Exploring the complexities of climate driver timing: Insights at the levels of vital rates and population dynamics

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Vorgelegt von
Sanne Maria Evers, M.Sc

Gutachter:
Professor Tiffany Knight
Professor Stan Harpole
Professor Eelke Jongejans

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“Only when our clever brain and our human heart work together in harmony can we achieve our true potential”

Jane Goodall

Table of Contents

Summary

The effect of climate change on population dynamics is a complex issue. Much research already been done to understand the effect climate drivers have on populations and species persistence. Part of this effort has been to develop a wide range of models, each designed to address particular questions, but also with their own assumptions. These models are built from vital rate regressions, and it is in these vital rates, that the effect of climate is often modelled. Much time has been spent trying to understand how different climate variables such as temperature and precipitation affect population dynamics, but much less time has been spent investigating, and re-evaluating prevalent assumptions, on when climate affects vital rates and thus population dynamics.

The aim of this dissertation is to specifically provide new insights in the timing aspect of climate drivers. To do so, this dissertation has been divided into three different research chapters. First, I will investigate which time frames are currently being used by researchers to investigate the effect of climate on plant vital rates, such as survival and flower probability. Moreover, I will analyse the effect of climate on four different plant species, to see which timeframes result in the best models when we loosen the assumptions of timeframes currently being used in the literature. Second, I will use simulations to see what the effects are on a population level of including different timeframes in our vital rate models. Here I will consider both the effect of more varied timeframes on population growth rates, but also on the effect and relative importance of other components that play an important part in population dynamics, such as climatic autocorrelation. Finally, I will analyse a long-term dataset of the endangered *Dracocephalum austriacum*, where I apply the lessons learned in the first two chapters.

The results of this dissertation shed light on an often-overlooked aspect of climate drivers. It provides insights and concrete advise on how to improve the selection of appropriate climate driver timeframes. As such, it will improve future research into the consequences of climate change on plant populations.

Zusammenfassung

Die Auswirkung des Klimawandels auf die Populationsdynamik ist ein komplexes Thema. Es wurde bereits viel geforscht, um die Auswirkungen des Klimawandels auf Populationen und den Fortbestand von Arten zu verstehen. Ein Teil dieser Bemühungen bestand darin, eine breite Palette von Modellen zu entwickeln, die jeweils auf bestimmte Fragen ausgerichtet sind, aber auch ihre eigenen Annahmen haben. Diese Modelle beruhen auf Regressionen der Vitalitätsraten, und die Auswirkungen des Klimas werden häufig anhand dieser Vitalitätsraten modelliert. Es wurde viel Zeit darauf verwendet, zu verstehen, wie sich verschiedene Klimavariablen wie Temperatur und Niederschlag auf die Populationsdynamik auswirken. Andererseits wurde deutlich weniger Zeit darauf verwendet, die vorherrschenden Annahmen darüber zu untersuchen und neu zu bewerten, wann das Klima die Vitalraten und damit auch die Populationsdynamik beeinflusst.

Ziel dieser Dissertation ist es, insbesondere neue Erkenntnisse über den zeitlichen Aspekt der klimatischen Einflüsse zu gewinnen. Um dies zu erreichen, ist diese Arbeit in drei verschiedene Forschungskapitel unterteilt. Zunächst werde ich untersuchen, welche Zeitrahmen derzeit von Forschern verwendet werden, um die Auswirkungen des Klimas auf die Vitalitätsraten von Pflanzen, wie Überleben und Blühwahrscheinlichkeit, zu untersuchen. Außerdem werde ich die Auswirkungen des Klimas auf vier verschiedene Pflanzenarten analysieren, um zu sehen, welche Zeitrahmen die besten Modelle ergeben, wenn wir die Annahmen der derzeit in der Literatur verwendeten Zeitrahmen lockern. Zweitens werde ich mit Hilfe von Simulationen untersuchen, welche Auswirkungen es auf Populationsebene hat, wenn wir verschiedene Zeitrahmen in unsere Modelle für die Vitalitätsrate aufnehmen. Dabei werde ich sowohl die Auswirkungen unterschiedlicher Zeitrahmen auf die Populationswachstumsraten als auch die Auswirkungen und die relative Bedeutung anderer Komponenten, die eine wichtige Rolle in der Populationsdynamik spielen, wie z. B. die klimatische Autokorrelation, untersuchen. Abschließend werde ich einen Langzeitdatensatz des gefährdeten *Dracocephalum austriacum* analysieren und dabei die in den ersten beiden Kapiteln gewonnenen Erkenntnisse anwenden.

Die Ergebnisse dieser Dissertation beleuchten einen oft übersehenen Aspekt der Klimatreiber. Sie bieten Einblicke und konkrete Ratschläge, wie die Auswahl geeigneter Zeitrahmen für Klimatreiber verbessert werden kann. Dadurch wird die künftige Erforschung der Auswirkungen des Klimawandels auf Pflanzenpopulationen verbessert.

Chapter 1

General Introduction

As ecologists, we seek to understand the spatial and temporal variation we observe in the species around us (Andrewartha & Birch, 1954; Sutherland et al., 2013). A large part of ecology is explaining population dynamics. Efforts have been made to explain the distribution (e.g., Kelly & Goulden, 2008), the temporal and spatial dynamics (e.g., Diez, Giladi, Warren, & Pulliam, 2014; Fréville et al., 2004) of populations within species (Compagnoni, Pardini, & Knight, 2021; Dostálek & Münzbergová, 2013), and even across species (Adler, Leiker, & Levine, 2009; Sæther et al., 2003). These topics are becoming more and more relevant. Understanding how climate affects these different aspects of population dynamics is a long-standing question (Sutherland et al., 2013). It has become clear that climate can play a large role in determining a population's fate (Urban, 2015). Moreover, climate change is causing, and will cause, previously unseen weather anomalies (IPCC, 2014), as well as changing historical weather correlations (Di Cecco & Gouhier, 2018). Therefore, researchers can no longer depend on historical correlations between climate drivers and population dynamics, unless it is the climate driver that is actually influencing the population dynamics.

Modelling population dynamics

Over the years, structured population projection models have emerged as a powerful tool to investigate the effects of climate on populations. However, different types of models have different strengths and assumptions, and researchers must carefully consider these when selecting an appropriate model for their study system.

One of the earliest types of population models, non-structured models, assume that all individuals within a population experience the same birth and death rates. While these non-structured models can be easy to parameterize and have been used to address questions regarding, for example, pest management (Liu, Zhang, & Chen, 2005), the assumption that all individuals are identical can often be un-realistic.

Age-based models, such as Leslie matrices (Leslie, 1945), offer a more realistic representation of individual variation within a population. These age structured Matrix Population Models (MPMs) assume that vital rates such as survival and reproduction are dependent on an individual's age. Moreover, as the name suggests, Leslie matrices summarize age specific vital rates (such as survival and reproduction) in a matrix. This enables research from using well established mathematical theory to perform inference on these models, including population growth rate and life history characteristics. Examples of Leslie matrices in the literature have been used to address conservation (Li et al., 2022) and evolutionary questions (Charlesworth, 1994). Although Leslie matrices incorporate more variation within a population compared to the non-structured population models, an age-based structure is not necessarily the defining intrinsic characteristic that correlates best with vital rates.

Researchers realised early on that plant demography often depends ontogeny or size, rather than age (e.g., Harper, 1967; Werner, 1975), and developed stage-structured matrix models (Keyfitz, 1964; L.P. Lefkovitch, 1965). Stage-structured MPMs classify individuals into discrete stages, such as size classes (e.g., Osunkoya, Perrett, Fernando, Clark, & Raghu, 2013) or reproductive state (e.g., Tremblay et al., 2009). This allows researchers to determine which characteristics best correlate with different vital rates. Moreover, the use of stage also allows stasis (where an individual remains in the same stage) and regression (where an individual transition into a stage against the normal direction of development) to occur within the modelled life cycle. The increased flexibility in stage selection and lifecycle structure, combined with the ease of analysis thanks to the matrix formulation of these models (Caswell, 2001), have made them a popular tool for analysing population dynamics. The open-access databases COMPADRE (Salguero-Gómez et al., 2015) and COMADRE (Salguero-Gómez et al., 2016), which contain thousands of matrices from hundreds of population studies in both plants and animals, highlight the widespread use of MPMs.

Despite their popularity, the discrete classifications of individuals forced by MPMs can be challenging. In some cases, these classifications can be clear, for example when using developmental stages such as seed, non-reproductive plant and reproductive plant. However, challenges can arise in cases where continuous traits, such as body mass, are the primary drivers of vital rates. Even in seemingly easy to divide lifecycles, researchers have sometimes been forced to create stages like "young" and "mature" reproductive adults (Marrero-Gómez, Oostermeijer, Carqué-Álamo, & Bañares-Baudet, 2007).

To address this limitation, integral projection models (IPMs) were developed (Easterling, Ellner, & Dixon, 2000). IPMs allow researchers to classify individuals based on continuous traits such as body weight (Simmonds & Coulson, 2015), volume (Ferrer-Cervantes et al., 2012) or length (Wallace, Leslie, & Coulson, 2013). Although the first IPMs developed consisted of a model with only a single continuous stage, IPMs can accommodate complex structures, such as discrete stages (Dahlgren, Ehrl, Dahlgren, & Ehrl, 2011), or an age-by-size structure (Childs, Rees, Rose, Grubb, & Ellner, 2003). Although these models are much more complicated to program than the other models discussed here, the development of excellent code guides (Merow et al., 2014) and R (R Core Team, 2021) packages (Levin et al., 2021; Metcalf, McMahon, Salguero-Gómez, & Jongejans, 2013) have made them accessible for ecologists. Moreover, because IPMs are implemented as large (>100 cells) matrices (Ellner, Childs, & Rees, 2016), many of the analyses developed for MPMs can also be performed on IPMs. All of these advantages have led to an increasing popularity of IPMs (Levin et al., 2022). However, IPMs too, make several assumptions. For examples, most IPMs assume that there is no environmental or heterogeneity or individual stochasticity (but see e.g., Snyder & Ellner, 2016).

Individual-based models (IBMs) explicitly model the behaviour of individuals within a population. As such, IBMs use equations and vital rates for individuals, rather than population level probabilities, regardless of stage or state dependence. This allows researchers to include different environmental values at the individual level, such as soil conditions, microclimatic variables, or light levels. As a result, IBMs allowing for a more flexible representation of the dynamics of a population. For example, IBMs allow for easily simulating demographic stochasticity (e.g. Compagnoni, Pardini, and Knight 2021), or asymmetric competition (Pacala et al., 1996). Thus, by incorporating individual-level behaviour into models, IBMs can provide insights into the mechanisms driving population dynamics and help inform management and conservation strategies.

There are several other models that I could discuss, some of which loosen the assumptions discussed above (e.g., Plard, Turek, Grüebler, & Schaub, 2019; Schaub & Abadi, 2011). However, these models too, make assumptions and have certain draw backs. In the end, each population model type has its advantages, challenges, and assumptions. It is the task of researchers to carefully select the appropriate model for their study system and question(s). The strength of all population models lies in acknowledging the assumptions each make, so we can utilize their strengths. New models continue to emerge as researchers strive to better understand the complexities of population dynamics.

