What have been your biggest mistakes? Oh, there have been plenty: not trusting my gut about collaborators, not recruiting the right people to my group, failing to set boundaries early, repeatedly giving too much benefit of the doubt. But mistakes are essential; they're often the only way to learn something without being told, and the lesson only sticks once you've felt the true cost of it yourself. As disappointing as they can be in the moment, they build character and resilience for the next setback.

Which aspect of science, your field or science in general, do you wish the general public knew more about? I wish the general public understood that science isn't a body of settled facts — it's an ongoing process of being wrong in increasingly precise ways. When a study is later overturned, that's not science failing; it's science working exactly as it should.

What big questions do you hope are asked next in your field? Biology leans heavily on a handful of model species. We've ended up knowing these species deeply, and we unconsciously treat them as stand-ins for life in general. But every species is really a model for itself, shaped by its own history and evolutionary pressures. So, I hope the big questions we ask next are drawn from the actual challenges animals face, rather than from the species that happen to be easiest to study.

If you had not made it as a scientist, what would you have become? Becoming a scientist was never my dream or ambition — watching and learning about animals clearly was. If I hadn't become a biologist, I'd most likely have become a wildlife photographer. I have occasionally been paid for my pictures, so I may have an alternative career to pursue.

DECLARATION OF INTERESTS

The author declares no competing interests.

School of Natural Sciences, Wallumattagal Campus, Macquarie University, Sydney, NSW, Australia.
E-mail: ajay.narendra@mq.edu.au

Quick guide

Heterodichogamy

Jeffrey S. Groh[1,2,3,4]

What is heterodichogamy? In many plant and animal lineages, the production of male and female gametes occurs in separate individuals. The majority of flowering plants, however, are hermaphroditic, and have evolved a wide variety of genetic and developmental mechanisms to navigate the fitness costs of self-fertilization and interference between male and female function. One common strategy is dichogamy, or temporal separation of the sexes. Dichogamy is typically monomorphic, meaning all individuals of a species show the same order of sex separation. However, some angiosperm lineages have taken this a step further by evolving a genetic dimorphism for the order of male *versus* female flowering — the mating system known as heterodichogamy.

In heterodichogamy, one morph is protandrous (male-first) while the other is protogynous (female-first). The timing of the sex switch is highly synchronized, such that one morph is male while the other is female, and *vice versa*. Thus, most matings should occur between individuals with different dichogamy phenotypes. Because of this, the rarer morph gains a reproductive advantage and rises in frequency until a 1:1 equilibrium ratio is reached. This maintenance of heterodichogamy through negative-frequency-dependent mating closely mirrors how Fisherian sex ratio selection maintains even sex ratios in countless species with separate sexes.

Heterodichogamy occurs on both seasonal and daily time scales (Figure 1A,B). In some species, protandrous and protogynous morphs switch functional sex midway through a growing season. In other systems, sex alternation occurs each 24-hour day/night cycle, with floral movements bringing the different sex organs into contact with incoming pollinators in succession.

How common is it? Heterodichogamy has convergently evolved at least a dozen times across angiosperms, and occurs in familiar crops such as walnut, pecan, and avocado. Where it has evolved, heterodichogamy often persists for tens of millions of years and is characteristic of entire clades. First discovered in walnut (Juglandaceae), seasonal heterodichogamy has since been confirmed in all five genera of subfamily Juglandoideae (ca. 50 species). Within the laurel family (Lauraceae), daily heterodichogamy evolved in the common ancestor of tribe Perseeae and is common among the ca. 400 species in this clade. Dichogamy is also known in bryophytes, ferns, and gymnosperms, and in animals (where it is called sequential hermaphroditism). In some corals, colonies even alternate between male and female across years. However, it remains unknown whether true dimorphic heterodichogamy exists outside of angiosperms.

Why does it evolve? It is commonly written that heterodichogamy is an adaptation to avoid self-pollination. However, dichogamy alone could accomplish this, and may even evolve for other reasons, such as avoidance of pollen wastage or sexual selection. The answer to why heterodichogamy evolves must directly address the evolution of dimorphism from an ancestrally monomorphic population. While the evolution of dichogamy may be a prerequisite, it seems likely that heterodichogamy *per se* evolves in response to a temporal skew in the sex ratio. For example, in a population where most individuals are male early in the season and female later in the season, early female function and late male function would be selectively favored. The evolution of heterodichogamy may be constrained by the existence of genetic variation allowing for these changes to be co-inherited.

