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Digest: Plant-pathogen coevolution extends to shifts in plant breeding systems*

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Plants and their pathogens are in a coevolutionary arms race. Some pathogens, such as anther smuts, use their host plants' pollinators for spore dispersal. In the plant *Dianthus pavonius*, gynodioecy (having female and hermaphroditic plants) has evolved to reduce flowering duration and therefore limit exposure to anther smut pathogens. Bruns et al. (2018) show that this shift in breeding system has evolved as a disease escape mechanism.

Plants and their fungal pathogens provide many examples of antagonistic coevolution (Burdon and Thrall 2009). Arms races may be fought gene-for-gene between plant receptors, which detect pathogens and trigger defense responses, and pathogen effectors, which evade detection or block defense signaling (Sánchez-Vallet et al. 2018). Pathogens successfully colonizing a plant can absorb nutrition from within their hosts' tissues, manipulate the host's body into producing galls, and even control whether host cells live or die. Plants may fight back with programmed cell death, toxin resistance, or defensive structures such as callose barriers (Underwood 2012). Changes in plant architecture or phenology may also evolve to reduce pathogen exposure or spread; these are known as "disease escape" strategies (Arraiano et al. 2009).

Some plant pathogens also exploit their host's would-be pollinators for spore dispersal in a variety of ways. The rust fungus *Puccinia punctiformis* produces spore pustules with a flower-like scent (Connick and French 1991), and *P. monoica* rusts make their hosts produce entire "pseudoflower" structures from leaf tissue (Cano et al. 2013), while anther smuts (*Microbotryum* sp.) cause their hosts' existing flowers to release fungal spores instead of pollen.

Anther smuts infect plants in the Caryophyllaceae family. These plants are model organisms for mating system evolution, with species ranging from complete hermaphrodites to full dioecy. In species with separate female plants, the anther smuts manipulate their hosts' floral development to form spore-bearing stamens in otherwise female flowers.

In this issue, Bruns et al. (2018) investigate whether having a mixture of female and hermaphroditic plants, a breeding system known as gynodioecy, can evolve as a mechanism of disease escape. Populations of alpine carnation *Dianthus pavonius* have varying frequencies of female and hermaphrodite flowers, as well as varying *Microbotryum* infection levels. The hermaphrodite flowers are protandrous: the stamens ripen before the stigmas (Fig. 1), reducing inbreeding. Through a combination of natural population studies and common garden experiments, Bruns et al. (2018) confirm that this system causes the hermaphrodite flowers to remain open for longer than female flowers, providing more opportunity for anther smut infection in hermaphrodite flowers than female flowers. However, the selection for female flowers is frequency-dependent: female flowers close after pollination, which happens more quickly when there are more pollen-producing (hermaphrodite) plants and female plants are rare. Bruns et al. (2018) show that populations where anther smut is present have more female plants, suggesting that *Microbotryum* presence has driven changes in sex ratios. The researchers also demonstrate inbreeding depression within *D. pavonius*, which further selects for gynodioecy and against loss of protandry in hermaphroditic flowers.

This study highlights an evolutionary conflict in which the same traits that increase mating success (through increased pollinator visits) also increase risk of disease. Pollinator-dispersed

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Figure 1. Flower types in *Dianthus pavonius*.(A) Hermaphrodite, protandrous flowers: the flowers open when the stamens are ripe; then the stigmas ripen, and flowers close after pollination. (B) Female flowers: the stigmas are ripe as soon as the flowers open, so flowering time is shorter. (C) Infected flowers: all flowers, whether genetically hermaphrodite or female, have spore-filled anthers and sterile carpels.

pathogens not only manipulate their hosts' reproductive systems directly, but also drive evolutionary changes in plant breeding systems through selection for disease escape.

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