

Forecasting range shifts of a dioecious plant species under climate change

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Global climate change has triggered an urgent need for predicting the reorganization of Earth's biodiversity. For dioecious species (in which female and male reproductive organs are not on the same individual), it is unclear how commonly unique climate sensitivities of females and males could influence projections for species-level responses to climate change. We developed demographic models of range limitation, parameterized from geographically distributed common garden experiments, with females and males of a dioecious grass species (*Poa arachnifera*) throughout and beyond its range in the south-central U.S. Female-dominant and two-sex model versions both predict that future climate change will alter population viability and will induce a poleward niche shift beyond current northern limits. However, the magnitude of niche shift was underestimated by the female-dominant model, because females have broader temperature tolerance than males and become mate-limited under female-biased sex ratios. Our result illustrate how explicit accounting for both sexes could enhance population viability forecasts and conservation planning for dioecious species in response to climate change.

global warming | matrix projection model | population dynamics | sex ratio

Rising temperatures and extreme drought events associated with global climate change are leading to increased concern about how species will become redistributed across the globe under future climate conditions (1–3). Species' range limits, when not driven by dispersal limitation, should generally reflect the limits of the ecological niche (4). Niches and geographic ranges are often limited by climatic factors including temperature and precipitation (5). Therefore, any substantial changes in the magnitude of these climatic factors could impact population viability, with implications for range expansions or contractions based on which regions of a species' range become more or less suitable (6, 7).

Forecasting range shifts for dioecious species (most animals and ca. 7% of plant species) is complicated by the potential for sexual niche differentiation, i.e. distinct responses of females and males to shared climate drivers (8–11). For instance, the lower cost of reproduction for one sex (male or female) may allow that sex to invest its energy toward other functions that result in higher growth rates, greater clonality, or even improved survival rates compared to the other sex, leading to sexual niche differentiation (12).^{*} Accounting for sexual niche differentiation is a long-standing challenge in accurately predicting which sex will successfully track environmental change and how this will impact population viability and range shifts (13, 14). Populations in which males are rare under current climatic conditions could experience low reproductive success due to sperm or pollen limitation that may lead to population

decline in response to climate change that disproportionately favors females (15). In contrast, climate change could expand male habitat suitability (e.g. upslope movement), which might increase seed set for mate-limited females and favor range expansion (16). Across dioecious plants, for example, studies suggest that future climate change toward hotter and drier conditions may favor male-biased sex ratios (10, 17). Although the response of species to climate warming is an urgent and active area of research, few studies have disentangled the interaction between sex and climate drivers to understand their combined effects on population dynamics and range shifts, despite calls for such an approach (10, 14).

The vast majority of theory and models in population biology, including those used to forecast biodiversity responses to climate change, ignore the complication of sex structure (but see 9, 18, 19). Traditional approaches instead focus exclusively on females, assuming that males are in sufficient supply as to never limit female fertility. In contrast, “two-sex” models are required to fully account for demographic differences between females and males and sex-specific responses to shared climate drivers (20, 21). Sex differences in maturation, reproduction, and mortality schedules can generate skew in the operational sex ratio (OSR; sex ratio of individuals available for mating) even if the birth sex ratio is 1:1 (15, 22). Climate and other environmental drivers can therefore influence the OSR via their influence on sex-specific demographic rates. In a two-sex framework, demographic rates both influence and respond to the OSR in a feedback loop that makes two-sex models inherently nonlinear and more data-hungry than corresponding

Significance Statement

The majority of models used to forecast population viability and range shifts in response to climate change overlook the complexity of sex structure, and thus the potential for females and males to differ in their sensitivity to climate drivers. Here, we used demographic data collected from a common garden experiment installed along environmental gradients in the south-central U.S. and mathematical models to demonstrate that accounting for only one sex could lead to an inaccurate estimates of the impact of climate change on dioecious species, particularly in regions of their range that are biased toward one sex.

J.K.M., A.C. and T.E.X.M. designed the study.
A.C. and T.E.X.M. collected the data.
All authors conducted the statistical analyses and modeling.
J.K.M. drafted the manuscript, and T.E.X.M. contributed to revisions.

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^{*} I added this to talk about the cost of reproduction explaining niche differentiation as you suggested

female-dominant models. Given the additional complexity and data needs, forecasts of range dynamics for dioecious species under future climate change that explicitly account for females, males, and their inter-dependence are limited (16, 23).