How is it regulated? In all studied cases, heterodichogamy is governed by simple Mendelian inheritance. Thus, to accomplish reciprocal synchrony of both sexes, a dominant allele found in one morph must simultaneously advance one sex while delaying the other. How might this occur? Recent work in several systems has identified the causal loci, yielding important insights into a variety of underlying mechanisms.

Across Juglandaceae, distinct genetic systems for seasonal heterodichogamy

All rights are reserved, including those for text and data mining, AI training, and similar technologies.

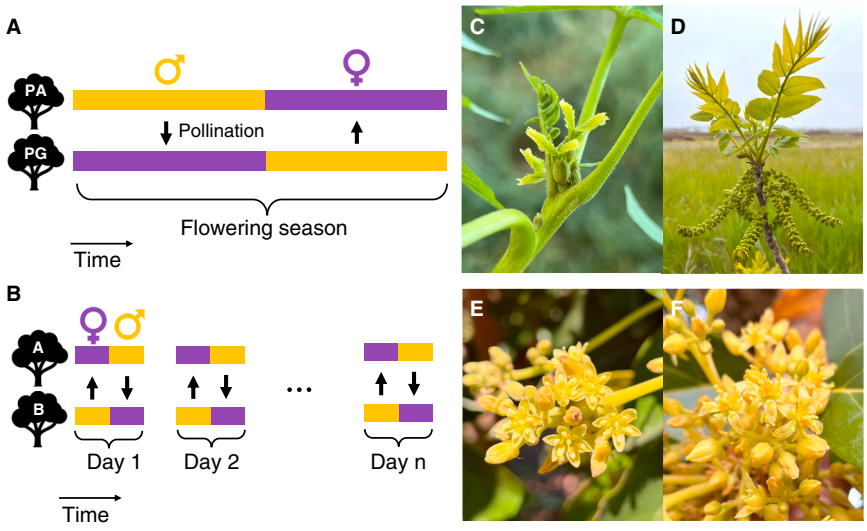


Figure 1. Heterodichogamy.
(A) Seasonal and (B) daily heterodichogamy. Arrows represent direction of pollen movement. (C) Female and (D) male flowers of Northern California black walnut (*Juglans hindsii*). (E) Female- and (F) male-phase flowers of avocado (*Persea americana*). (Photos by J.S. Groh.)

exist in walnuts, wingnuts, and hickories. An emerging theme is that the causal loci drive allele- and tissue-specific expression of single gene candidates. In walnuts (Figure 1C,D), *TPPD1* shows allele-specific expression in developing male flowers. In wingnuts, differential regulation of *GFAFL* alleles in male and female flowers illustrates a minimal model for single gene control. In both groups, context-specific expression changes appear to be in part regulated by small RNAs encoded by the dominant allele. In contrast, hickories (e.g., pecan) have a 'supergene' locus; the two alleles are non-recombining haplotypes spanning 20 genes, including several flowering time candidates. The functional changes in these seasonal heterodichogamy systems begin to act early in flower development, prior to winter dormancy.

In daily heterodichogamy, the causal loci must rapidly coordinate sex organ maturation with floral movements. In tropical gingers (Zingiberaceae), the style flexes upward or downward, staggering pollen release and pollen receipt. The causal locus is a regulatory region of *SMPED1*, a gene with pleiotropic effects on both style movement and anther dehiscence. Morphs show distinct daily rhythms of *SMPED1* expression, although the protein alleles are identical.

An intricate form of heterodichogamy exists in avocado (Figure 1E,F) and its relatives. Flowers on A-type plants first open in female-phase one morning and reopen in male-phase the following day in the afternoon. Flowers on B-type plants first open in female-phase one afternoon, then again in male-phase the following morning. The result is that each day of flowering, A-types switch from female to male, and B-types do the reverse. This reciprocal dance is staged by the floral transcription factor *SDMYB*. The dominant allele has a phase-shifted expression rhythm mirroring the temporal offset of male-phase and contains amino acid changes that likely play an additional role.

In summary, inheritance systems for heterodichogamy involve genes with diverse roles in flower development, but general regulatory principles are beginning to emerge. In both seasonal and daily heterodichogamy, changes to the regulation of a few or single genes in specific developmental contexts ultimately establish the remarkable synchrony of sex alternation.