Understanding the effect of climate on population dynamics

Population models are essential tools for ecologists to understand and analyse population dynamics. However, the accuracy of these models depends on the accuracy of their underlying vital rate models. Vital rate models should reflect the data closely and incorporate appropriate coefficients and structure to answer researchers' questions accurately. Inaccurate models can lead to misleading results, impacting conservation and management strategies. In the next paragraphs I will introduce several challenges in creating accurate, climate sensitive vital rate models. These vital rate models are crucial in our efforts to understand how climate change will affect population dynamics.

Ecologists use population models to analyse and understand population dynamics. However, these tools are only useful in that they help us answer important ecological questions. Moreover, the accuracy of these population models is limited by the accuracy of their underlying vital rate models. Therefore, it is crucial that vital rate models are built to reflect the data as closely as possible, as well as incorporate the right coefficients and structure that is needed to address the questions being asked by researchers. In this dissertation I will focus on one topic: The effect of climate on plant population dynamics.

Identifying the right climate driver is crucial for ecologists because climate fluctuations can affect vital rates such as survival and reproduction. These fluctuations can lead to transitions where populations have more surviving individuals or higher reproduction rates, but also to transitions where vital rates are below average. This will lead to different annual population growth rates (λ). Inter-annual variance in population growth rate has been shown to result in a long-term population growth rate that is lower than the average (Tuljapurkar, 1990, but see, e.g., Koons, Pavard, Baudisch, & Jessica E. Metcalf, 2009). Investigating the effect of climate on population dynamics is therefore an increasingly salient question, with climate change no longer a problem for the future, but already clearly present in our everyday life (IPCC, 2014).

There are two general approaches to investigating the effect of climate on population dynamics. The first is to correlate population-level inferences like annual population growth rate to selected climate drivers. This relatively straightforward analysis was common in earlier studies (e.g., Knape & de Valpine, 2011; Picó, De Kroon, & Retana, 2002) but can be limited by low sample sizes. Moreover, this approach can obscure opposing effects from lower-level vital rates. In and of itself, this is not necessarily a disadvantage when the aim is to predict or forecast rather than to understand (Tredennick, Hooker, Ellner, & Adler, 2021). However, correlations between a population's growth rate and climate may become less accurate under climate change as previously unobserved climate values and changes in observed climatic autocorrelation arise under climate change (Di Cecco & Gouhier, 2018; IPCC, 2014).

Correlating climate drivers with vital rates

The second approach that is becoming the norm, is to analyse correlations at the vital rate scale. This approach enables the detection of opposing climate effects across vital rates and the use of individual observations as data points. It more accurately represents the level at which climate influences populations. However, selecting the best climate driver for vital rate models is a significant challenge. Pinpointing the exact time frame in which a climate variable best predicts a vital rate requires a significant amount of data (Tenhumberg, Crone, Ramula, & Tyre, 2018; van de Pol et al., 2016), and researchers have therefore historically made *a priori* selections of climate drivers due to computational and data limitations.

In the literature, climate driver and climate variable can often be used interchangeably, however in this dissertation, I will be using them as two distinct definitions. Climate variables are the different aspects of weather that are measured or calculated, such as temperature or precipitation. Climate drivers on the other hand, are a combination of climate variables and a specific time frame, e.g., the total precipitation from June to August.

The biggest challenge is in the component that distinguishes climate driver from climate variable. Being able to pinpoint the exact time frame in which a climate variable best predicts a vital rate requires significant amount of data, anywhere from 10 years for strong climate signals ($R^2 = 0.4$-0.8) to 47 years for weaker climate signals ($R^2 = 0.2$) (van de Pol et al., 2016). In comparison, the median study duration for plant demography is five years (Salguero-Gómez et al., 2015). Because of this, and because of computational challenges, historically, researchers have been forced to make *a priori* selection of climate drivers.

Although I will address this topic in more detail in the next chapter, this practice of selecting the most recent growing season climate *a priori* has become a prevalent routine among population ecologist, despite studies that point to alternative time frames (Dalgleish, Koons, Hooten, Moffet, & Adler, 2011; Fox, Ribeiro, Brown, Masters, & Clarke, 1999; Hacket-Pain et al., 2018; Inouye & McGuire, 1991). Furthermore, several new model selection methods have been developed (Gasparrini, Scheipl, Armstrong, & Kenward, 2017; Teller, Adler, Edwards, Hooker, & Ellner, 2016; Tenhumberg et al., 2018) that can assist in the selection of the best climate drivers. These methods can reduce the number of assumptions made in the climate driver timing.

Aims and scope of thesis

In this dissertation, I aim to challenge several assumptions on climate driver timing at the vital rate and population levels. This research will contribute to a better understanding of how to model the effect of climate on population dynamics and will evaluate and refine existing methods for selecting climate drivers. By re-evaluating assumptions and applying new tools to our analyses, we can make progress in population ecology and contribute to our understanding of the effects of climate change on natural systems. I will also provide a case study of an herbaceous perennial with a long-term dataset to show how such analysis can be done.

Outline of research chapters

In this dissertation, I aim to investigate the effect of climate driver timing on different levels (Fig. 1). First, in chapter 2, I investigate the timeframes that link climate to vital rate regressions (Fig. 1). The aim is to evaluate more concretely what timeframes are commonly used in recent literature. Moreover, I use one of the recently developed model selection methods to select the best timeframes for several plant species, stepping away from many of the assumptions made in the literature about the best timeframe. Next, in chapter 3 I analyse the effect of including more varied climate driver timing in vital rate regressions on population dynamics (Fig.1). I use MPM simulations to investigate the effect of including more varied timeframes, as suggested by the results of Chapter 2. These simulations include MPMs for a wide range of life histories, as well as many other components that are known to influence population dynamics, such as vital rate correlations and climate autocorrelation. Finally, in chapter 4, I incorporate the conclusions of chapter 2 and 3 into the population analysis of *Dracocephalum austriacum*. I investigate the effect of climate and its interaction with several (a)biotic variables on both the population dynamics and forecasts of several *D. austriacum* populations in the Czech Republic.

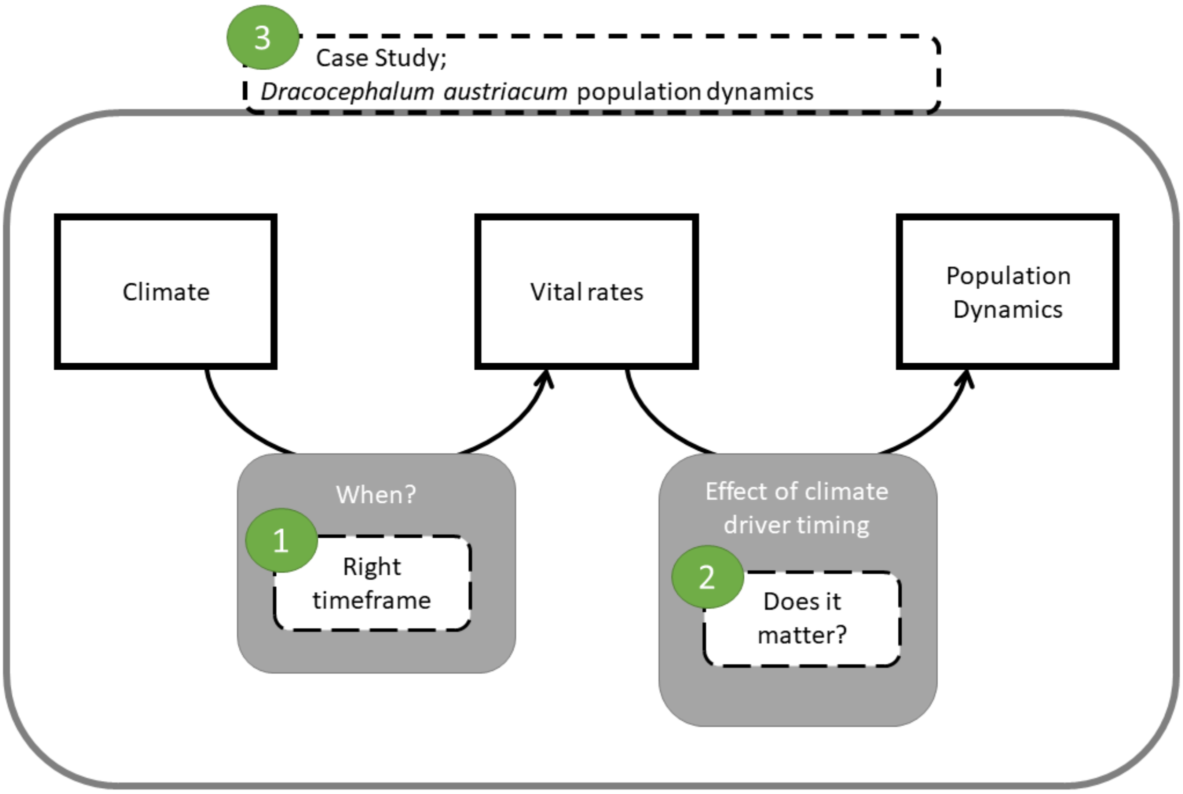

Figure 1. This dissertation addresses the complexity of climate driver timing on three different levels. First, in Chapter 2, I investigate the timeframe of climate drivers. Here I focus on the effect of climate drivers on vital rates. Next, in Chapter 3, I focus on the effect of different time frames in the vital rates might have at a population level. Finally, Chapter 4 combines the conclusions of the previous chapters into a case study of Dracocephalum austriacum.

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Chapter 2

Lagged and dormant season climate better predict plant vital rates than climate during the growing season

Sanne M. Evers, Tiffany M. Knight, David W. Inouye, Tom E.X. Miller, Roberto Salguero-Gómez, Amy M. Iler & Aldo Compagnoni

