



RECOMMENDATION

Sometimes, sex is in the head

Cite as: Arroyo J. Sometimes, sex is in the head. *Peer Community In Evolutionary Biology*, 100069 (2019). DOI: 10.24072/pci.evolbiol.100069

Published: 12th February 2019

Based on reviews by:
three anonymous reviewers

Correspondence:
arroyo@us.es

Juan Arroyo¹

¹ Dept. de Biología Vegetal y Ecología. Dept. of Plant Biology and Ecology, Universidad de Sevilla – Sevilla, Spain

A recommendation of

Torices R, Afonso A, Anderberg AA, Gómez JM, and Méndez M. Architectural traits constrain the evolution of unisexual flowers and sexual segregation within inflorescences: an interspecific approach. *bioRxiv* 356147, ver 3 peer-reviewed and recommended by *PCI Evol Biol* (2019). DOI: 10.1101/356147

 CC-BY-ND 4.0

This work is licensed under the Creative Commons Attribution-NonCommercial 4.0 International License.

Plants display an amazing diversity of reproductive strategies with and without sex. This diversity is particularly remarkable in flowering plants, as highlighted by Charles Darwin, who wrote several botanical books scrutinizing plant reproduction. One particularly influential work concerned floral variation [3]. Darwin recognized that flowers may present different forms within a single population, with or without sex specialization. The number of species concerned is small, but they display recurrent patterns, which made it possible for Darwin to invoke natural and sexual selection to explain them. Most of early evolutionary theory on the evolution of reproductive strategies was developed in the first half of the 20th century and was based on animals. However, the pioneering work by David Lloyd from the 1970s onwards excited interest in the diversity of plant sexual strategies as models for testing adaptive hypotheses and predicting reproductive outcomes [1]. The sex specialization of individual flowers and plants has since become one of the favorite topics of evolutionary biologists. However, attention has focused mostly on cases related to sex differentiation (dioecy and associated conditions [7]). Separate unisexual flower types on the same plant (monoecy and related cases, rendering the plant functionally hermaphroditic) have been much less studied, apart from their possible role in the evolution of dioecy [2] or their association with particular modes of pollination [6].

Two specific non-mutually exclusive hypotheses on the evolution of separate sexes in flowers (dicliny) have been proposed, both anchored in Lloyd's views and Darwin's legacy, with selfing avoidance and optimal limited resource allocation. Intermediate sex separation, in which sex morphs have different combinations of unisexual and hermaphrodite flowers, has been crucial for testing these hypotheses through comparative analyses of optimal conditions in

suggested transitions. Again, cases in which floral unisexuality does not lead to sex separation have been studied much less than dioecious plants, at both the microevolutionary and macroevolutionary levels. It is surprising that the increasing availability of plant phylogenies and powerful methods for testing evolutionary transitions and correlations have not led to more studies, even though the frequency of monoecy is probably highest among diclinous species (those with unisexual flowers in any distribution among plants within a population [8]).

The study by Torices *et al.* [9] aims to fill this gap, offering a different perspective to that provided by Diggle and Miller [4] on the evolution of monoecious conditions. The authors use heads of a number of species of the sunflower family (Asteraceae) to test specifically the effect of resource limitation on the expression of sexual morphs within the head. They make use of the very particular and constant architecture of inflorescences in these species (the flower head or “capitulum”) and the diversity of sexual conditions (hermaphrodite, gynomonocious, monoecious) and their spatial pattern within the flower head in this plant family to develop an elegant means of testing this hypothesis. Their results are consistent with their expectations on the effect of resource limitation on the head, as determined by patterns of fruit size within the head, assuming that female fecundity is more strongly limited by resource availability than male function.

The authors took on a huge challenge in choosing to study the largest plant family (about 25 thousand species). Their sample was limited to only about a hundred species, but species selection was very careful, to ensure that the range of sex conditions and the available phylogenetic information were adequately represented. The analytical methods are robust and cast no doubt on the reported results. However, I can’t help but wonder what would happen if the antiselfing hypothesis was tested simultaneously. This would require self-incompatibility (SI) data for the species sample, as the presence of SI is usually invoked as a powerful antiselfing mechanism, rendering the unisexuality of flowers unnecessary. However, SI is variable and frequently lost in the sunflower family [5]. I also wonder to what extent the very specific architecture of flower heads imposes an idiosyncratic resource distribution that may have fixed these sexual systems in species and lineages of the family. Although not approached in this study, intraspecific variation seems to be low. It would be very interesting to use similar approaches in other plant groups in which inflorescence architecture is lax and resource distribution may differ. A whole-plant approach might be required, rather than investigations of single inflorescences as in this study. This study has no flaws, but instead paves the way for further testing of a long-standing dual hypothesis, probably with different outcomes in different ecological and evolutionary settings. In the end, sex is not only in the head.

References

- [1] Barrett SC and Harder LD. David G. Lloyd and the evolution of floral biology: from natural history to strategic analysis. In: *Ecology and evolution of flowers*. Ed. by Harder LD and Barrett SC. Oxford University Press, 2006, pp. 1–21.
- [2] Charlesworth D. Theories of the evolution of dioecy. In: *Gender and sexual dimorphism in flowering plants*. Ed. by Geber MA, Dawson TE, and Delph LF. Springer, 1999, pp. 33–60.
- [3] Darwin C. *The different forms of flowers on plants of the same species*. John Murray, 1877.
- [4] Diggle PK and Miller JS. Developmental plasticity, genetic assimilation, and the evolutionary diversification of sexual expression in *Solanum*. *American journal of botany* 100 (2013), 1050–1060. DOI: 10.3732/ajb.1200647.
- [5] Ferrer MM and Good-Avila SV. Macrophylogenetic analyses of the gain and loss of self-incompatibility in the Asteraceae. *New Phytologist* 173 (2007), 401–414. DOI: 10.1111/j.1469-8137.2006.01905.x.
- [6] Friedman J and Barrett SC. A phylogenetic analysis of the evolution of wind pollination in the angiosperms. *International Journal of Plant Sciences* 169 (2008), 49–58. DOI: 10.1086/523365.
- [7] Geber MA, Dawson TE, and Delph LF. *Gender and sexual dimorphism in flowering plants*. Springer Science & Business Media, 1999.
- [8] Renner SS. The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of botany* 101 (2014), 1588–1596. DOI: 10.3732/ajb.1400196.
- [9] Torices R, Afonso A, Anderberg AA, Gómez JM, and Méndez M. Architectural traits constrain the evolution of unisexual flowers and sexual segregation within inflorescences: an interspecific approach. *bioRxiv* 356147, ver 3 peer-reviewed and recommended by *PCI Evol Biol* (2019). DOI: 10.1101/356147.

Appendix

Reviews by three anonymous reviewers, DOI: 10.24072/pci.evolbiol.100069