of a sex determination gene, *Masculinizer* (responsible for male-specific splicing of *dsx* and repression of transcription from Z chromosomes), has been similarly attributed to misregulation of dosage compensation (*33*).

Dosage compensation in *A. gambiae* also relies on hyperactivation of the X-chromosome genes in males (*34*). Therefore, in the presence of YOB, dosage compensation may be directly or indirectly induced in the XX embryos, leading to their death as a result of abnormal overtranscription from both X chromosomes (fig. S10). Conversely, in the absence of YOB, lack of dosage compensation and concomitant insufficient transcription from the X chromosome should be male-lethal, rather than leading to feminization of the XY individuals. Indeed, we observed highly significant male deficiency in mosquitoes surviving transient knockdown of *Yob* in nonsexed embryos (Fig. 3C). All tested female survivors had the XX karyotype.

Involvement of the Y chromosome factor in sex determination in *Anopheles* was first supported by the finding of a single, triploid *Anopheles culicifacies* male with the XXY sex chromosomes (*15*). Such a karyotype, apparently extremely rare and not reported elsewhere in numerous mutational and cytogenetic studies in *Anopheles*, seems to counter overtranscription of the X-chromosome genes as a cause of female embryo lethality observed in our study. However, the genetic background of this male must have been severely compromised through the mutagenic effects of irradiation on his parents (*15*). It thus seems likely that the XXY male may have carried multiple mutations, including those causing loss of function of dosage compensation machinery that allowed his survival to adulthood despite possessing two X chromosomes.

A. gambiae and *A. arabiensis* are the most important African vectors of human malaria. Control of the disease depends heavily on the use of insecticides, but emergence of resistance in mosquito populations severely threatens the effectiveness of these approaches (*35*). The sterile insect technique and other genetic control methods have been proposed to complement current efforts to suppress mosquito populations (*36*, *37*). Such programs must incorporate male-only releases, because released females would contribute to pathogen transmission. However, no effective methods to sex the large number of *Anopheles* needed for releases currently exist. The fitness and mating competitiveness of adults is highly dependent on larval density; therefore, removing females from the release generation during the embryonic stage would drastically decrease the costs of rearing of high-quality males (*38*). *Yob* represents an excellent tool to be used in transgenic technology to conditionally eliminate female embryos and efficiently produce male-only generations of both malaria-transmitting *Anopheles* species (*37*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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References (*39*–*48*)

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CLIMATE CHANGE

Sex-specific responses to climate change in plants alter population sex ratio and performance

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Males and females are ecologically distinct in many species, but whether responses to climate change are sex-specific is unknown. We document sex-specific responses to climate change in the plant *Valeriana edulis* (valerian) over four decades and across its 1800-meter elevation range. Increased elevation was associated with increased water availability and female frequency, likely owing to sex-specific water use efficiency and survival. Recent aridification caused male frequency to move upslope at 175 meters per decade, a rate of trait shift outpacing reported species' range shifts by an order of magnitude. This increase in male frequency reduced pollen limitation and increased seedset. Coupled with previous studies reporting sex-specific arthropod communities, these results underscore the importance of ecological differences between the sexes in mediating biological responses to climate change.

Differences between the sexes in morphology and physiology can result in sex-specific responses to the environment (*1*–*3*). Given this, climate change may affect the sexes differently, potentially creating an imbalance in the frequency of males and females and altering patterns of fertility and population dynamics (*4*–*6*). In so doing, climate change might ameliorate or exaggerate existing sex ratio biases, alternatively driving population growth or decline (*4*, *7*) and affecting the ability of species' ranges to track shifting climate envelopes (*8*, *9*).

We investigated whether climatic variation differentially affects the performance of the sexes and whether these differences are sufficient to bias population sex ratios. We studied *Valeriana edulis* (valerian, Caprifoliaceae), a dioecious herb with fixed, genetically based sex expression (*10*, *11*), over its entire elevation range from arid low-elevation scrublands to mesic alpine tundra (2000 to 3790 m) and in response to 33 years of climate change. We assessed (i) sex ratio change along these two complementary axes of climate variation, (ii) the sex-specific mechanisms underlying this change, and (iii) how biased sex ratios influence individual fitness.

Climate varies considerably across the elevation range of *V. edulis* (fig. S1, A to D, and table S2). Contemporary climate data for our study area in the Rocky Mountains of Colorado (fig. S2 and table S1) showed that increasing elevation is accompanied by a decrease in mean growing season (June–August) temperature (−0.59°C per 100 m), an increase in growing season precipitation (1.5 mm per 100 m), a delay in the date of snowmelt (4.1 days later per 100 m), and a marginally significant trend for increasing growing season soil moisture (1.09% per 100 m). Collectively, these changes produce a gradient of decreasing aridity with increasing elevation.