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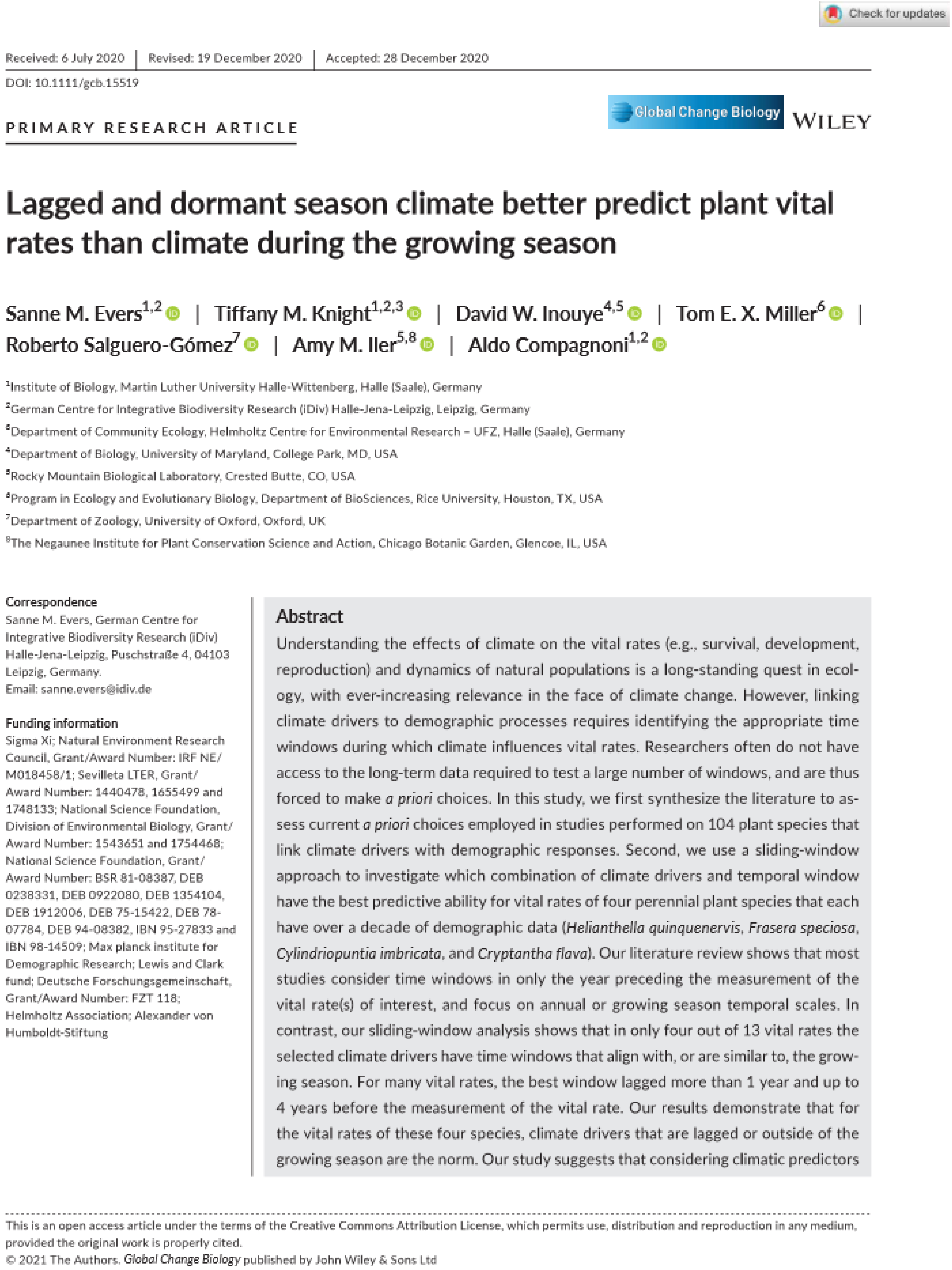

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Lagged and dormant season climate better predict plant vital rates than climate during the growing season

Sanne M. Evers[1,2] | Tiffany M. Knight[1,2,3] | David W. Inouye[4,5] | Tom E. X. Miller[6] | Roberto Salguero-Gómez[7] | Amy M. Iler[5,8] | Aldo Compagnoni[1,2]

[1]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany
[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[3]Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle (Saale), Germany
[4]Department of Biology, University of Maryland, College Park, MD, USA
[5]Rocky Mountain Biological Laboratory, Crested Butte, CO, USA
[6]Program in Ecology and Evolutionary Biology, Department of BioSciences, Rice University, Houston, TX, USA
[7]Department of Zoology, University of Oxford, Oxford, UK
[8]The Negaunee Institute for Plant Conservation Science and Action, Chicago Botanic Garden, Glencoe, IL, USA

Correspondence
Sanne M. Evers, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany.
Email: sanne.evers@idiv.de

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Abstract

Understanding the effects of climate on the vital rates (e.g., survival, development, reproduction) and dynamics of natural populations is a long-standing quest in ecology, with ever-increasing relevance in the face of climate change. However, linking climate drivers to demographic processes requires identifying the appropriate time windows during which climate influences vital rates. Researchers often do not have access to the long-term data required to test a large number of windows, and are thus forced to make *a priori* choices. In this study, we first synthesize the literature to assess current *a priori* choices employed in studies performed on 104 plant species that link climate drivers with demographic responses. Second, we use a sliding-window approach to investigate which combination of climate drivers and temporal window have the best predictive ability for vital rates of four perennial plant species that each have over a decade of demographic data (*Helianthella quinquenervis*, *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava*). Our literature review shows that most studies consider time windows in only the year preceding the measurement of the vital rate(s) of interest, and focus on annual or growing season temporal scales. In contrast, our sliding-window analysis shows that in only four out of 13 vital rates the selected climate drivers have time windows that align with, or are similar to, the growing season. For many vital rates, the best window lagged more than 1 year and up to 4 years before the measurement of the vital rate. Our results demonstrate that for the vital rates of these four species, climate drivers that are lagged or outside of the growing season are the norm. Our study suggests that considering climatic predictors that fall outside of the most recent growing season will improve our understanding of how climate affects population dynamics.

KEYWORDS
carryover effects, environmental driver, lagged effects, plant demography, precipitation, sliding window, temperature

1 | INTRODUCTION

Understanding the effects of climate on population dynamics is a central, long-standing quest in ecology (Andrewartha & Birch, 1954; Sutherland et al., 2013). This topic is increasingly salient because climate change is expected to alter dramatically population dynamics of many species, which is key for predicting local extinction risk and species' range shifts (Bellard et al., 2012; Kelly & Goulden, 2008; Urban, 2015). In the last decades, ecologists have been working toward understanding (Harper & White, 1971; Hindle et al., 2019; Sarukhan, 1974) and, more recently, forecasting the effects of climate on population dynamics (Iler et al., 2019; Urban et al., 2016). Models that link climate to biological processes such as population dynamics (Merow et al., 2014; Pagel & Schurr, 2012) have higher predictive ability in novel climates than those based on species occupancy, such as species distribution models (Zurell et al., 2016). However, one challenge in linking climate drivers to demographic processes is to identify the appropriate time window during which climate influences demography, as well as the specific climatic variable that best predicts vital rates (e.g., temperature, precipitation, etc.). This task is challenging because environmental drivers are often correlated, researchers often do not know the most relevant time window nor environmental variable for plant physiological responses to climate, and researchers typically do not have access to long-term data to analyze different temporal windows (Salguero-Gómez et al., 2015).

Investigators often link climate drivers to population dynamics based on pre-existing knowledge of their focal species (van de Pol et al., 2016). The most common approach for plant species is to consider climate within the growing season of the year preceding the vital rate(s) (i.e., survival, development, reproduction; e.g., Chu et al., 2016; Clark et al., 2011). While these choices are supported by strong *a priori* expectations (e.g., Menges & Quintana-Ascencio, 2004), some evidence suggests at least two alternative time windows that might provide better predictive ability. First, several studies show that climate conditions during the dormant season can have a substantial effect on vital rates (Fox et al., 1999; Inouye & McGuire, 1991; Kreyling, 2010). For example, temperature and precipitation during the dormant season influence snowpack, which protects plants from frost damage through insulation (Groffman et al., 2001). A decrease in snowpack has been shown to decrease flower production, most likely through frost damage (Boggs & Inouye, 2012; Inouye & McGuire, 1991). Second, some researchers have found evidence of lagged effects, in which vital rates are affected by climate more than 1 year prior to the year in which vital rates are measured (Dalgleish et al., 2011; Hacket-Pain et al., 2018; Tenhumberg et al., 2018). For example, decreased snowfall can cause a shortage of soil water later in the season, depleting an individual's stored resources and thus decreasing growth and survival in the following year (Dalgleish et al., 2011). These studies highlight that the most appropriate time window of climate to predict vital rates might not be during the growing season or the current year.

In the literature, authors also tend to select specific climate variables, such as temperature and precipitation, *a priori*, as opposed to using a model selection approach. Authors generally select the climate predictor according to the main limiting factor of the system: for example, precipitation in a warm desert (Huxman et al., 2004; Noy-Meir, 1973). However, testing alternative climate variables is justified when these variables could also affect the limiting resources within a system. For example, in warm deserts, temperature can deplete soil moisture (Sherry et al., 2008), and therefore may be just as likely to predict vital rates as precipitation. Moreover, different climate variables could change idiosyncratically during the upcoming century (IPCC, 2014), disrupting historical correlations between climate variables. The choice of climate variable could thus affect the accuracy of future predictions.

Recently, new statistical techniques have emerged that facilitate selecting a specific climate variable and time window(s) during which this climate variable has a high predictive ability (Ogle et al., 2015; van de Pol & Cockburn, 2011; Teller et al., 2016). Among these, the sliding-window approach (e.g., Brommer et al., 2008; Husby et al., 2010; van de Pol et al., 2016) compares the predictive ability of models whose climate predictor is represented by different time windows (Figure 1). If we subdivide a year into months, then the "time window" is defined as a time period of consecutive month(s). In this scenario, predictive time windows comprise all possible combinations of opening (i.e., beginning) and closing (i.e., end) months during the year. The climatic predictor is then computed by taking an aggregate measure of the monthly climatic values within each window. Although the sliding-window approach holds much promise in increasing predictive ability when linking climatic drivers to demographic processes, it requires large amounts of data. Using simulated datasets, van de Pol et al. (2016) showed that a sample size of 10, referred to either years, sites, or both, was enough to detect strong climate signals reliably ($R^2 = 0.4$ and 0.8); a sample size of 47 years detected weak climate signals ($R^2 = 0.2$). These data requirements present a challenge, as the median study duration for plant demography research is 5 years (Salguero-Gómez et al., 2015).

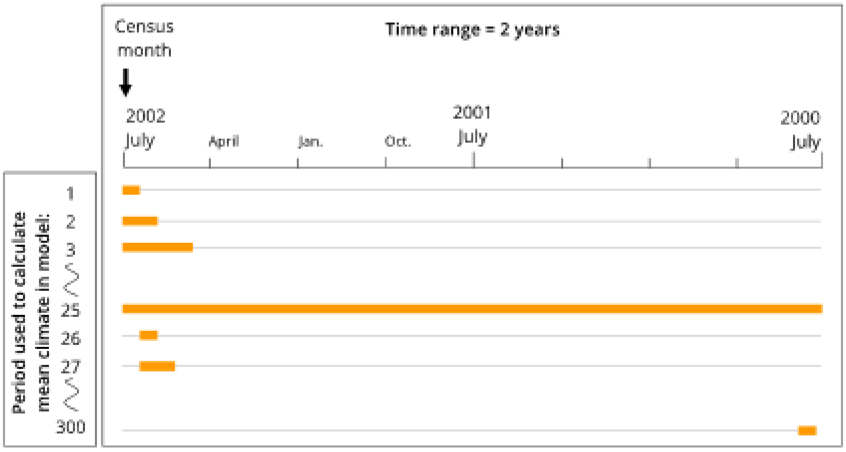

FIGURE 1 Graphical representation of the sliding-window approach, showing time windows in orange. In this article, the sliding-window approach is applied for each of the seven climate variables (three temperature variables, precipitation, snowfall, snow depth, and Standardized Precipitation–Evapotranspiration Index; SPEI). For each climate variable, models are run including the mean climate variable anomaly in all possible time windows within a certain range (in this example, 2 years). Using monthly data, these time windows consist of all possible start and end months. In this example, this means that for model 1 the mean monthly temperature anomaly is calculated in the time window July 2002. The time window for model 2 is July and June 2002, the time window used for model 3 is July, June and May 2002, etc. until model 25 where the time window used are the full 2 years. The time window for model 26 is June 2002, and for model 27 June and May, etc., until 300 different time windows are created for temperature over the 2-year timeframe

Here we will address two questions. First, we review recent literature that links climate drivers to plant vital rates to evaluate which time windows are used to define climate drivers in plant demographic studies. Second, we apply a sliding-window analysis to long-term datasets of four temperate perennial plant species (*Helianthella quinquenervis*, *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava*). We focus on several climate variables (temperature, precipitation, snow depth, and a drought index) and ask, for each species: when selecting one climate driver, what is the best time window for predicting plant vital rate responses to climate? We predicted that vital rates will depend mostly on the climate during the respective growing seasons of these plants (Angert et al., 2007; Körner, 2003). However, by explicitly testing for the time window with the best predictive ability, we evaluate how strong the alternative cases are. Our analyses aim to clarify whether, and how often, the dormant season (Hacket-Pain et al., 2018; Kruuk et al., 2015; Sherry et al., 2008; Thompson & Ollason, 2001) and lagged effects (Fox et al., 1999; Harsch et al., 2014; Kreyling, 2010) play a role in the effects of climate on plant demographic processes.