What are the consequences for genome evolution? Structural variation is a common feature of heterodichogamy inheritance systems. Structural variants may play a direct role in gene regulation, for example through the production of small RNAs from tandem repeats, as seen in walnuts and wingnuts. Structural variants may also enhance linkage between epistatic mutations by suppressing recombination, precipitating further divergence between alternative haplotypes. In hickories, the non-recombining dominant haplotype has expanded two-fold in length through elevated transposon accumulation. This bloated haplotype also shows lower genetic diversity, hallmark signs of degeneration shared by other non-recombining supergenes like Y and W chromosomes. Nonetheless, the causal loci don't expand to the same extent as many heteromorphic sex chromosomes. Why might heterodichogamy loci differ from sex chromosomes in this way? Perhaps occasional recombination in rare dominant allele homozygotes slows Muller's Rachet, and/or there is relatively little genetic variation with morph-specific fitness effects to drive the spread of recombination suppression.

What remains unknown? Despite recent progress, little remains known about the molecular mechanisms controlling heterodichogamy. Even where the causal genes are known, often much remains unclear as to how these mechanisms jointly regulate the timing of both sexes. How did these systems evolve in the first place? Theoretical and empirical work is needed to elucidate steps in the initial evolution of heterodichogamy from a dichogamous ancestor. This may also help explain the phylogenetic distribution and relative rarity of heterodichogamy. Although genetic systems for heterodichogamy are remarkably stable (e.g., >40 Myr in Juglandaceae and Lauraceae), their diversity within Juglandaceae suggests that they may occasionally turn over and even reverse the direction of dominance. What might drive such turnover? The causes remain unknown, yet might be due to environmental shifts, meiotic drive, or accumulation of deleterious variation. Further comparative studies are also needed to better understand the role of heterodichogamy in the evolutionary transition to separate sexes.

Why does it matter? While fascinating in its own right, heterodichogamy offers a useful comparative system to understand general principles in the evolution of sexual reproduction strategies and balanced polymorphisms.

CellPress

Studying the underlying genetics may shed light on molecular mechanisms of dominance and adaptation of biological rhythms. Finally, identification of the causal variants will accelerate breeding programs in slow-growing tree crops such as walnut, pecan and avocado — a valuable tool for sustainable agriculture in a changing climate.

Where can I find out more?

Bai, W.-N., Zeng, Y.-F., and Zhang, D.-Y. (2007). Mating patterns and pollen dispersal in a heterodichogamous tree, *Juglans mandshurica* (Juglandaceae). New Phytol. *176*, 699–707.

Bertin, R.I., and Newman, C.M. (1993). Dichogamy in angiosperms. Bot. Rev. *59*, 112–152.

Endress, P.K. (2020). Structural and temporal modes of heterodichogamy and similar patterns across angiosperms. Bot. J. Linn. Soc. *193*, 5–18.

Gleeson, S. (1982). Heterodichogamy in walnuts: inheritance and stable ratios. Evolution *36,* 892–902.

Groh, J.S., Ackerman, G., Wenzel, M., and Coop, G. (2025). Distinct haplotypes and reversed dominance at a single-gene balanced polymorphism controlling heterodichogamy in two genera of wingnuts. Curr. Biol. *35*, 5192–5209.e11.

Groh, J.S., Vik, D.C., Davis, M., Monroe, J.G., Stevens, K.A., Brown, P.J., Langley, C,H., and Coop, G. (2025). Ancient structural variants control sex-specific flowering time morphs in walnuts and hickories. Science *387*, eado5578.

Groh, J.S., Soares dos Santos, M.F., de Dios, E.A., Ackerman, G., Solares, E., Iturrieta, R.A., Focht, E., Seymour, D., Gaut, B.S., Arpaia, M.L., *et al*. (2026). Balanced polymorphism in a floral transcription factor underlies the ancient rhythm of daily sex alternation in avocado. Proc. Natl. Acad. Sci. USA *123*, e2606876123.

Liu, H.-S., Wang, W.-H., Song, Y.-F., Yang, Y., Zhang, D.-Y., Bai, W.-N., and Zhang, B.-W. (2025). A pan-genome framework reveals structural variation and small RNA regulation underlying heterodichogamy in *Pterocarya*. Curr. Biol. *35*, 5179–5191.

Pendleton, R.L., Freeman, D.C., Macarthur, E.D., and Sanderson, S.C. (2000). Gender specialization in heterodichogamous *Grayia brandegei* (Chenopodiaceae): evidence for an alternative pathway to dioecy. Am. J. Bot. *87*, 508–156.

Renner, S.S. (2001). How common is heterodichogamy? Trends Ecol. Evol. *16*, 595–597.