Tracking the impact of climate change on population viability (λ) and distributional limits of dioecious taxa depends on our ability to build mechanistic models that take into account the spatial and temporal context of sex specific response to climate change, while accounting for sources of uncertainty (6, 24). Structured population models built from demographic data collected from geographically distributed observations or common garden experiments provide several advantages for studying the impact of climate change on species' range shifts (25–27). First, demographic models link individual-level life history events (mortality, development, and regeneration) to population demography, allowing the investigation of factors explaining vital rate responses to environmental drivers (28–30). Second, demographic models have a natural interface with statistical estimation of individual-level vital rates that provide quantitative measures of uncertainty and isolate different sources of variation, features that can be propagated to population-level predictions (31, 32). Finally, structured demographic models can be used to identify which aspects of climate are the most important drivers of population dynamics. For example, Life Table Response Experiments (LTRE) built from structured models have become widely used to understand the relative importance of covariates in explaining variation in population growth rate (33–35).

In this study, we combined geographically-distributed common garden experiments, hierarchical Bayesian statistical modeling, two-sex population projection modeling, and climate back-casting and forecasting to understand demographic responses to climate change and their implications for past, present, and future range dynamics. Our work focused on the dioecious plant Texas bluegrass (*Poa arachnifera*), which is distributed along environmental gradients in the south-central U.S. corresponding to Our previous study showed that, despite evidence for differentiation of climatic niche between sexes, the female niche mattered the most in driving longitudinal range limits of Texas bluegrass (36). However, that study used a single proxy variable (longitude) to represent environmental variation related to aridity and did not consider variation in temperature, which is the much Developing a rigorous forecast for the implications of future climate change requires that we transition from implicit to explicit treatment of multiple climate drivers, as we do here. Leveraging the power of Bayesian inference, we take a probabilistic view of past, present, and future range limits by quantifying the probability of population viability ($Pr(\lambda \geq 1)$) in relation to climate drivers of demography, an approach that fully accounts for uncertainty arising from multiple sources of estimation and process error. Specifically, we asked:

1. What are the sex-specific vital rate responses to variation in temperature and precipitation across the species' range?
2. How do sex-specific vital rates combine to determine the influence of climate variation on population growth rate (λ)?
3. What is the impact of climate change on operational sex ratio throughout the range?

4. What are the likely historical and projected dynamics of the Texas bluegrass geographic niche and how does accounting for sex structure modify these predictions?

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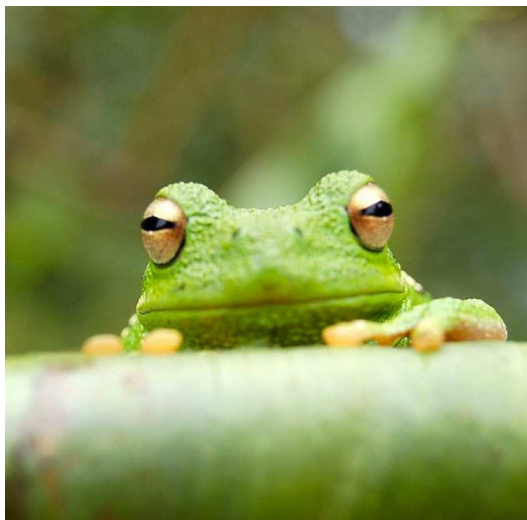


Fig. 1. Placeholder image of a frog with a long example caption to show justification setting.

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Table 1. Comparison of the fitted potential energy surfaces and ab initio benchmark electronic energy calculations

Species	CBS	CV	G3
1. Acetaldehyde	0.0	0.0	0.0
2. Vinyl alcohol	9.1	9.6	13.5
3. Hydroxyethylidene	50.8	51.2	54.0

nomenclature for the TSs refers to the numbered species in the table.

starting with S1, S2, etc.

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Fig. 2. This caption would be placed at the side of the figure, rather than below it.

$$\begin{aligned}
 (x + y)^3 &= (x + y)(x + y)^2 \\
 &= (x + y)(x^2 + 2xy + y^2) \\
 &= x^3 + 3x^2y + 3xy^2 + y^3.
 \end{aligned}
 \tag{1}$$

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