2 | METHODS

2.1 | Literature review

To create a comprehensive overview of what time windows are used to define climate drivers, we conducted a literature review. We investigated two aspects of time windows: (i) the relative time window(s) within the year that are used (annual, growing season, and/or dormant season) and (ii) how far removed the time windows are from the census date. We used studies published between 1997 and 2017 that contain structured population projection models (either matrix population models [Caswell, 2001] or integral projection models [Easterling et al., 2000]) and that linked macro-climatic drivers to plant vital rates. We identified these studies performing a search on Web of Science using the same Boolean expression employed by Compagnoni et al. (2020; Appendix S1).

For each study (n = 76 studies), we identified whether the time window examined for climate driver(s) was within the growing season, dormant season, and/or whether it was an annual driver (i.e., climate aggregated over a 12-month period). If investigators considered multiple drivers across different periods, the study was assigned to all applicable time windows. For example, a study considering the effect of annual and growing season precipitation was assigned to both the annual and growing season time window. As a single study could consider multiple periods, we used Cochran's Q tests implemented through the *RVAideMemoire* package (Hervé, 2020) in R (R Core Team, 2018) to test whether certain time windows were considered more often than others (annual, growing season, and dormant season). When Cochran's Q test identified significant differences in the selection of periods, McNemar's χ^2 tests (*RVAideMemoire* package; Hervé, 2020) were used for further pairwise comparisons among the three time windows. Second, we identified the length of the timeframe over which climate was considered before each demographic census to quantify how many studies considered lagged time windows (i.e., occurring more than 12 months prior to the census month). For each study, we identified the census date of the vital rates, whether the climate driver(s) were temperature-related (mean, minimum, etc.) or precipitation-related (including precipitation, snowfall, soil moisture, etc.), and the date of the time window(s) considered for the climate driver relative to the census date. We chose temperature and precipitation because most studies investigated at least one climate driver that could be classified as one of these two categories. When a study tested both temperature and precipitation, we scored both of these as present for the study. We included the presence of a climate driver if it was considered by the author, and regardless of significance of the results, the model types used, and whether it was analyzed for its effect on population growth rate or only one vital rate. We tested whether temperature and precipitation were considered equally often as possible climate drivers across biomes. As temperature and precipitation could both be considered in the same study, we again used McNemar's χ^2 tests.

2.2 | Demographic modeling

2.2.1 | Study species and study sites

To identify which climate variables and time windows best predict plant vital rates, we applied the sliding-window analysis to long-term datasets. We identified four perennial plant species datasets for our demographic modeling that had over a decade of demographic data. Our selected species come from biomes whose growing season is clearly defined by an abiotic limitation: temperature for montane habitats (Bryson, 1974) and precipitation for arid habitats (Huxman et al., 2004; Noy-Meir, 1973).

Montane species

We used data collected in the West Elk Range of the Colorado Rocky Mountains, USA, on two herbaceous montane plant species, *Helianthella quinquenervis* (Hook.) A. Gray and *Frasera speciosa* Douglas ex Griseb. *Helianthella quinquenervis* (Asteraceae), the aspen sunflower, is a long-lived iteroparous perennial (Inouye & Taylor, 1979) for which three populations were censused across its elevation range for up to 15 years (Iler et al., 2019). In this study, we used data from 1998 to 2012 for the "mid" population (38°57.5′N, 106°59.3′W, 2886 m a.s.l.), 2005 to 2012 for the "high" population (38°58.612′N, 106°58.690′W, 3407 m a.s.l.), and 1999 to 2012 for the "low" population (38°51.774′N; 107°09.556′W, 2703 m a.s.l.). *Frasera speciosa* (Gentianaceae), the monument plant or green gentian, is a long-lived semelparous perennial (Inouye, 1986) whose population was censused in an alpine meadow at 3750 m, near Cumberland Pass (Che-Castaldo & Inouye, 2011). This population was censused for 47 years (1973–2019).

Populations of both *H. quinquenervis* and *F. speciosa* were censused annually in July, which is in the middle of the growing season (roughly June–August, Iler et al., 2019). Each census measured survival, size, reproduction, and the number of reproductive structures of each plant. Size was measured as the number of rosettes for *H. quinquenervis* and as the number of leaves in the basal rosette for *F. speciosa*. The reproductive measurements of *H. quinquenervis* and *F. speciosa* are the number of flowering stalks and the number of flowers, respectively. Climate data for the three *H. quinquenervis* populations were estimated using PRISM (PRISM Climate Group, Oregon State University, n.d.) because separate weather stations were not available for each population (Figure S1.1). Climate data for the single population of *F. speciosa* come from the closest NOAA (National Oceanic and Atmospheric Administration, USA) weather station that has data going back to the 1970s (18 km away from the population, Figure S1.2), retrieved using the R package rnoaa (Chamberlain, 2019).

Arid species

We used data from a cactus, *Cylindriopuntia imbricata* (Haw.) DC., and an herbaceous perennial, *Cryptantha flava* L. (A. Nelson) Payson. For *C. imbricata* (Cactaceae), the tree cholla cactus, we used 15 years of data (2004–2018) from a population located at the Sevilleta National Wildlife Refuge, a Long-Term Ecological Research site (SEV-LTER) in central New Mexico, USA (34°20′5.3″N, 106°37′53.2″W, 1660 m a.s.l.; see [Miller et al., 2009] and [Ohm & Miller, 2014] for more details). *Cryptantha flava* (Boraginaceae), Brenda's yellow cryptantha, is a short-lived iteroparous perennial. The data used in this study come from a population near Redfleet State Park, Utah, USA (40°35′42.63″N, 109°25′55.92″W, 1790 m a.s.l.). Demographic monitoring was set up in several plots, distributed among six blocks (see Lucas et al., 2008 for details). The dataset contains 16 years of demographic information (1997–2012; Salguero-Gómez et al., 2012).

Annual demographic censuses were conducted in May for both species, coinciding with the beginning of the growing season for *C. imbricata* (May–September; Miller et al., 2009) and *C. flava* (April–July; Salguero-Gómez et al., 2012). Each census measured survival, size changes (growth/shrinkage), probability of reproduction, and number of reproductive structures of each individual. For *C. imbricata*, size measures consisted of plant height, maximum width, and the width perpendicular to the maximum width. *Cryptantha flava*'s size was measured as the number of rosettes. Reproductive structures quantified during the annual censuses were flower buds and flowering rosettes for *C. imbricata* and *C. flava*, respectively. Climate data for *C. imbricata* were obtained from the nearest climate station of the SEV-LTER (<0.1 km, Figure S1.3, Moore, 2016). Data for *C. flava* came from the nearest NOAA station (16.6 km, Figure S1.4).

2.2.2 | Analyses

2.2.1 | *Baseline models*

We modeled vital rates based on generalized linear mixed models that followed previous studies published by the data originators. Because of data limitations, and for consistency with previous literature, all vital rate models are density-independent. Testing for density dependence would require data on the location of each individual and possibly the location of other species, which are not available for our species. Baseline models did not include climate drivers, were size-dependent, and included year as a random intercept. We used a log-transformed size predictor in all models to improve model fit. For *C. imbricata*, size was calculated as the log-transformed volume (cm^3) of an individual, calculated as a cone using plant height and average width. For *H. quinquenervis* in every baseline model, population was added as a fixed effect (Iler et al., 2019) and block was used as a fixed effect for *C. flava* (Salguero-Gómez et al., 2012). Plot identity was added to every baseline model for *C. imbricata* as a random effect (Elderd & Miller, 2016).

Survival and changes in size were modeled as dependent on the size in the previous year (Table S3.1). Because *F. speciosa* is semelparous, survival for this species was modeled conditional on not flowering. Data for *C. flava* suggested senescence, with decreased survival at larger sizes; therefore, the survival baseline for this vital rate also included a quadratic response to size (Table S3.1) as we assume size correlates with age. For *H. quinquenervis*, *C. imbricata*, and *C. flava*, flowering probability and number of reproductive structures were modeled as a function of size during the same census (Table S3.1). For *F. speciosa*, the flowering probability and flower numbers (in year $t + 1$) were modeled as dependent on size of the previous census (year t). In this species, size was not measured at the time of flowering (except for flowering stalk height and number of flowers).

Survival and flowering probability were modeled as Bernoulli regressions. Because the size measure of *C. imbricata* is continuous, the size change model for this species was modeled as a Gaussian regression. The size change model of the other species, which have count data as size variables, was modeled as Poisson regressions. Flower numbers also consisted of count data and thus were also modeled as Poisson regressions. See Table S3.1 for an overview of the full set of baseline models.

2.2.2 | *Climate variables*

We tested a total of seven climate variables for *F. speciosa* and five climate variables for the other species, based on monthly temperature or monthly precipitation anomalies. Previous studies have shown that temperature, precipitation, snow cover, and drought indices (which integrate temperature and precipitation) can be key drivers of population dynamics (e.g., Dalgleish et al., 2011; Doak & Morris, 2010; Salguero-Gómez et al., 2012; Siepielski et al., 2017; Tenhumberg et al., 2018). We used climate anomalies rather than absolute values because plants are expected to be adapted to their mean climate (Peterson et al., 2018), and should therefore respond to climatic anomalies. We considered both average and extreme temperature anomalies because climate extremes have also been shown to influence vital rates (Easterling, Meehl, et al., 2000). Specifically, mean minimum and mean maximum temperature should correlate with limitations to vegetation processes. For example, the mean minimum temperature should influence nighttime respiration costs (Criddle et al., 1997; Maier et al., 1998; Wright et al., 2006) while the mean maximum temperature should influence photorespiration costs (Hagemann & Bauwe, 2016). The monthly climate variables included total precipitation (P), mean average daily temperature (T_{avg}), mean maximum daily temperature (T_{mean_max}), and mean minimum daily temperature (T_{mean_min}). We used precipitation data, and the latitude of our study populations, to calculate a drought index, the Standardized Precipitation–Evapotranspiration Index (SPEI), on a scale of 12 months, using the *SPEI* R package (Beguería & Vicente-Serrano, 2017). Finally, for *F. speciosa*, we also included monthly snowfall (S_{fall}) and mean snow depth (S_{depth}). S_{fall} and S_{depth} were not available for the separate populations of the other montane species, *H. quinquenervis*. We used P, SPEI, S_{fall}, S_{depth}, and T_{avg} to quantify the cumulative effect of water availability and temperature on vegetation processes. We used S_{fall} and S_{depth} to account for the physical effects of snow. Finally, we used T_{min_mean} and T_{max_mean} to quantify the effect of climatic extremes in driving demographic rates.

