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How climate change affects plants' sex lives

Shifts in plant sex ratios help plant species to expand upslope in a warmer climate

By **Julie R. Etterson¹** and **Susan J. Mazer²**

Climate change affects wild plant species across their geographical ranges. Studies at the margins of species' ranges reveal upslope expansion, low-elevation range contraction, and, in some cases, a lack of geographic response to climate change (1). However, all populations, including those in the core of species' ranges, are subject to climate-driven natural selection that promotes adaptation to a warmer world (2). Theoretical models show that coupled spatial and temporal responses of populations can mediate the negative effects of climate change (3, 4), but it remains unclear whether these processes can occur fast enough to rescue populations from extinction (5). On page 69 of this issue, Petry *et al.* (6) report rapid spatial and temporal change in plant sex ratios in response to changing climatic conditions. These changes could facilitate geographic range shifts in the montane perennial herb valerian (*Valeriana edulis*).

The authors examine change across an elevation gradient in a dioecious species, in which individuals are either male or female, over the course of 33 years (see the figure). In warmer and drier low-elevation sites, populations harbor more males than those in cooler and wetter high-elevation sites, apparently because of gender-specific differences in water-use efficiency and, ultimately, life expectancy. Because it has become warmer and drier in central Colorado over the past three decades, the proportions of males in high-elevation populations have increased (see the figure, top panel), resulting in greater pollination success and increased seed set for females—conditions that could facilitate upslope range expansion. This con-

dance between temporal and spatial change supports the assumption that space can substitute for time when forecasting responses to climate change.

Although a novel and compelling finding, this mechanism of change only applies to the ~6% of angiosperms composed of unisexual individuals. The vast majority of flowering

plants are hermaphroditic—that is, they produce flowers that include both male and female reproductive parts (see the photo). Some hermaphrodites have sophisticated means of preventing self-fertilization (7), but ~42% have mixed mating systems where a single fruit can contain seeds from self-pollination and seeds pollinated by a different individual.

Mixed mating systems provide reproductive assurance, which is especially beneficial when mates or pollinators are scarce (8). However, this mating system also promotes self-fertilization, which is even more genetically risky than mating between close relatives. Any inbreeding increases the expression of deleterious mutations, thereby reducing reproductive fitness. Natural selection can gradually purge populations of harmful mutations, but mixed mating systems persist even in the presence of the negative effects of inbreeding; unfortunately, this also increases susceptibility to extinction (9).

How might climate change alter the sex lives of these hermaphroditic species? Clearly, warmer and drier conditions should favor attributes that directly benefit both male and female function, such as drought tolerance. But some climate responses could directly or indirectly lead to increased self-fertilization, along with its genetic risks.

First, in extreme environments, smaller flowers may be produced as a passive response to a stressful and deteriorating environment (10). This could also reduce the temporal and/or spatial separation between male and female organs (11), facilitating self-fertilization (see the figure, middle panel).

Second, smaller flowers may evolve indirectly through climate-driven selection that favors traits promoting rapid completion of the life cycle, including early flowering and rapid floral development. These two traits

Sex matters

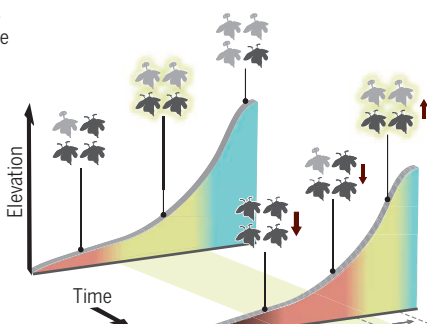
Plant responses to climate change depend on their method of reproduction

Unisexual (dioecious) plants

Plants are either male or female



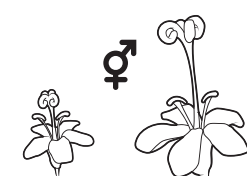
Gender-specific range shifts may help these plants to adapt to climatic conditions in some locations



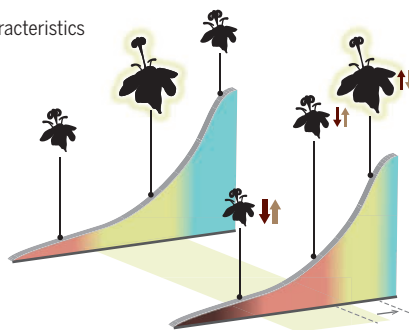
↓ Population growth rate ↑ Self-fertilization