We surveyed population operational sex ratios (OSRs; the proportion of flowering individuals that are male) across this elevation gradient to test whether elevational variation in climate was accompanied by parallel variation in *V. edulis* population OSR. Surveys of 31 *V. edulis* populations across the species' elevation range in 2011 showed that males decrease in frequency with increasing elevation (linear regression, $F_{1,\,29} = 10.33$, $P = 0.003$, $R^2 = 0.26$) (Fig. 1A), falling from 50.0% of flowering individuals at the lowest elevation population to 22.7% at the highest population, for an average change of –0.88% per 100 m of elevation. Spatial climatic variation thus affects *V. edulis* OSR, suggesting that similar shifts may occur in response to climate change over time.

Recent climate change has warmed and dried our study area, driving climatic isoclines up in elevation and providing a temporal axis of climate variation that parallels that which occurs over the elevation gradient (fig. S1, E to H, and table S2). Data collected during the growing season over the past four decades (1978–2014) show that mean temperature increased 0.21°C/decade, precipitation decreased 1.91 mm/decade, and soil moisture decreased 1.5%/decade, whereas snowmelt date marginally advanced 2.9 days/decade (tables S1 and S2). This change over time is equivalent to an upslope shift in the isoclines for growing season mean temperature, precipitation, advancement of snowmelt, and soil moisture at rates of 36 ± 8, 133 ± 26, 72 ± 40, and 195 ± 523 m/decade (±SEM), respectively. Climate change over the past four decades has advanced the onset of flowering in *V. edulis* by 3.1 days/decade (linear regression, $P = 0.062$, $R^2 = 0.091$) (fig. S3), likely because of an advancing date of snowmelt, which is strongly associated with flowering phenology in this species (linear regression, $P < 0.0001$, $R^2 = 0.47$) (*12*). Regional climatic projections suggest that climate will continue to change (*13*).

Recent climate change has in turn significantly shifted *V. edulis* OSR in a manner consistent with the upslope shift in climate. Surveys of OSR from nine populations in both 1978 and 2011 showed that males have become more frequent across the species' elevation range at a rate of 1.28%/decade (paired *t* test, $t_9 = 2.29$, $P = 0.047$) (Fig. 1B). Comparing this temporal shift with the independent, parallel pattern of OSR variation over space shows that OSR isoclines are moving upslope at a rate of 175 m/decade (lower SE = 87 m/decade, upper SEM = 316 m/decade), mirroring the rates at which precipitation and soil moisture have changed. The parallel changes in OSR over elevation and time implicate climate as the driver of OSR variation but do not reveal the processes by which this occurs.

To explore the mechanisms underlying sex-specific responses to climate change, we quantified life history differences between the sexes in four populations spanning 1167 m of elevation (2470 to 3637 m) and varying 22% in OSR (48 to 26% male). We used sex- and size-structured rates of annual growth and mortality collected from 1978–1980 to calculate male and female life expectancy upon reaching reproductive maturity in each population. This metric integrates sex differences in demographic performance across the life span and reflects the average duration during which a plant contributes to OSR. Sex differences in reproductive life expectancy were concordant with population OSR, so that female-biased OSRs were associated with longer reproductive life spans than those of males (fig. S4) and suggesting that sex-specific effects of climate on life history drive population variation in OSR.

We sought to determine the proximate, physiological basis for the sex-specific effects of climate by focusing on water, a key resource. A plant's water use efficiency (WUE; carbon assimilation per unit of water transpiration) mediates its ability to acquire energy within the short, water-limited growing season (fig. S5). We hypothesized that sex differences in WUE—a trait known to differ between the sexes in many plant species, likely resulting from higher costs of reproduction in females (*14*)—underlie sex differences in plant performance and drive patterns in OSR. We measured the integrated WUE of each sex as indicated by leaf carbon isotope ratios collected from eight populations varying in OSR (*15*). Sex differences in WUE strongly predicted population OSR (Deming regression, $t_6 = 2.06$, $P = 0.043$) (Fig. 2); females had higher WUE than that of males in strongly female-biased populations (low OSR), but males had higher WUE than that of females in populations with a higher proportion of males (higher OSR). Although these findings do not directly link WUE to differential performance of the sexes, in other species this trait drives sex differences in performance that produce intrapopulation variation in OSR among arid and mesic microsites (*16*).