We calculated climate anomalies as a *z*-score, by subtracting the monthly climate mean from each annual monthly value, and dividing by the standard deviation of the monthly climate. We calculated the means and standard deviations of monthly climate across a minimum period of 30 years (World Meteorological Organization, 2017). However, for *C. imbricata*, we could only calculate climate anomalies for the 20-year period (1998–2018) during which climate data were available.

We computed the climatic predictors of our generalized linear models using the climate observed from the start of the annual census backwards (e.g., if survival was measured in mid-July 2018, we considered the monthly climate anomalies starting in July 2018; see Figure 1). Our demographic datasets consist of censuses made on the same month each year. As a result, the start and end months of the range tested for climate signals were the same across years for each species.

Our time range started from the census where the response variable was measured (e.g., survival or flower probability). Thus, for all vital rates and species except for *F. speciosa*, our range includes the month during which the response variable was measured in year $t + 1$, and the preceding 36 months. For *F. speciosa*, we considered a more extended range; 6 years for survival and size changes, and 4 years for fertility. While this increased range increased the possibility of spurious correlations, previous research indicates that this species commits to flowering 4 years before flowering (Inouye, unpublished), and increases the number of leaves in the rosette every 4 years on average (Inouye, 1986), suggesting it may be particularly slow growing and prone to lagged climate effects.

2.2.3 | *Sliding-window analysis*

We identified the climate driver with the best ability to predict demographic rates using the sliding-window approach (van de Pol et al., 2016, Figure 1), implemented with the *climwin* package (Bailey & van de Pol, 2016) in R (R Core Team, 2018). This package compares the predictive ability of models that include climate from all possible time windows within a specified time frame (range). Because our data are monthly, possible time windows include windows of 1-month duration, 2-month duration, and all the way up to the full extent of the range tested. Moreover, all possible starting months were considered for each window duration. In other words, a time window of 2 months could start 2 months before and end at the census date, or it could start 7 months before and end 5 months before the census month. Subdividing a range of 3 years into the constituting 36 months implies testing the predictive ability of 703 time windows of each climate driver for each response variable. The monthly climate variables were aggregated within each window by taking the mean.

The sliding-window analysis included a single linear effect of climate for each vital rate and species. This resulted in a total of seven models for each vital rate for the montane species, and five models for each vital rate of the arid species, for which the predictive ability of all time windows was tested. We selected the best model (and thus best climate driver) using AIC_c. We subtracted the AIC_c of the baseline models (i.e., models not considering climate) from the AIC_c of the climate models. The climate driver with the lowest AIC_c was selected for further analysis. We focus on identifying a single, best climate variable for each vital rate. Additional climate variables may also predict vital rates, and over different timeframes, but our goal was to assess whether the best climatic predictor occurred within a timeframe that is typically considered (e.g., the growing season). Additionally, adding multiple climatic predictors would amplify the number of climate windows, increasing the chance of spurious correlations (see section below). Finally, we evaluated the predictive ability of our selected climate driver models. This was done by comparing the AIC_c scores of the selected climate driver models with the models using the same climate variable observed during the most recent growing season.

2.2.4 | Potential for spurious correlations

Due to the high number of windows tested in our analysis, we examined potential spurious correlations between the climate drivers and vital rates. There are two ways in which selected models might reflect a spurious relationship. First, due to the high number of models tested, significant climate signals could arise by chance. Second, there may be a correlation between the selected climate driver and other time windows and/or climate variables. To address the first possibility, we used a randomization procedure that randomizes the date of the demographic data (van de Pol et al., 2016). This randomization removed the observed correlation between response variable and climatic drivers. However, this randomization maintained the original data structure, as well as the structure of the climate variables. Then, we re-ran the sliding-window analysis described above, saving the AIC_c of the best model. This model selection was done 2000 times, creating a distribution of the best AIC_c values obtained on each randomized dataset. This distribution was then used to test whether the AIC_c of the best model found in the sliding-window analysis is due to chance, indicating a spurious correlation.

To address the second possibility that there is a correlation between the selected climate driver and other climate drivers, we investigated the influence of correlation between competing climatic windows. While high correlations would not decrease the predictive abilities of the selected climate drivers, they could indicate that the causal relationship could be found in other time windows and/or climate variables. We first quantified the autocorrelation between the selected climate window, and all other competing windows. We then also tested the correlation between the selected climate window and the climate windows of all the climate variables that were not selected.

3 | RESULTS

3.1 | Literature review

Out of 76 studies (Table S1.1) with 246 different populations of 103 plant species, few considered the possibility of climate effects in the dormant season, or the possibility of lagged effects. The studies had a mean duration of 8.04 years (with a range of 1–40 years). A total of 11 studies had a duration greater than 15 years, and all studies selected climate drivers *a priori*, rather than using a model selection approach such as the sliding window. We found that researchers do not consider different periods (annual, growing, and dormant season) equally when examining the effects of temperature ($\chi^2 = 7.294$, df = 2, $p = 0.026$) and precipitation ($\chi^2 = 19.471$, df = 2, $p < 0.001$) on vital rates (Figure 2). When authors considered temperature as a possible climate variable, the growing season was considered significantly more often than the dormant season ($\chi^2 = 8.642$, df = 1, $p = 0.003$). Moreover, a tendency emerged for climate effects in an annual period to be investigated more often

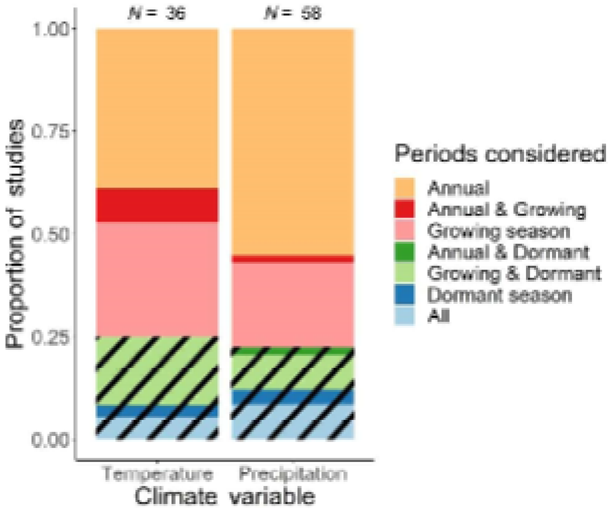

FIGURE 2 The literature review reveals that 25% or fewer studies examining temperature and precipitation as climate drivers explicitly consider climate during the dormant season. Studies that include temperature and/or precipitation drivers are categorized by the periods within the year over which climate is considered as a potential driver (annual, dormant season, and growing season). The black lines indicate studies that explicitly include dormant season as a possible climate driver

than in the dormant season (χ^2 = 3.375, df = 1, p = 0.066). When authors investigated precipitation, the annual timeframe was most commonly considered (Figure 2). Authors considered the annual period (χ^2 = 15.625, df = 1, p < 0.001) and the growing season (χ^2 = 5.063, df = 1, p = 0.024) significantly more often than the dormant season. Additionally, authors also investigated precipitation during an annual period more often than during the growing season (χ^2 = 4.5, df = 1, p = 0.034).

A total of 85% of the examined studies (n = 65 out of 76 studies) considered windows inside the transition year only (Figure 3b shows Arid studies; all studies can be found in Figures S1.1 and S1.2). Of the 11 studies including lagged windows, only six considered two full years prior to the census. Finally, only the publications from arid biomes had a strong preference of one type of climate driver over the other. Studies in arid regions investigated precipitation climate drivers significantly more often (χ^2 = 9.091, n = 17, df = 1, p = 0.003) than temperature.

3.2 | Demographic modeling

3.2.1 | Potential for spurious correlations

Randomizations showed that of the 16 climate signals detected, 13 had a significantly low chance of being spurious results (p < 0.05; Appendix S6). On the other hand, the climate drivers selected for the survival of *F. speciosa* (p = 0.369; Figure S6.5) and for the size changes and flower numbers in *C. imbricata* (p = 0.217; Figure S6.10 and p = 0.520; Figure S6.12, respectively) did have a chance of being spurious. We therefore did not present the results for these three climate drivers.

Correlation results showed that shorter windows have fewer auto-correlations or correlations with other climate variables (e.g., Figure S9.4), whereas longer windows have many other neighboring windows that are highly correlated, both within the same climate variable and in others (e.g., Figure S9.14). Correlation was more common between the temperature climate variables (e.g., Figure S9.1), between P and SPEI (e.g., Figure S9.6), and between snowfall and depth (e.g., Figure S9.5). Correlation was less common between P and SPEI, and between the temperature and snow variables (but see Figures S9.9 and S9.12).

3.2.2 | Sliding-window analysis

We found that in many cases the climate variable most predictive of demographic rates fell outside of the growing season, and many climatic predictors were lagged (i.e., their effect occurred farther back than one transition year; Figure 4). One climate driver had a time window that resembled the growing season: average temperature

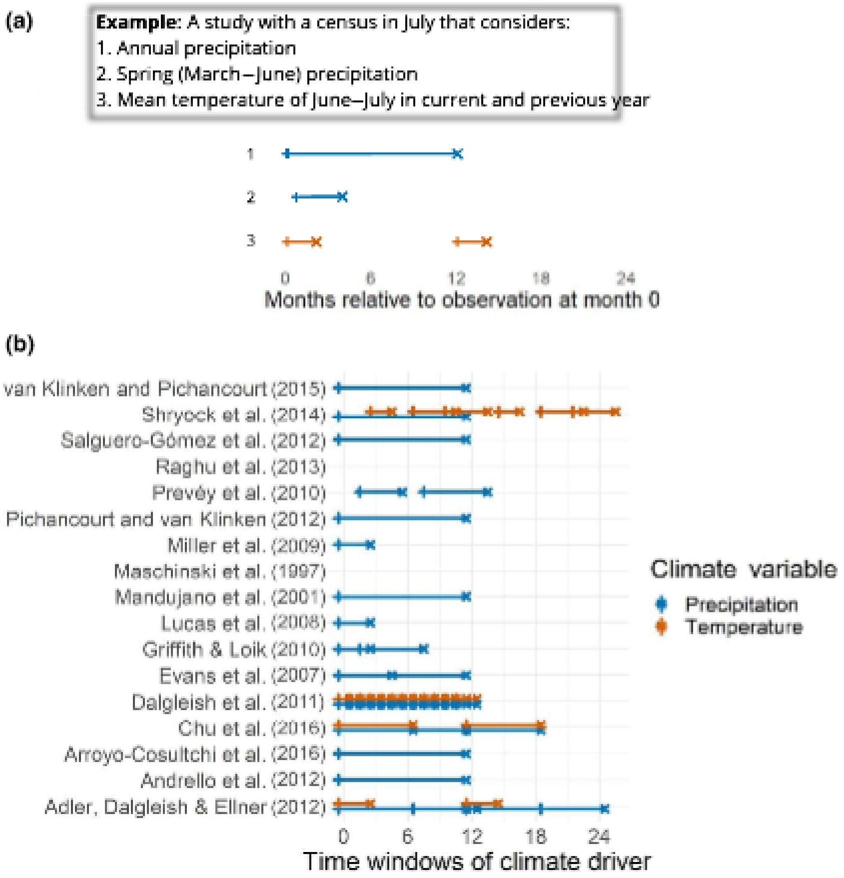

FIGURE 3 Few studies consider climate drivers more than 12 months prior to the census month. (a) shows the hypothetical example with written climate driver descriptions and the appropriate time windows in graphical form. (b) shows the subset of studies conducted in arid regions. The time windows that are considered in studies conducted in two biomes; arid and temperate coniferous forest relative to the census of the response variable. Few studies consider the potential for lagged effects (climate drivers more than 12 months prior to the census). Both precipitation and temperature drivers are included

