://thomsonreuters.com/web-of-knowledge>) with the search terms (gynodioec\* and plant\*) and (seed\* or germin\*) on 8 November 2018, which returned 338 papers. In addition, two papers were included from secondary literature (Appendix S1 for the PRISMA flow and the list of papers included: see Supplementary Data). Studies were included if they reported at least one seed/seedling quality trait and reported the results with sample size, mean and a measure of variance (SD or SE). In total, 50 papers were included, reporting traits for 34 species. If means and measures of variance were presented only in graphical form, I extracted them using GraphClick (Arizona-Software, 2008). Standard deviations were back-calculated from SE and sample sizes as  $SD = SE \times \sqrt{n}$ . Some papers included measurements of different populations and/or years. These case studies were all included, for a total of 123 case studies. In most studies done with natural populations, the authors did not control or specify whether the seeds produced by hermaphrodites were obtained by selfing or outcrossing. In those that reported seed traits obtained from selfing hermaphrodites *versus* outcrossing, only the latter were included.

### Statistical analysis

All statistical analyses were carried out with R version 3.6.2 (R Core Team, 2019). I used the standardized mean difference with heteroscedastic population variances (SMDH) to estimate effect size Hedges' *g* (Bonett 2008; Bonett, 2009), which was calculated using the function 'escalc' in the package 'metafor' (Viechtbauer, 2010). Effect sizes were therefore calculated by subtracting the difference between female and hermaphrodite plants. Effect sizes were weighted to ensure that more robust studies (with smaller variances) were given more weight in the calculations (Harrison, 2011). The weighted effect size was calculated using the inverse variance as the weight and is presented in the figures. Positive effect sizes indicate that females

had a significant advantage over hermaphrodites for that trait; whereas negative results indicate the opposite. An effect size of zero indicates no significant difference between the sexes. Heterogeneity was assessed by inspection of forest plots and by examining  $Q^2$  and  $I^2$  (Thompson & Sharp, 1999). Significant heterogeneity indicates that the studies do not share a common effect size. Subsequently, I tested whether plant family could predict effect sizes by fitting a linear mixed-effects model. Mean weighted effect sizes and their 95% CIs were estimated using restricted maximum likelihood (REML).

Publication bias was visually inspected with funnel plots and also tested with Egger's regression test (Egger *et al.*, 1997) and a Rank correlation test (Begg & Mazumdar, 1994). These tests are used to examine whether there is a significant asymmetry in the funnel plot, which may be indicative of publication bias. Finally, Cohen's  $d$  effect sizes correlations between traits were examined using Spearman's rank correlation. Effect sizes were calculated using the function 'mes' in the package 'metafor' (Viechtbauer, 2010).

## RESULTS

### Number of seeds produced

Overall, the mean weighted effect size across all studies for seed production was positive and significant, indicating that females produced significantly more seeds than hermaphrodites ( $0.16 \pm 0.03$ ;  $z = 5.53$ ,  $P < 0.001$ ; Fig. 1). Heterogeneity was moderate and statistically significant (33.4%;  $Q_M = 155.72$ ,  $df = 107$ ,  $P = 0.001$ ) and there was publication bias ( $z = 2.91$ ,  $P = 0.003$ , Kendall's tau = 0.20,  $P < 0.01$ ; Appendix S2A). The visual analysis of the funnel plot indicated a significant trend to publish results with a positive female advantage in seed number (Appendix S2A).

When plant family was accounted for as a moderator, heterogeneity was still moderate and statistically significant (29.8%;  $Q_M = 25.59$ ,  $df = 15$ ,  $P = 0.04$ ), with significant publication bias (both tests  $P < 0.02$ ). A significant difference between sexes was detected within the Campanulaceae and the Geraniaceae families (Fig. 1), with a mean positive difference effect size in seed production of 0.35 and 0.36, respectively.

### Seed mass

Seed mass data were obtained from 93 cases in 15 families. Overall, the effect size for seed mass showed no differences between the sexes, as shown by the standardized grand mean difference of  $-0.01 \pm 0.09$  ( $z = -0.1049$ ,  $P = 0.91$ ; Fig. 2). Total heterogeneity was high and significant (91.55%;  $Q_M = 1352.41$ ,  $df = 92$ ,  $P < 0.001$ ), with significant publication bias as measured by the Egger's test ( $z = -5.27$ ,  $P < 0.001$ ; Appendix S2B) but not the Rank test (Kendall's tau =  $-0.08$ ,  $P = 0.25$ ). In this case, there was a publication bias towards negative effect sizes (*e.g.* with hermaphrodite plants producing larger seeds than females).