Variation in OSR may feed back to affect population growth by altering pollen availability and seedset rates (*7*, *17*). We measured the response of female seedset to an index of pollen availability

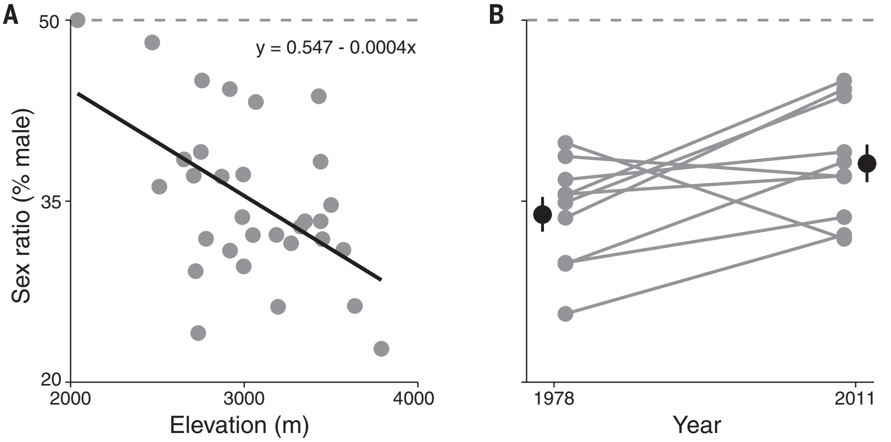

Fig. 1. OSR of *V. edulis* populations declines with climatic variation over elevation and increases in response to climate change. (**A**) OSR becomes significantly more female-biased with increasing elevation across the species elevation range in contemporary surveys (2011). (**B**) Males have significantly increased in frequency with climate change between 1978 and 2011 by an average of 5.5% (black points ± SEM) representing nine resurveyed populations (linked gray time points). A mean of 294 plants were surveyed in each population; populations with <100 flowering plants were censused completely.

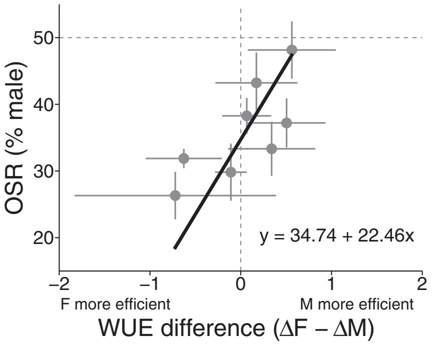

Fig. 2. Sex differences in WUE predict OSR. Each point represents a single population (*n* = 8 populations; 2470 to 3637 m). WUE is inferred from ^{13}C fractionation (Δ), and positive differences between the sexes (ΔF − ΔM) indicate that WUE of females is lower than that of males and vice versa. Data are means ± SEM.

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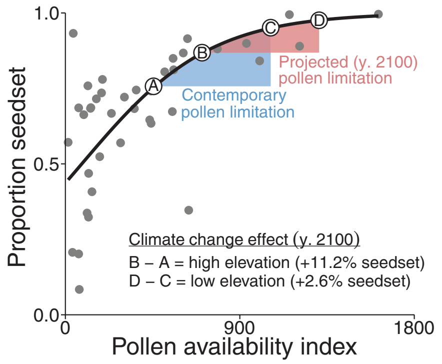

Fig. 3. Pollen availability limits female reproductive success. Each point represents one focal female controlling for competition with neighboring females for pollen. Estimated mean pollen availability for the range of contemporary OSRs observed across the *V. edulis* elevation range and expected OSRs in the year 2100 are indicated by the shaded regions where labeled points ("A" to "D") graphically show the expected change in pollen availability and seedset at the species' range margins. A linear model was fit to logit-transformed data; the back-transformed model fit is shown (*12*).

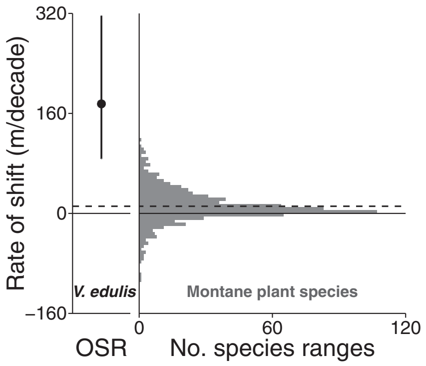

Fig. 4. Elevation range shifts of montane plant species are on average an order of magnitude slower than the rate of *V. edulis* OSR change. (**Left**) The black point ± SEM indicates the pace of OSR shift in *V. edulis*. (**Right**) A histogram shows the observed distribution of range shifts (677 observations encompassing 643 species reported in the literature), and the mean range shift (dashed black line) is indicated.