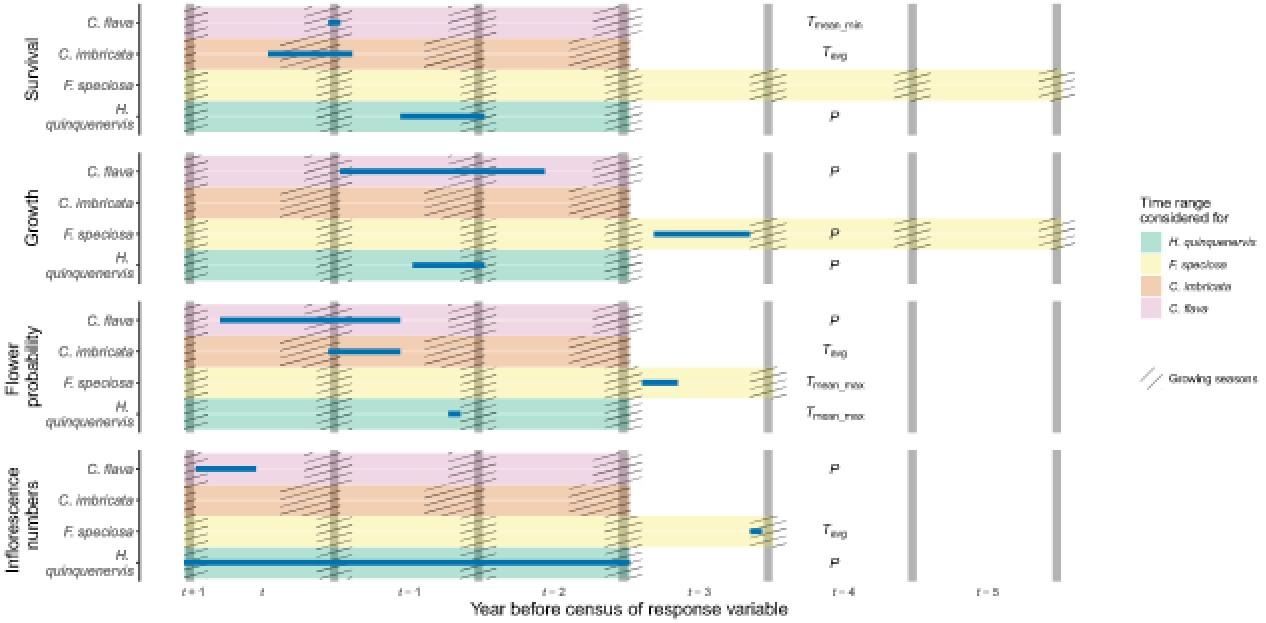

FIGURE 4 The climate drivers that best predict vital rates in *Helianthella quinquenervis*, *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava* mostly fall outside the growing season and before the first year prior to the population census. For each vital rate and each species, the time window with the best predictive ability is shown with blue horizontal lines. The best driver is listed on the right side of the graph. The grid lines indicate census months and the shaded areas show the time range considered in the sliding-window analysis. The dashed areas indicate the growing seasons for each population

for *C. imbricata* survival extends 1 month before and after the growing season (Figure 4). Other windows included only 1 month during the growing season or fell fully outside the growing season (e.g., *C. flava* survival and *F. speciosa* changes in size, respectively, Figure 4). Moreover, lagged windows were common: out of the 13 non-spurious time windows, six open and close before the transition year (i.e., >1 year before the census in time t), and one window closes in the transition year, but opens in year $t - 1$ (*C. flava* flower probability, Figure 4). We also found windows spanning more than 12 months. We found that eight of the 13 best climate predictors were related to temperature. Finally, all but one of the selected models with a time window different from the growing season had AIC_c scores that were at least 2 units lower than models with time windows in the recent growing season (Appendix S5).

For *H. quinquenervis*, we found that precipitation (*P*) from July in year $t - 1$ (July$_{t-1}$) to January in year $t - 1$ (January$_{t-1}$) has the best predictive ability for survival from year t to year $t + 1$ (with 59.32 AIC units lower than the baseline; from now on presented as $\Delta AIC_c = -59.32$; Figure 4; Table S5.1). *P* in this time period has a positive effect on survival of *H. quinquenervis* (Figure 5). An increase of two standard deviations (from mean −SD to mean +SD) changed survival probability of an average-sized individual from 79.5% to 96.0% (Figure S8.1). Size changes were best predicted by *P* from July$_{t-1}$ to December$_{t-1}$ ($\Delta AIC_c = -51.33$; Figure 4; Table S5.2). *P* during this time window had a positive effect on *H. quinquenervis* (Figure 5). An increase of 2-SD in *P* increased the size in year $t + 1$ by 43.8% (for an average-sized individual; Figure S8.1). Flower probability was best predicted by mean maximum temperature (T_{mean_max}) in September$_{t-1}$ ($\Delta AIC_c = -67.2$; Figure 4; Table S5.3). A 2-SD increase in T_{mean_max} decreased flower probability from 85.0% to 1.5% (Figure 6; Figure S8.2). Finally, the number of flowering stalks was best predicted by *P* from July$_{t-2}$ to July$_{t+1}$ ($\Delta AIC_c = -31.66$; Figure 4; Table S5.4), which is the full time range in our analysis. An increase of 2-SD increased the number of flowering stalks by 70.2% (Figure 6; Figure S8.2).

Frasera speciosa changes in size were best predicted by *P* in September$_{t-3}$ to April$_{t-3}$ ($\Delta AIC_c = -9.52$; Figure 4; Table S5.6), where an increase of 2-SD decreased size in $t + 1$ by 4.1% (Figure 5; Figure S8.1). Flower probability was best predicted by T_{mean_max} from March$_{t-3}$ to May$_{t-3}$ ($\Delta AIC_c = -11.69$; Figure 4; Table S5.7), when a 2-SD increase increases flower probability from 0.02% to 0.16% (Figure 6; Figure S8.2). Finally, average temperature (T_{avg}) in August$_{t-3}$ best predicted the number of flowers ($\Delta AIC_c = -12.99$; Figure 4; Table S5.8). A 2-SD increase in temperature increased the number of flowers by 38.0% (Figure 6; Figure S8.2). All vital rates of *F. speciosa* had at least one secondary climate variable whose predictive ability was close to the best models (i.e., within 2 AIC_c units; T_{mean_max}, *P*, and T_{mean_max} for size changes, flower probability and flower numbers, respectively; Table S5.6–5.8).

Our results show that for *C. imbricata*, survival was best predicted by T_{avg} from April$_{t-1}$ to October$_t$ ($\Delta AIC_c = -8.43$; Figure 4; Table S5.9). An increase in temperature of 2-SD during this period decreased survival probability (Figure 5) from 98.7% to 95.9% for an average-sized individual (Figure S8.1). There was also a second climate variable with a ΔAIC_c score that was within 2 units of the selected survival model (T_{mean_max}; Table S5.9). The best predictor for flower probability was T_{avg} from December$_{t-1}$ to May$_t$ ($\Delta AIC_c = -9.88$;

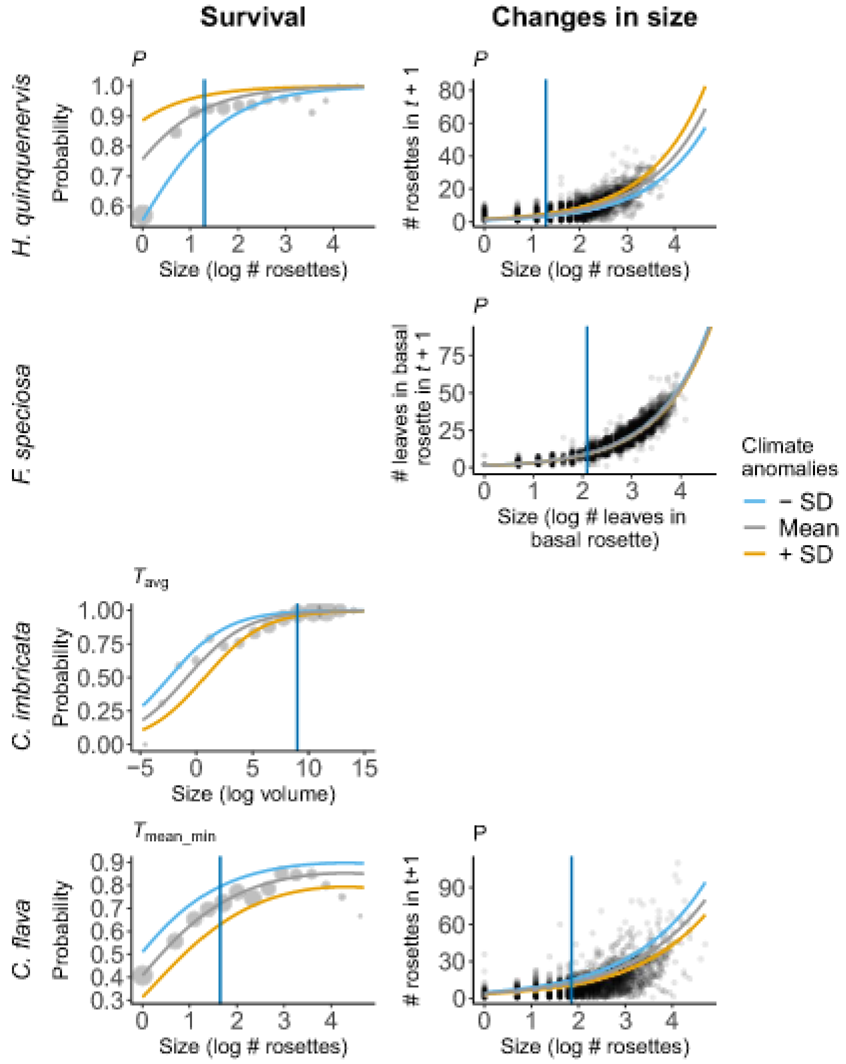

FIGURE 5 The model prediction for survival and changes in size with the best climate driver plotted against the datapoints for *Helianthella quinquenervis* ("mid" population), *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava* (Block I). Climate effect was calculated on three levels; mean climate anomaly during this time window as well as + and − one standard deviation climate anomaly. The vertical blue lines are the mean size of the individuals used to parameterize the models. Data used for the model parameterization are also plotted. In the survival column, the points are the binned proportions of survival, with the size of the points proportional to the number of observations in each bin. The points in the changes of size column are individual observations

Figure 4; Table S5.11), where flower probability increased from 0.9% to 5.9% with a 2-SD increase in T_{avg} (Figure 6; Figure S8.2).