Even though significant differences between the sexes were observed in Brassicaceae, Caryophyllaceae and Poaceae (Fig. 2), the moderator plant family did not significantly predict heterogeneity ( $Q_M = 13.12$ ,  $df = 14$ ,  $P = 0.51$ ), probably due to the low weight of these families combined with the significant publication bias (Appendix S2B). Positive effect sizes were detected

in Brassicaceae and Poaceae, but a negative effect size was observed in the Caryophyllaceae, indicating a hermaphrodite advantage in this family for seed mass.

### Seed nutrient content and seed viability

Data for seed nutrient content were restricted to only five studies for species belonging to the Caryophyllaceae (*Silene acaulis*, mean =  $-0.15$  [ $-0.54$ ,  $0.24$ ], 61% weight), Geraniaceae (*Geranium sylvaticum*, mean =  $-0.41$  [ $-1.04$ ,  $0.23$ ], 23% weight) and Malvaceae (*Sidalcea spicata*, mean =  $0.00$  [ $-0.75$ ,  $0.75$ ], 16% weight), with a grand mean difference of  $-0.18$  [ $-0.48$ ,  $0.12$ ]. Because of the low number of studies, no further analyses were carried out.

Similarly, only one study reported seed viability. Del Castillo (1993) reported proportion of viable seeds of  $0.44 \pm 0.7$  SD ( $n = 14$ ) versus  $0.54 \pm 1.3$  in seed from female and hermaphrodite ( $n = 43$ ) *Phacelia dubia* (Hydrophyllaceae).

### Seed germination

Seed germination rates were reported in 56 cases including nine different families, with seeds from female plants showing significantly higher germination rates than seeds from hermaphrodites (Fig. 3). For this model, heterogeneity was very high and significant (96.2%;  $Q_{55} = 294.28$ ,  $P < 0.001$ ) and contained significant publication bias towards studies reporting a female advantage ( $z = 9.001$ ,  $P < 0.001$ ; and Kendall's tau = 0.37,  $P < 0.01$ ; Appendix S2C). The moderator family did not significantly explain the results and, thus, heterogeneity was still high and significant (96.7%;  $Q_M = 5.54$ ,  $df = 9$ ,  $P = 0.78$ ). Significant differences between sexes were only observed in the Brassicaceae (Fig. 3).

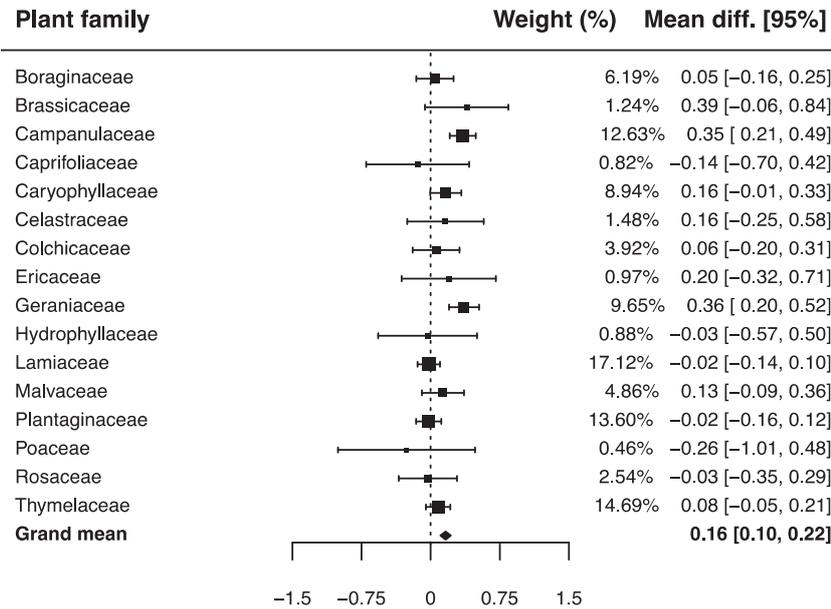
### Seedling survival and performance

Data on seedling survival were available from only three studies from members of the Caryophyllaceae (mean =  $0.01$  [ $-0.31$ ,  $0.33$ ], 80% weight) and Rosaceae (mean =  $0.67$  [ $0.03$ ,  $1.31$ ], 20% weight). The grand mean difference was  $0.14$  [ $-0.14$ ,  $0.43$ ], even though no further statistical analyses were performed due to the low number of studies available.

