Using mechanistic insights to predict climate-induced expansion/contraction for a dioecious range-limited species

Jacob K. Moutouama¹, Aldo Compagnoni², and Tom E.X. Miller¹

¹Program in Ecology and Evolutionary Biology, Department of BioSciences, Rice University, Houston, TX USA

²Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany; and German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

June 14, 2023

* Corresponding author: jmoutouama@gmail.com

Submitted to Ecological Monographs

Manuscript type: Article

Open Research statement: All of our data and code are available during peer review at https://github.com/jmoutouama/POAR-Forecasting. This manuscript and its contents can be reproduced from this file: https://github.com/jmoutouama/POAR-Forecasting/Manuscript/Forescasting.Rnw. Upon acceptance, all data will be provided via creation and publication of an Environmental Data Initiative (EDI) data package, and code will

be archived via Zenodo.

Abstract

² Gender-specific response to rising temperature and drought raises the questions of whether

3 global change could lead to a drastic change in the sex ratio and whether that change

in the sex ratio could drive population extinction. Answering these questions requires

5 an understanding of the mechanism by which a change in vital rates under future cli-

mate conditions for each sex, could be translated into a significant change in population

⁷ dynamics. Here, we took the first step toward building a forecast model for dioecious

8 plants by understanding sex-specific demographic responses to environmental change.

9 Combining a demographic data set for a dioecious species with a Bayesian hierarchical

modeling approach, we fit models in which vital rates are driven by seasonal precipita-

tion and temperature.

12

Keywords

Introduction

13

Rising temperatures and extreme drought events have already caused broad-scale vul-14 nerability of native species, leading to increased concern about how species will redis-15 tribute across the globe under future climate conditions. Dioecious species might be particularly vulnerable to climate change because they often display skewed sex ratios 17 that are reinforced by differentiation of sexual niches (Tognetti, 2012). Accounting for 18 such a niche differentiation between male and female within a population is a long-19 standing challenge in accurately predicting which sex will successfully track environ-20 mental change and how this will impact population dynamics (Jones et al., 1999). As a 21 result, accurate forecasts of colonization-extinction dynamics for dioecious species under future climate scenarios are hampered by limited mechanistic research on the demographic response of these species to climate change. 24

The effect of climate conditions on species distributions is often derived by correlative 25 relationships between species occurrence record or abundance patterns and current climate conditions (Elith and Leathwick, 2009). These established relationships serve as the 27 basis for predicting how species will redistribute across the globe in a changing world. 28 However, the responsiveness of species abundance patterns often lags behind environmental change, which can lead to pronounced mismatches in current and future climate 30 conditions and colonization-extinction dynamics (Lee-Yaw et al., 2022). In addition, most 31 of these models do not take into account niche difference between male and female be-32 cause they rely on species occurrence. More recently, "mechanistic approaches" of species 33 distribution model (SDM) using species physiology have been proposed as an alterna-34 tive to the correlative approach of SDM. Although the application of these approaches have been successful for some species, these approaches have several limitations. First,

"mechanistic approaches" of SDM require details information that is not often available
for most species. For example, getting information such as individual physiological parameters (thermal conductivity, oxygen extraction efficiency, body posture change,diet)
is often difficult. Second, this information if available; are often derived from allometric
relation from related species. Thirdly, scaling up individual physiological information
to the population or landscape level is very challenging. Finally, most of species distribution models do not take into account differentiation of sexes distribution base due to
resource acquisition.

Theory predicts that if cost of reproduction for each sex is equal and if males and 45 females differ in reproductive fitness equality with increasing size, then natural selection will act to balance a population sex ratio at 1:1 (Fisher, 1930). However, deviances from 47 those assumptions have been observed. In several plant species, females are more sensitive to stress-related resource availability conditions than males, leading to high female mortality and, therefore, to a male bias sex ratio (Hultine et al., 2016; Freeman et al., 50 1976). Furthermore, the lower cost of reproduction of males may allow them to invest 51 their energy in other functions that produce higher growth rates, higher clonality, or even higher survival rates compared to females (Bruijning et al., 2017), causing a skew 53 sex ratio. 54

Climate change could therefore magnify skewed sex ratios and potentially reduced population growth rate if individuals are unable to find a mate and reproduce (Morrison et al., 2016). Furthermore, as the drier, warmer climate moves "up slope", so will adapt arid males shift the sex ratios (Petry et al., 2016). Because of this, populations in which males are rare under current climatic conditions could experience less mate limitation, allowing females to successfully produce more seed under warmer conditions and favor range shifts (Petry et al., 2016).

55

56

57

Our ability to track the impact of climate change on the population dynamics of dioe-62 cious plants depends on our ability to build mechanistic models that take into account 63 the spatial and temporal context in which survival, reproduction, and growth occur due 64 to the sessile nature of these plants. Several studies found that climate change affects 65 demographic processes in distinctive and potentially contrasting ways (Dalgleish et al., 66 2011). For example, while climate has a significant effect on the probability of survival and growth, it has no effect on the probability of flowering (Greiser et al., 2020). Addi-68 tionally, under warmer conditions, some native species will fail to establish reproductive 69 populations due to the extremely low germination rate and seedling survival (Reed et al., 70 2021a). Therefore, climate change will reduce the population growth rate and the range size of these species (Reed et al., 2021b). Other species will persist or even increase their 72 range in response to climate change (Williams et al., 2015; Merow et al., 2017). In seabird 73 populations, climate change by increasing the survival rate of both sexes favored their population growth rate (Gianuca et al., 2019). 75