Shikina, S., Tsai, P.-H., Chiu, Y.-L., and Chang, C.-F. (2024). The stony coral *Fimbriaphyllia* (*Euphyllia*) *ancora*'s reproductive strategy involves a sex change every year. Commun. Biol. *7*, 1093.

Zhao, J.-L., Dong, Y., Huang, A.-D., Duan, S.-C., Peng, X.-C., Liao, H., Chen, J.-H., Luo, Y.-L., Lan, Q.-Y., Wang, Y.-L., *et al*. (2025). Ginger genome reveals the *SMPED1* gene causing sex-phase synchrony and outcrossing in a flowering plant. Nat. Plants *11*, 2254–2267.

DECLARATION OF INTERESTS

The author declares no competing interests.

[1]Miller Institute for Basic Research in Science, University of California, Berkeley, CA, USA.
[2]Department of Molecular and Cellular Biology, University of California, Berkeley, CA, USA.
[3]Department of Plant and Microbial Biology, University of California, Berkeley, CA, USA.
[4]Department of Integrative Biology, University of California, Berkeley, CA, USA.
E-mail: jgroh@berkeley.edu

Primer

Fungal–bacterial interactions

Jessie Uehling*, Daniyal Gohar, and Hayden Johnson

The study of fungal–bacterial interactions is an emerging field of biology with relevance for environmental health, medicine, and agriculture, among other sectors. The frequent co-occurrence of fungi and bacteria in many habitats has facilitated the evolution of their symbioses. Both groups are key players in host-associated microbiomes and in nutrient cycling, and these roles often intersect in dynamic ways. Interactions between fungi and bacteria can be mutualistic, commensal, or pathogenic, and they can vary in a context-dependent manner. In mutualistic interactions, fungi and bacteria can exchange nutrients, ameliorate each other's stress, enhance growth, enable dispersal, and facilitate novel niche exploration via metabolite exchange. In contrast, antagonistic interactions frequently involve competition for limited nutrients, such as iron, and active chemical warfare with secreted and bioactive compounds. Bacteria associated with fungi can occur inside of fungal cells (endosymbiotic) or on the surface of fungal hyphae (exosymbiotic). Endosymbiotic bacteria can be further differentiated into facultative symbionts, which retain the ability to enter fungal hyphae but also live independently, and obligate endosymbionts, which are always intracellular and not capable of independent life outside of hyphae. Whereas free-living bacteria can be pathogenic or mutualistic, endosymbiotic bacteria are often regarded as commensals or mutualists, although some can exhibit parasitic attributes in some conditions. A combination of molecular genetics, genomics, and microscopy has been used to study free-living bacteria. In addition to these approaches, fluorescence and electron microscopy have been used as the gold standards to study and differentiate endosymbiotic bacteria based on their intracellular location. More recently, researchers have started using systems-biology approaches to study fungal–bacterial interactions including high-throughput -omics assays. These methods produce expansive datasets that are ideally suited to artificial intelligence (AI)-based approaches to tackle long-standing questions about the basic biology and evolution of fungal–bacterial interactions. In this primer we give an overview of fungal–bacterial interactions, including their diversity, community structure, and symbiotic evolution. We highlight two research systems in particular: the intracellular endosymbionts of Mucoromycota fungi and the free-living bacteria associated with edible fungi. We focus on these systems because fungi remain understudied relative to other groups, and only a handful of fungal taxa with their bacterial symbionts are backed by large enough data sets to explore these concepts in detail. Our aim here is not to be comprehensive, but instead to use the most well-understood systems to illustrate emerging principles. We then discuss advances in using AI to infer new aspects of microbial biology and provide suggestions for how these technologies could advance research on fungal–bacterial interactions utilizing existing genomic datasets.

Endosymbiotic bacteria and fungi

Endosymbiotic bacteria are documented across the fungal tree of life but are especially prevalent in the Mucoromycota, an early diverging clade of largely plant-associated fungi. Bacterial endosymbionts of fungi are unequivocally established using a combination of sequencing and imaging data to robustly demonstrate their intracellular location. The best characterized endosymbionts of Mucoromycota fungi are related to *Burkholderia* and *Mollicutes*, and are referred to respectively as *Burkholderia*-related endosymbionts (BREs) and *Mollicutes*-related endobacteria (MREs). Both BREs and MREs have reduced genomes compared to free-living relatives, and it is widely assumed that both are vertically transmitted. MRE bacteria have more recently been described as symbionts of Mucoromycota fungi. Because the BREs have been better studied, more is known about their diversity, the mechanisms of their host interactions,

All rights are reserved, including those for text and data mining, AI training, and similar technologies.