Hermaphroditic plants

Plants have male and female characteristics



Smaller flowers or accelerated development in extreme environments may reduce spatial or temporal separation of male and female organs, hence more self-fertilization and inbreeding

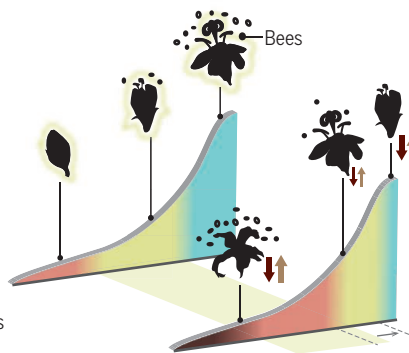


Plant-pollinator interactions

Plants are hermaphroditic



Climate change may cause plants to flower when few pollinators are present. This may reduce reproductive success and favor self-fertilizing plants





Hermaproditic flower of *Chamerion angustifolium*, a species that can self-fertilize.

are associated with the production of small flowers with synchronously developing and proximate male and female organs (11), also facilitating self-fertilization.

Finally, coevolved biotic interactions between flowering plants and their pollinators can be disrupted if warmer temperatures cause a mismatch between the timing of flowering and pollinator abundance or presence (see the figure, bottom panel). In this case, natural selection could directly favor self-fertilization as a mechanism of reproductive assurance (12). If these processes occur very rapidly, the rate of self-fertilization could increase faster than the rate at which deleterious mutations are purged. This could ultimately cause population declines.

Petry *et al.*'s findings were possible because historical data was fortuitously available. In a few rare circumstances, it has been possible to observe evolutionary change between two time points by germinating ancestral seeds that were fortuitously available (e.g. preserved in tundra soils or seed vaults) simultaneously

with contemporary seeds (2, 13). Such direct comparison between ancestral and descendent populations show that climate change is already affecting traits associated with plant mating systems, such as the timing of flowering. Efforts are under way to vastly expand the availability of these rare and valuable historical seed resources (14, 15). These collections should help to more definitively answer the knotty question of whether evolution can rescue populations of native species, including the wild relatives of crops, from climate change across their geographic ranges. ■

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SEX DETERMINATION

Yob makes mosquitoes male

A gender-switch gene opens avenues to malaria control

By Steven P. Sinkins

Most developmental processes show deep conservation across great phylogenetic distances. In contrast, the signal that triggers the primary genetic switch between the sexes has evolved with remarkable rapidity—entirely lacking the “respectable antiquity” (1) seen in other comparable systems. Coupled with the repeat-rich structure of Y chromosomes, this has made the identification of genetically dominant “M” male-determining factors especially challenging. On page 67 of this issue, Krzywinska *et al.* (2) compared gene transcript sequences from male and female embryos of the malaria mosquito *Anopheles gambiae* and identified an early-expressed gene on the Y chromosome, designated *Yob*. Crucially, they show that it controls sex-specific splicing of *dsx* (*double-sex*), the conserved binary switch between male and female development (3), fulfilling the criteria for M. *Yob* partly overlaps, and probably is a better-annotated version of, a previously identified gene called *YG2* (4), recently shown to be conserved across the *An. gambiae* species complex (5).

This landmark follows the identification of *Nix*, the male-determining M gene in *Aedes aegypti*—the primary mosquito vector of dengue and Zika viruses (6). *Yob* and *Nix* are certainly not homologous. *Aedes* and *Culex* mosquitoes, unlike *Anopheles*, do not possess Y chromosomes, and *Nix* is located in a nonrecombining region of chromosome 1. Dosage compensation, the equalization of gene expression between males and females, is thus not needed in *Aedes*, but in *Anopheles* operates by up-regulation of genes on the single male X (7). *Yob* seems to control both sex determination and dosage compensation, because embryos die when genetic females receive ectopically delivered *Yob* messenger RNA or when *Yob* is silenced in genetic males (2). In contrast, in *Aedes*,



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