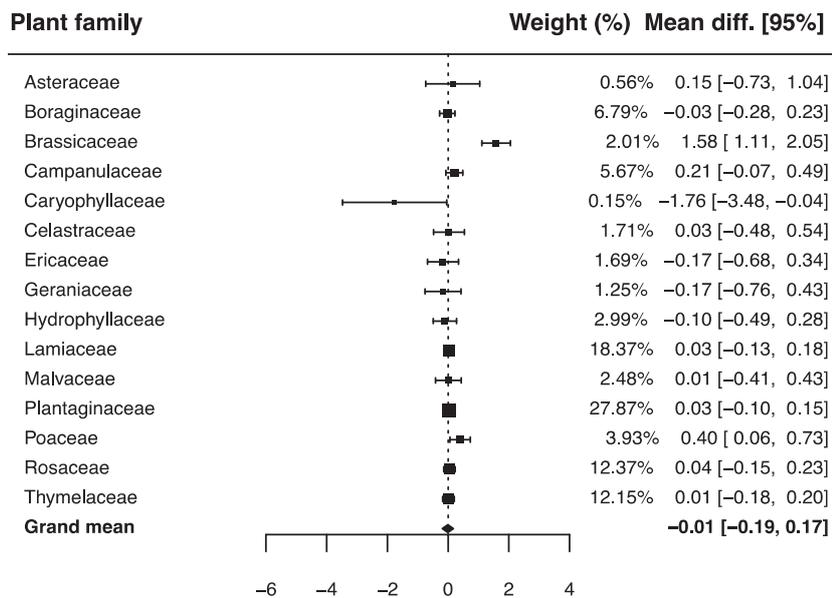
Finally, seedling performance was reported on 13 occasions, including plants of three different families. In this case, heterogeneity was medium and statistically significant (51.4%;  $Q_M = 22.76$ ,  $df = 12$ ,  $P = 0.02$ ), and no publication bias was detected ( $z = -1.07$ ,  $P = 0.28$ , Kendall's tau =  $-0.30$ ,  $P = 0.16$ ; Appendix S2D). Effect sizes were similar between the sexes (Fig. 4) and the inclusion of plant family as a moderator did not explain heterogeneity ( $Q_M = 2.61$ ,  $df = 2$ ,  $P = 0.27$ ).

### Correlations between traits

There was no statistically significant relationship in female advantage between seed number and seed mass ( $\rho = 0.12$ ,  $P = 0.25$ ), seed number and seed germination ( $\rho = 0.04$ ,  $P = 0.76$ ) or seed number and seedling performance ( $\rho = -0.20$ ,  $P = 0.53$ ). Similarly, female advantage in seed mass was not related to a female advantage in seed germination ( $\rho = 0.18$ ,  $P = 0.24$ ). However, species that showed higher female advantage in seed mass also show a positive tendency



**Fig. 1.** Standardized mean differences (SMDH) and 95% confidence intervals in seed number between females and hermaphrodites for individual families included in the meta-analysis. The grand mean difference is indicated with a diamond. Weight indicates the influence of each family on the pooled result.



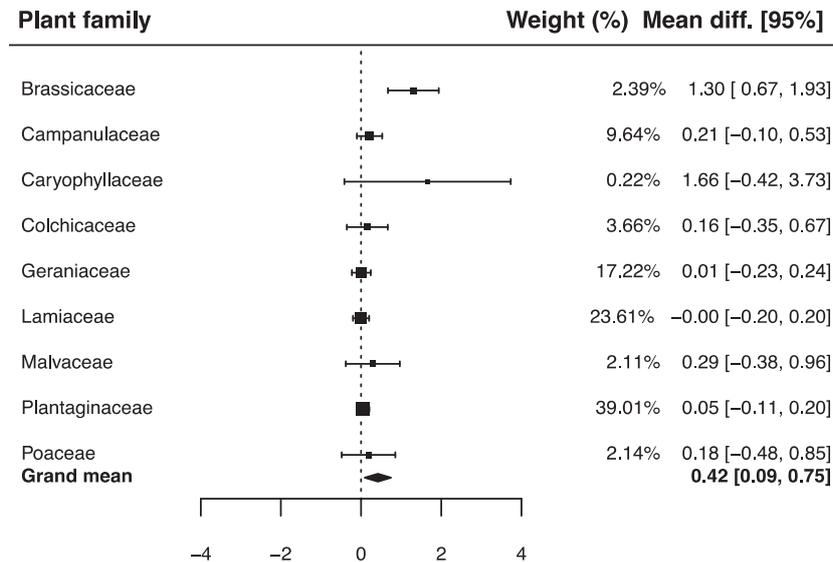
**Fig. 2.** Standardized mean differences (SMDH) and 95% confidence intervals in seed mass between females and hermaphrodites for individual families included in the meta-analysis. The grand mean difference is indicated with a diamond. Weight indicates the influence of each family on the pooled result.