Finally, for *C. flava*, the best predictor for survival probability was T_{mean_min} in May$_t$ (ΔAIC_c = −12.71; Figure 4; Table S5.13). Survival decreased from 79.5% to 63.0% with a 2-SD increase of T_{mean_min} in this period (Figure 5; Figure S8.1). The second best climate variable for predicting survival (T_{mean_max} from September$_t$ to January$_t$) also had a low ΔAIC_c score (ΔAIC_c = −12.35). Changes in size were best predicted by *P* from Dec$_{t-2}$ to April$_{t-1}$ (ΔAIC_c = −14.03; Figure 4; Table S5.14). Average-sized individuals in year *t* were 27.9% smaller in *t* + 1 when *P* increased with 2-SD in this period (Figure 5; Figure S8.1). Flower probability was best predicted by *P* from December$_{t-1}$ to February$_t$ (ΔAIC_c = −13.07; Figure 4; Table S5.15). A 2-SD increase in *P* increased flower probability of an average-sized individual from 10.5% to 31.3% (Figure 6; Figure S8.2). The number of flowering rosettes was also best predicted by *P*, but from December$_t$ to April$_t$ (ΔAIC_c = −12.14; Figure 4; Table S5.16). Number of flowering rosettes increased by 54.3% with a 2-SD increase in precipitation over this timeframe (Figure 6; Figure S8.2).

4 | DISCUSSION

Changes in climate are projected to be heterogeneous across space and time (IPCC, 2014). Thus, it is important for ecologists to select the right climate variables and time windows to understand and forecast responses of their specific study systems/locations to current and future climate (van de Pol et al., 2016). We found that plant population ecologists typically only consider in their demographic models the climate during the transition year, over either annual or growing season time frames. This choice makes the implicit assumption that climatic effects on vital rates—and thus emergent population dynamics—are short term. However, our sliding-window analyses reveal that in the four species for which we have long-term (>10 years) demographic data, lagged windows are the rule rather than the exception. Moreover, our analyses demonstrated that the influence of climate drivers on demography often occurred outside of the most-recent growing season. Thus, these results indicate that lagged climate variables and dormant season climate might be important drivers of plant population dynamics. Consequently,

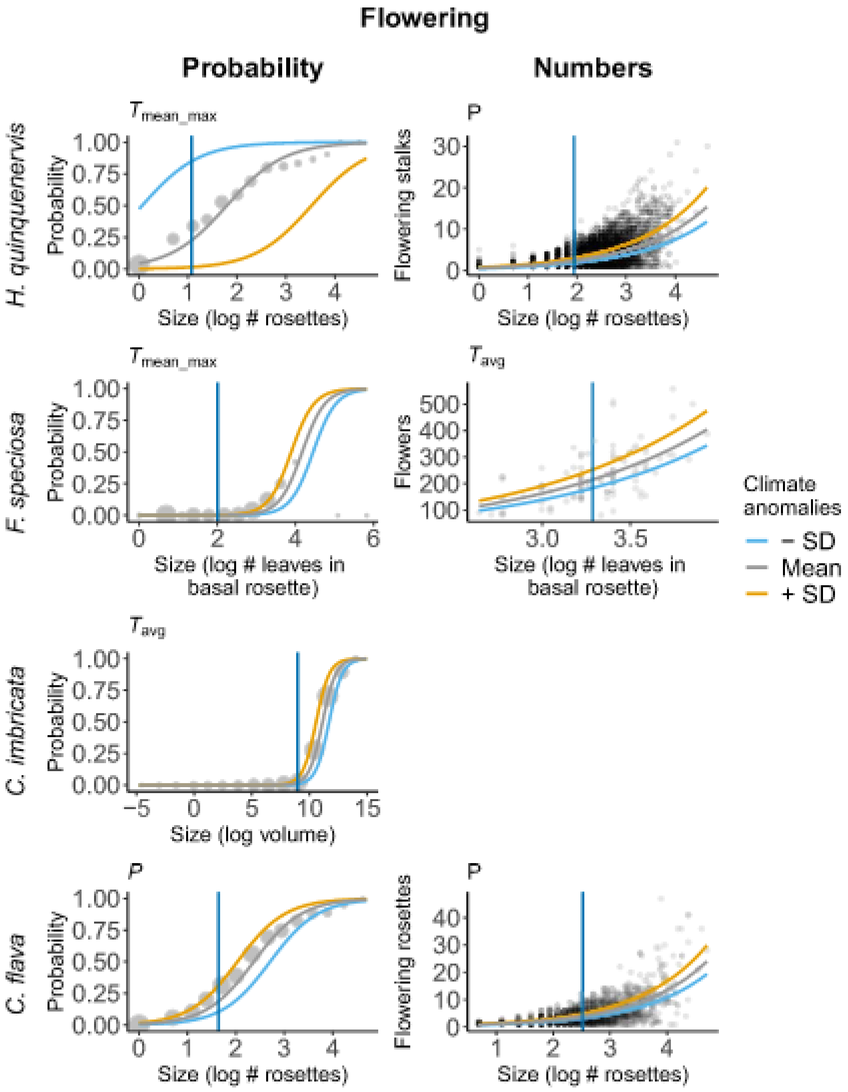

FIGURE 6 The model prediction for flower probability and numbers with the best climate driver plotted against the datapoints for *Helianthella quinquenervis* ("mid" population), *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava* (Block I). Climate effect was calculated on three levels; mean climate anomaly during this time window as well as + and − one standard deviation climate anomaly. The vertical blue lines are the mean size of the individuals used to parameterize the models. In the probability column, the points are the binned proportions of flower probability with the size of the points proportional to the number of observations in each bin. The points in the number column are the individual observations

investigators are justified in considering dormant season and lagged climate as (*a priori*) climate predictors.

Our results suggest that lagged climate might commonly mediate the effect of climate on vital rates. The literature provides some key examples of how a lagged effect of climate could result from physiological mechanisms. For instance, in *Astragalus scaphoides*, Tenhumberg et al. (2018) found a lagged negative effect of spring precipitation on survival. This lagged effect was linked to the biannual flowering peaks of this species (Crone & Lesica, 2004) where a large proportion of individuals flower after a wet spring. This flowering peak led to depleted non-structural carbohydrate stores in the following year (Crone et al., 2009), which negatively influenced survival (Tenhumberg et al., 2018). The prevalence of lagged effects we report here across our species could result from similar physiological mechanisms. Correlating residuals from the changes in size models from 1 year to the next revealed significant negative relationships for *H. quinquenervis* and *F. speciosa* (data not shown), but not *C. flava*. This finding suggests that the former two species could be similarly limited by resources after a year of better than average growth.

Another way in which plant physiology might result in lagged climate effects is the preformation of leaves and inflorescences. Belowground bud banks are common among herbaceous plants (Ott et al., 2019). For instance, in alpine environments, up to 4 years can be required for each leaf and inflorescence to progress from initiation to functional and structural maturity (e.g., Diggle, 1997; Garcia et al., 2011). This preformation happens in *F. speciosa* as well 4 years before emergence (Inouye, 1986). Accordingly, the climate most influential to the changes in number of leaves and flowering probability in *F. speciosa* occurs 4 years before the census (Figure 4). Our second result on flowering probability agrees with another analysis carried out on this same *F. speciosa* dataset. Flowering by *F. speciosa* is correlated with summer precipitation 4 years prior to inflorescence emergence (Inouye, in prep). Our analysis selected mean maximum temperature, rather than precipitation occurring 4 years prior to flowering as the best predictor of flowering probability; however, precipitation was a close second best model (Table S5.7). Temperature was also a significant predictor of flowering, with a 2-year lag, of *Veratrum tenuipetalum* (Melanthiaceae) in the same habitats as lower-altitude *Frasera* populations (Iler & Inouye, 2013).

An alternative hypothesis to explain lagged climate drivers during the dormant season is their indirect effects. Indirect effects of climate drivers occur when these influence certain biotic drivers, such as soil microbiomes or pollinators, rather than plant physiology. Examples include the reported long, lagged window in which precipitation has a negative effect on the growth of *C. flava*. Yu et al. (2019) showed that under wetter conditions, *B. eriopoda*, a C_4 grass, had a competitive advantage over *C. imbricata*. Indirect effects can also include interspecific (Aschehoug et al., 2016) or intraspecific density dependence (Dahlgren et al., 2016). Specifically, lagged climate drivers for survival could point to intraspecific density dependence, but we do not find such lagged climate drivers for our species. Previous authors who emphasized the importance of dormant season climate also pointed to indirect biotic effects (Kreyling, 2010; Stahl et al., 2006). Accordingly, biotic drivers are known to have large effects on population growth rates (Morris et al., 2020). Identifying possible indirect effects of climate on vital rates would require additional data on, for example, insect populations (Stahl et al., 2006) or the soil community (Bever et al., 1997; Maherali, 2020), and is an exciting area for future research.

The mechanisms by which dormant season climate influences vital rates likely depend on the habitat. For example, snow cover duration during the dormant season might be important for vital rates of montane and cold desert species such as *C. flava* (which requires vernalization to flower), whereas physiological activity outside of the growing season might be important for arid species. In the montane species *F. speciosa*, the dormant season was important for size changes and flower probability. Less precipitation during the winter might be linked to earlier snow melt, a longer growing season, and more growth. An earlier snow melt might also correlate with a warmer $T_{\text{mean\_max}}$, which led to a higher probability of flowering. Snow melt timing generally has a substantial effect on the dynamics or physiology of alpine plant populations (Campbell, 2019; Iler et al., 2019; Wipf et al., 2009). However, it is possible that dormant season snowfall and snow depth anomalies do not correlate well with snow melt timing, or that the ecological effects of snow cover on vital rates might be nonlinear (e.g., because snow cover insulates the ground only above the 40 cm threshold; Cline, 1997).

The climate driver that best predicted the flowering of our arid species, *C. imbricata*, is most likely linked to the importance of physiological processes during the dormant season. Both our results and Czachura and Miller (2020) found that flowering probability was positively affected by temperature anomalies observed during the dormant season. Wetter and cooler seasons might allow dormant season photosynthetic activity, as has been documented in other species, such as winter annuals (Regehr & Bazzaz, 1976) and conifers in oceanic climates (Waring & Franklin, 1979).

We hypothesize that the diversity of selected climate variables and time windows could explain an earlier finding showing mostly uncorrelated vital rates in *C. imbricata* and *H. quinquenervis* (Compagnoni et al., 2016). Specifically, our results suggest that vital rates might fluctuate independently because they respond to a diversity of climatic windows, climate drivers, and effect sizes. Testing this hypothesis would also require ruling out the effect of other factors producing positive or negative correlations among vital rates, such as density dependence and individual-level trade-offs between vital rates.

Despite the computational burden of our sliding-window analyses, we still make assumptions that could be relaxed by more complex models. First, we assumed that each month within the time window is equally important. However, generalized additive models (Teller et al., 2016) and regularization (Tredennick et al., 2017) can estimate the effect sizes, and therefore the relative importance, of single monthly or seasonal climate anomalies. This could be especially important in the long windows such as the flower numbers of *H. quinquenervis*, which includes several growing and dormant seasons. Second, we focused on selecting only one climate driver per vital rate, which allowed us to address the main question of this article: what are the best climate variables and time windows for our species, and how do these relate to what is common in the literature? However, other research questions could benefit from selecting multiple drivers (van de Pol et al., 2016), for example, when maximizing predictive ability of predicting population trends under climate change. Finally, we did not consider more complex relationships between climate and vital rates, such as nonlinear effects (Ehrlén et al., 2016), density dependence (Gornish, 2013), climate and size interactions (Iler et al., 2019), and interactions between vital rate parameters. Including these factors could increase the predictive ability of vital rate models or even change the climate driver selected. Our approach is an important first step in assessing the relative importance of climate conditions that fall outside of typically considered time windows in studies of plant demography.