In this study, we combined a demographic survey and a Bayesian hierarchical model 76 to understand the demographic response of dioecious species to climate change and its implications on range dynamics. Our study system is a dioecious plant species (Poa 78 arachnifera) distributed along an aridity gradient. A previous study on the system showed 79 that, despite the differentiation of the niche between sexes, the female niche mattered the 80 most in driving the environmental limits of the viability of Poa arachnifera populations 81 (Miller and Compagnoni, 2022). Thus, under current climate conditions, we hypothe-82 sized that a high value of the growing temperature and a lower value of precipitation have negative effects on the population growth rate through a reduction in the growth of female survival and the flowering rate. Under future climate will, we hypothesized that

Materials and methods

Study system

- Texas blue grass (Poa arachnifera) is a perennial cool season plant. The species occurs in
- 89 Texas, Oklahoma, and Southern Kansas. Texas blue produces a dark green ground cover
- 90 throughout the summer between October and May, with onset of Dormancy often from
- June to September. When flowering, males often have anthers, and females have stigmas.
- The species is pollinated by wind.
- We studied n populations along the distribution of these species in the United States in 2014 and 2015.

Literature Cited

- ⁹⁶ Bruijning, M., M. D. Visser, H. C. Muller-Landau, S. J. Wright, L. S. Comita, S. P. Hubbell,
- 97 H. de Kroon, and E. Jongejans. 2017. Surviving in a cosexual world: A cost-benefit
- analysis of dioecy in tropical trees. The American Naturalist 189:297–314.
- Dalgleish, H. J., D. N. Koons, M. B. Hooten, C. A. Moffet, and P. B. Adler. 2011. Climate
- influences the demography of three dominant sagebrush steppe plants. Ecology 92:75–
- 101 85.

86

87

95

- 102 Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explana-
- tion and prediction across space and time. Annual review of ecology, evolution, and
- systematics **40**:677–697.
- Fisher, R. A. 1930. The genetical theory of natural selection .

- Freeman, D. C., L. G. Klikoff, and K. T. Harper. 1976. Differential resource utilization by the sexes of dioecious plants. Science **193**:597–599.
- Gianuca, D., S. C. Votier, D. Pardo, A. G. Wood, R. B. Sherley, L. Ireland, R. Choquet,
- R. Pradel, S. Townley, J. Forcada, et al. 2019. Sex-specific effects of fisheries and
- climate on the demography of sexually dimorphic seabirds. Journal of Animal Ecology
- **88**:1366–1378.
- Greiser, C., K. Hylander, E. Meineri, M. Luoto, and J. Ehrlén. 2020. Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. Ecography **43**:637–647.
- Hultine, K. R., K. C. Grady, T. E. Wood, S. M. Shuster, J. C. Stella, and T. G. Whitham.

 2016. Climate change perils for dioecious plant species. Nature Plants 2:1–8.
- Jones, M. H., S. E. Macdonald, and G. H. Henry. 1999. Sex-and habitat-specific responses of a high arctic willow, Salix arctica, to experimental climate change. Oikos pages 129–138.
- Lee-Yaw, A. J., J. L. McCune, S. Pironon, and S. N. Sheth. 2022. Species distribution models rarely predict the biology of real populations. Ecography **2022**:e05877.
- Merow, C., S. T. Bois, J. M. Allen, Y. Xie, and J. A. Silander Jr. 2017. Climate change both facilitates and inhibits invasive plant ranges in New England. Proceedings of the National Academy of Sciences 114:E3276–E3284.
- Miller, T. E., and A. Compagnoni. 2022. Two-Sex Demography, Sexual Niche Differentiation, and the Geographic Range Limits of Texas Bluegrass (Poa arachnifera). The

 American Naturalist 200:17–31.

- Morrison, C. A., R. A. Robinson, J. A. Clark, and J. A. Gill. 2016. Causes and conse-
- quences of spatial variation in sex ratios in a declining bird species. Journal of Animal
- Ecology **85**:1298–1306.
- Petry, W. K., J. D. Soule, A. M. Iler, A. Chicas-Mosier, D. W. Inouye, T. E. Miller, and K. A.
- Mooney. 2016. Sex-specific responses to climate change in plants alter population sex
- ratio and performance. Science **353**:69–71.
- Reed, P. B., S. D. Bridgham, L. E. Pfeifer-Meister, M. L. DeMarche, B. R. Johnson, B. A.
- Roy, G. T. Bailes, A. A. Nelson, W. F. Morris, and D. F. Doak. 2021a. Climate warming
- threatens the persistence of a community of disturbance-adapted native annual plants.
- Ecology **102**:e03464.
- Reed, P. B., M. L. Peterson, L. E. Pfeifer-Meister, W. F. Morris, D. F. Doak, B. A. Roy, B. R.
- Johnson, G. T. Bailes, A. A. Nelson, and S. D. Bridgham. 2021b. Climate manipulations
- differentially affect plant population dynamics within versus beyond northern range
- limits. Journal of Ecology **109**:664–675.
- ¹⁴² Tognetti, R. 2012. Adaptation to climate change of dioecious plants: does gender balance
- matter? Tree Physiology 32:1321-1324. URL https://doi.org/10.1093/treephys/
- 144 tps105.
- ¹⁴⁵ Williams, J. L., H. Jacquemyn, B. M. Ochocki, R. Brys, and T. E. Miller. 2015. Life history
- evolution under climate change and its influence on the population dynamics of a
- long-lived plant. Journal of Ecology **103**:798–808.