for higher female advantage in seedling performance ( $\rho = 0.78$ ,  $P = 0.04$ ; Fig. 5).

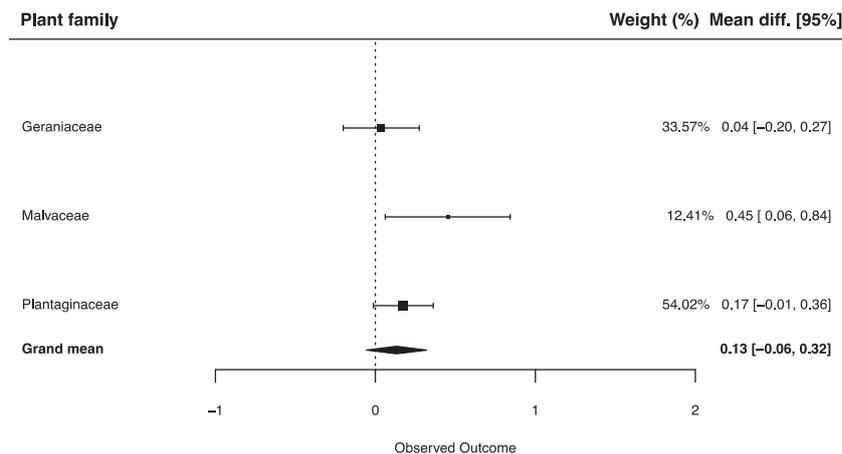
## DISCUSSION

In gynodioecious plants, a female fecundity advantage is used to explain how female plants can be maintained within the same population as hermaphrodites and this is usually measured and analysed in terms of larger seed production

(reviewed in Shykoff *et al.*, 2003; Dufaÿ & Billard, 2012). Few studies have specifically compared female advantage in seed quantity *versus* offspring quality in natural populations of gynodioecious plants (van der Meer *et al.*, 2017). Moreover, it is well known that female advantage depends on the population sex ratio and the pollination context (*e.g.* Delph *et al.*, 2007; Stone and Olson, 2018). Therefore, the use of meta-analyses allows us to standardize all of these other factors known to modify female advantage and, thus, it is a powerful tool to



**Fig. 3.** Standardized mean differences (SMDH) and 95% confidence intervals in germination success between seeds produced by females and hermaphrodites for individual families included in the meta-analysis. The grand mean difference is indicated with a diamond. Weight indicates the influence of each family on the pooled result.



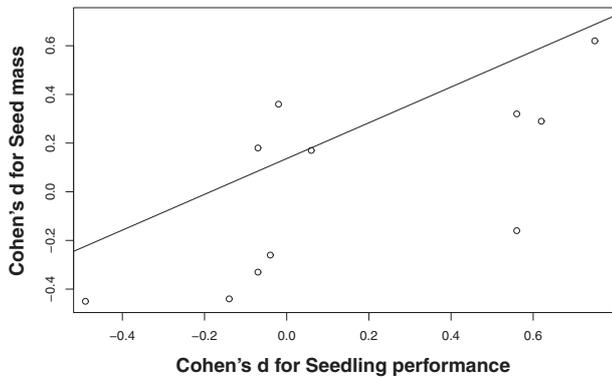
**Fig. 4.** Standardized mean differences (SMDH) and 95% confidence intervals in seedling performance between seeds produced by females and hermaphrodites for individual families included in the meta-analysis. The grand mean difference is indicated with a diamond. Weight indicates the influence of each family on the pooled result.

investigate the true occurrence of female advantage. In addition, meta-analysis tools allow us to examine whether publication bias exists in the available literature.