within the range of pollen movement (*12*). The majority (~90%) of pollen was received from males within 10 m of focal females (fig. S6). Female seedset in turn increased with pollen availability in this mating neighborhood (Fig. 3), rising from 39.3 to 99% of flowers producing seed across the observed range of neighborhood pollen availability. Simulating the effect of population OSR on seedset across the range of observed OSRs (Fig. 1A and supplementary materials, materials and methods), we found that the observed spatial variation in OSR was sufficient to alter female fitness. The low frequency of males at high elevation (22.8%) reduced median pollen availability by 55% compared with low-elevation populations with balanced OSR, corresponding to a reduction in seedset from 95 to 76% (Fig. 3). The demographic consequences of these effects are unclear because population growth rate in long-lived species is often relatively insensitive to changes in seed production (*18*). Nevertheless, *V. edulis* disperses only by seed, and climate effects on seedset may thus have important consequences for range shifts.

A mechanistic understanding of OSR dynamics in this system enables projections of the future state of *V. edulis* populations. Assuming the rate of increase in male frequency continues (1.28%/decade) (Fig. 1B), pollen limitation of reproduction at high-elevation populations could be halved by the year 2100 (a median seedset increase of 11.2%) (Fig. 3), facilitating the upslope range expansion of this species. In contrast, increasing male frequency at low elevation could have little effect on seedset (+2.6%) because females in those populations are pollen-saturated under contemporary, balanced OSRs (Fig. 3). Instead, increasingly male-biased OSRs at low elevation may threaten population viability by replacing females with males and thus reducing population-level seed production (*7*). Moreover, our previous work shows that female *V. edulis* support dramatically higher densities of arthropods than do males, including several specialist herbivores that depend exclusively on *V. edulis* (*19*, *20*). Accordingly, the effects of a climate-driven decline in female frequency may extend to higher levels of ecological organization.

Our data are distinctive in that they provide a pace of trait change (the upslope shift in plant sex distributions), whereas past studies of distribution responses to climate change have focused on species range shifts. Although trait changes are predicted to occur more rapidly than range shifts (*21*, *22*), the magnitude of such differences is hitherto unknown. Previously reported rates of species range shifts in montane plants show a mean upslope shift of 11.1 m/decade (*12*), which is dramatically slower than the 175 m/decade upslope pace of OSR change in *V. edulis* (Fig. 4). The pace of species range shifts frequently lags behind the pace of climate change (*12*), and such range disequilibria are frequently attributed to dispersal limitation (*23*). In contrast, shifts in traits within species ranges may track climate change more closely because they are based on differential performance of genetically based types that often already exist in many populations across the range. Here, we show that the pace of OSR change in *V. edulis* tracked climate change; it has kept pace with shifts in precipitation and soil moisture and has exceeded those of temperature and snowmelt (fig. S1).

We have demonstrated the occurrence of a potentially widespread form of biological response to climate change. We show that sex specificity of these responses can be exceptionally rapid, with broad effects across multiple scales of ecological organization. Within populations, sex-specific responses to climate change can skew sex ratios—through sex differences in physiology and performance or otherwise (*5*, *9*, *24*)—and the resulting sex ratio biases may, by mediating reproduction, affect population growth rate, the risk of population extinction, and the rate of adaptation to changing climate by altering the effective population size (*25*, *26*). In so doing, climate-driven changes in sex ratio may also control the tempo of species range shifts by mediating mate limitation at the leading or trailing range margins (*8*, *9*). Accordingly, a full understanding of biological responses to climate change requires a multiscale approach that integrates the underlying, but often cryptic, changes in intraspecific traits that give rise to higher-order patterns.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/353/6294/69/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S8
Tables S1 to S5
References (*27*–*60*)

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Sex-specific responses to climate change in plants alter population sex ratio and performance

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Editor's Summary

Changing sex ratios

Climate-warming temperatures might be expected to affect the sex ratio of species if sex determination is temperature-dependent. Petry *et al.* show that indirect climate effects could also alter sex ratios in species in which sex is genetically determined and damage reproductive fitness (see the Perspective by Etterson and Mazer). Over four decades, sex ratios in populations of a dioecious alpine plant have shifted toward females as a result of the different water needs of the male and female plants. The lack of males has reduced the reproductive success and fitness of the females. Similar subtle differences between sexes in environmental sensitivities could eventually lead to population declines.

Science, this issue p. 69; see also p. 32