The results of this meta-analysis corroborate the widely reported finding of female advantage in seed number and seed germination in gynodioecious plants. However, these two traits were the only ones that were significantly different between females and hermaphrodites in this meta-analysis. Although effect sizes were not strongly predicted by plant family in most cases, there were clear differences in female advantage in some families, namely Brassicaceae, Campanulaceae, Caryophyllaceae, Geraniaceae, Rosaceae and Poaceae. Moreover, this is the first study to statistically investigate the existence of publication bias in reporting female advantage in seed traits. Significant publication bias was detected for seed number and seed germination, but not for seedling performance, with a trend to

publish a positive female advantage in seed number and germination, but the opposite trend for seed mass.

The existence of a female advantage in gynodioecious plants for reproductive traits is relatively well-established for traits related to seed production, including flower production, fruit production, seed production, seed size and seed germination (Shykoff *et al.*, 2003; Dufäy & Billard, 2012). The present meta-analysis goes a step further as it includes not only seed traits but also seedlings traits, as ultimately, female advantage in gynodioecious plants will only be achieved if their seeds are able to germinate and establish. Based on previous results and the present study, a female advantage in seed germination was corroborated, but seedlings produced by female plants did not show a consistent advantage in survival and performance. A possible explanation for the lack of differences in seedling survival may be that the relatively short duration of the experimental approached



**Fig. 5.** The relationship between female advantages (positive Cohen's  $d$ ) for seed mass and seedling performance.

used does not allow for the effects to be detectable. Usually, seeds are germinated in greenhouse conditions and followed up in most cases until flowering (e.g. months, see e.g. Eckhart, 1992; Molina-Freaner & Jain, 1992) even though exceptions occur where offspring produced by females and hermaphrodites have been followed for years (e.g. Schultz & Ganders, 1996; Ramsey & Vaughton, 2002; Varga & Kytöviita, unpublished). This short duration would imply that differences in seedling performance cannot be observed because secondary sexual dimorphism in the seedlings themselves will only appear after attaining a certain size or due to the existence of mechanisms, physiological and/or demographic, to compensate the costs of reproduction in plants (see Obeso, 2002 and references therein).

Jennions & Moller (2002) examined the datasets of effects sizes from 40 peer-reviewed published meta-analyses in evolutionary ecology and concluded that publication bias was present and may have affected the main conclusions for up to 21% of these meta-analyses. The present work suggests that there is a tendency to publish studies reporting a positive female advantage in seed number and seed germination (which agrees with the well-established theory to explain female maintenance in gynodioecious systems) and a tendency to publish against female advantage for seed mass. This is an issue that should be addressed or at least taken into account when making generalizations about the factors determining female maintenance in gynodioecious systems.

To conclude, gynodioecy is a breeding system reported in at least 81 of the 449 currently accepted angiosperms plant families (Dufaj et al., 2014) but data from only 17 families were suit-

able to be included in the present meta-analysis focused on seed quality. Around 57% of the studies that could be included belong to only three families: Caryophyllaceae, Geraniaceae and Campanulaceae. This is similar to the number of available families in the previous analyses of Shykoff *et al.* (2003) and Dufaj & Billard (2012) (23 and 27 families, respectively) and highlights the need for further research in other families to fully elucidate female advantage in gynodioecious species and, as such, would open new possibilities to investigate at what evolutionary time female advantage has evolved. Female advantage was only observed in seed number and seed germination, but could not be further detected at the seedling stage. Moreover, when analysed at the family level, female advantage was variable across families and traits analysed. The power to detect effects in some traits was limited by insufficient data on seed nutrient content, seedling survival and seedling performance, highlighting the need for long-term studies where seeds from female and hermaphrodite plants are germinated and grown in appropriate conditions. This could help understanding and quantifying whether female advantage occurs and at what stage during an individual's life.

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## DATA AVAILABILITY STATEMENT

Data are available on Figshare (<https://doi.org/10.6084/m9.figshare.14128541.v1>).

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** PRISMA flow diagram showing the decision process to whether or not to include the studies.

**Appendix S2.** Contour-enhanced funnel plots (left panels) and influential study plots (right panels) for (A) Seed number, (B) Seed mass, (C) Seed germination, and (D) Seedling performance in the meta-analysis of gynodioecious plants. In the funnel plots, dots indicate publication bias ( $P \geq 0.1$ , white area;  $0.05 \leq P < 0.01$ , grey area;  $0.01 \leq P < 0.05$ , dark grey area; and  $P < 0.01$  for area outside the funnel plot).

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