When selecting the best climate driver, closely related time windows, or different climate variables can have similar model support. Selecting among climate variables, nine of our vital rates had a climate variable with a much lower ΔAIC_c (at least 2 units) than all other variables (e.g., Table S5.2), but other vital rates had at least one other climate variable with ΔAIC_c scores close to the best climate driver (e.g., Table S5.6). This lack of a clear winner could indicate highly correlated climate drivers, complex relations between vital rates and climate mentioned previously or a strong influence of more than one climate driver (van de Pol et al., 2016). When multiple models have similar support, investigators can opt to perform model averaging. However, the ability of these models to predict future responses to climate might still be low. For example, when correlations between separate climate drivers are high, it may be impossible to establish causality. This is especially relevant when predicted climatic changes include novel correlations between climatic drivers (IPCC, 2014).

In this analysis, we have used large-scale, macro-climatic predictors which, however, can differ from the micro-climate experienced by plants (Scherrer & Körner, 2010). This can be especially important when investigating plant populations in spatially variable habitats, such as montane grasslands (Körner, 2003; Oldfather & Ackerly, 2019). Because it is currently unclear how climatic anomalies correlate at the macro- and micro-scale, employing micro-climatic conditions in a sliding-window analysis could improve our understanding of timeframes over which climate affects vital rates.

Our results motivate several recommendations for researchers with shorter-term datasets for which the sliding-window method may not—yet—be feasible, and for those with longer-term datasets. In short-term datasets, a sliding-window method has a high chance of not detecting the climate signal, or identifying true signals as spurious through the randomization tests (van de Pol et al., 2016). We therefore suggest to first compare the predictive ability of climatic predictor types over larger and fewer timeframes (e.g., "dormant season temperature"), rather than continuously sliding climatic windows. According to our findings, these climate predictors should include both precipitation and temperature during the growing season, the dormant season, and in previous years. Second, considering natural history information (e.g., presence of belowground bud banks, or of dormant season physiological activity) when selecting climate drivers can improve the chance of selecting relevant time periods (including lagged time windows). Third, with shorter datasets, researchers should account for potential overfitting, for example by performing cross-validation (Wenger & Olden, 2012) or by fitting regularized regression models (Dahlgren, 2010). Finally, for the researchers with longer-term datasets, we encourage the use of model selection methods to select climate drivers. In these cases, it is vital to consider the life-history information of their specie(s) to select a time range that allows for appropriate lagged effects. This time range should include climate drivers during the growing and dormant season.

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DATA AVAILABILITY STATEMENT

The demographic datasets of all four species used for the demographic modeling are available online (*H. quinquenervis*; https://doi.org/10.5061/dryad.863c8sk, *Frasera speciosa*; https://osf.io/qubhx/, *Cylindriopuntia imbricata*; https://doi.org/10.6073/pasta/dd06df3f950afe4a4642306182237d13, *Cryptantha flava*; https://doi.org/10.6084/m9.figshare.c.3306537.v1. The R code used in all the analyses is available on GitHub at github.com/SanneE1/Climate-windows.

ORCID

Sanne M. Evers https://orcid.org/0000-0002-8002-1658
Tiffany M. Knight https://orcid.org/0000-0003-0318-1567
David W. Inouye https://orcid.org/0000-0003-2076-7834
Tom E. X. Miller https://orcid.org/0000-0003-3208-6067
Roberto Salguero-Gómez https://orcid.org/0000-0002-6085-4433
Amy M. Iler https://orcid.org/0000-0002-3354-7593
Aldo Compagnoni https://orcid.org/0000-0001-8302-7492

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Chapter 3

The inclusion of immediate and lagged climate responses amplifies the effect of climate autocorrelation on long-term growth rate of populations

Sanne M. Evers[1,2], Tiffany M. Knight[1,2,3] & Aldo Compagnoni[1,2]

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Affiliations

[1] Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle (Saale), Germany.

[2] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany.

[3] Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

Abstract

1. Climate variability will increase with climate change, and thus it is important for population ecologists to understand its consequences for population dynamics. Four components are known to mediate the consequences of climate variability: the magnitude of climate variability, the effect size of climate on vital rates, covariance between vital rates, and autocorrelation in climate. Recent studies have pointed to a potential fifth component: vital rates responding to climate in different time frames, with some responding more immediately and some having lagged responses.
2. We use simulations to quantify how all five components modify the consequences of climatic variability on long-term population growth rates across a range of life histories defined by life expectancy and iteroparity. We use an established method to compose Matrix Population Models (MPM) for 147 life histories.
3. Our simulations show that including different timeframes for vital rates responses to climate can either reduce or amplify the negative influence of climate variability on long-term population growth rates. The negative effect of different timeframes for vital rates responses on population growth is amplified when climatic autocorrelations are negative, and when species are long-lived.
4. *Synthesis:* The existing literature shows that vital rates often respond to climate in different time frames, and that studies often ignore climate autocorrelation. Our results show that simultaneously including both of these factors can substantially increase or decrease a population’s expected growth rate. Moreover, the relative magnitude of this change increases with the generation time of a life history. Our results are relevant to conservation, population forecasts, and population modeling in general.

Introduction

In recent years, the threat of climate change to both plant and animal populations has become a central topic in ecology (Clark et al., 2001; Urban et al., 2016). Climate variability is projected to increase in the future (IPCC, 2014), and studies suggest that this could pose a larger threat to populations than changes in mean climate (e.g., Vasseur et al., 2014). Thus, it is important to understand how climate variability influences the vital rates (survival, reproduction, etc.) of species, their annual population growth rate (λ), and their long-term stochastic population growth rate (λs; Barraquand & Yoccoz, 2013; Lewontin & Cohen, 1969). The literature has examined four components that influence the effect of climate variation to long-term population growth: (1) the magnitude of climate variability (Boyce et al., 2006), (2) the susceptibility of vital rates to climate, in particular vital rates with high sensitivity (Morris et al., 2008), (3) the covariances among vital rates (Iles, Rockwell, & Koons, 2019), (4) the environmental autocorrelation in the climate (Fey & Wieczynski, 2017). Recent studies identified a fifth component that could affect long-term population growth: the timeframe in which vital rates respond to climate drivers (Evers et al. 2021). For example, some vital rates might respond almost immediately while others have lagged responses to climate drivers. We do not know how much temporally varied responses (i.e., the fifth component) influence long-term population growth. It is also unclear what the relative effect and importance of the first four components are in the presence of temporally varied responses.

Climate variability (component 1) and the susceptibility of a species' vital rates to climate (component 2) play a large role in determining the interannual variation in λ. The higher the interannual variation in λ, the lower the λs (Lewontin & Cohen, 1969; Tuljapurkar, 1990). As a result, populations for which sensitive vital rates (vital rates that strongly influence λ, Caswell, 2001) respond strongly to climate drivers are expected to change the most from increases in climate variance (e.g., Boyce et al., 2006). Covariation among vital rates (component 3) can mediate climatic effects. In particular, positive covariation increases, while negative covariation dampens, interannual variation in λ, and thus decreases and increases λs respectively (Doak et al., 2005). In the context of climate drivers, positive covariation arises if all vital rates respond in the same direction to a certain climate driver, whereas negative covariation arises when two (or more) vital rates respond in opposite directions to the same climate driver.

The environmental autocorrelation in climate (component 4), in which the climate at each point in time is correlated to the previous environment, also influences interannual variation in λ and extinction risk. Positive environmental autocorrelation tends to increase extinction risk because populations in decline tend to stay in decline. On the other hand, negative environmental autocorrelation tends to stabilize populations, as declines are followed by increases (Heino & Sabadell, 2003; Pilowsky & Dahlgren, 2020; Schwager, Johst, & Jeltsch, 2006). The effect of environmental autocorrelation generally has a small effect on population growth rates when compared to the effects of other components, such as vital rate covariation (e.g., Morris et al., 2011). However, environmental autocorrelation can be important for species that recover slowly from perturbations (Tuljapurkar & Haridas, 2006), such as those with long lifespans and high reproductive output (Salguero-Gómez et al., 2016).

The fifth component, when different vital rates respond to climate drivers in different time frames (hereafter, Temporally Varied Responses or TVR), has been shown to occur by recent research that considers climate timeframes other than the typical first 12 months prior to vital rate responses (Evers et al., 2021; Tei et al., 2017; Tenhumberg, Crone, Ramula, & Tyre, 2018). Here, we show that TVR and climate autocorrelation affect λs via their effect on vital rates covariations. For example, consider a species with two vital rates that respond positively to the same climate driver. In the absence of TVR, the correlation between the vital rates will be strongly positive. However, in the presence of TVR (e.g., survival responds to climate in the current year, and fecundity responds to climate in the previous year), the correlation between the vital rates will depend on the temporal autocorrelation of the climatic driver. Specifically, strong negative autocorrelation will produce a strong negative vital rate covariation, thus increasing λs; vice versa for a strong positive autocorrelation.

We also expect that life history of a species will influence the extent to which TVR will influence populations growth rate. Species with low life expectancies typically have low juvenile survivorship, and species with high iteroparity typically have high adult survivorship. When the means of survivorship are close to zero or to one, high coefficients of variation are not possible (Morris & Doak, 2004), and we expect the effects of TVR to diminish in magnitude. This leads us to the expectation that the relative effects of TVR will vary with life history (e.g., longevity and parity).

Here, we use simulations to investigate how the five components we described above mediate the effect of climate variation on λs. We simulate matrix population models that represent a wide range of life histories. We then run stochastic simulations in which TVR is either present or absent, while modifying the first four components (climate variability, climate effect strength, vital rate covariation, and climatic environmental autocorrelation). By doing so, we elucidate how long-term viability responds to TVR across a large range of life histories.

Methods

In order to investigate the effect of TVR on long-term population growth rate across a broad range of life histories, we used a well-established framework to create Matrix Projection Models (MPMs) representing a wide range of life histories (Neubert and Caswell 2000). We use these MPMs to conduct stochastic simulations of their dynamics under different scenarios of environmental autocorrelation, environmental variance, strength of climatic signal, vital rate covariation, and TVR (Figure 1).

Simulating temporal sequences

We simulated variation in the vital rates of MPMs starting from normally distributed environmental sequences (V) with standard deviation σ_V. These environmental sequences reflect the response of a vital rate to both a climate driver, C, and unexplained environmental variation represented as random noise, ε (Figure 1a). We control the environmental variance (V) explained by climate (C) using signal strength (p). Signal strength varies between 0 and 1, where for example 0.5 and 1 imply that climate explains, respectively, 50% and 100% of the environmental variance ${\sigma_V}^2$. We then converted these normally distributed sequences to the beta and gamma distributions that characterize the survival and fecundity rates, respectively (see “Environmental sensitive Matrix Population Models” below, Figure 1c).

We simulated the environmental sequences (V) by adding two separate random processes, the climate sequence (C), and the unexplained variation (ε). We first simulated climate sequences, C, using 35 combinations of standard deviation and autocorrelation (see S1.1 for detailed methods). We included five levels of the environmental standard deviation, σ_V (0.01, 0.258, 0.505, 0.753 and 1). We chose these values to scale standard deviation of vital rates (see “Population Models across life histories”) from 1 to 100% (component 1). We incorporated seven levels of autocorrelation in the climate sequences (component 4): -0.6, -0.3, -0.1, 0, 0.1, 0.3 and 0.6. For each combination of σ_V and autocorrelation (N=35 combinations), we simulated 30 different sequences, resulting in 1050 climate sequences.

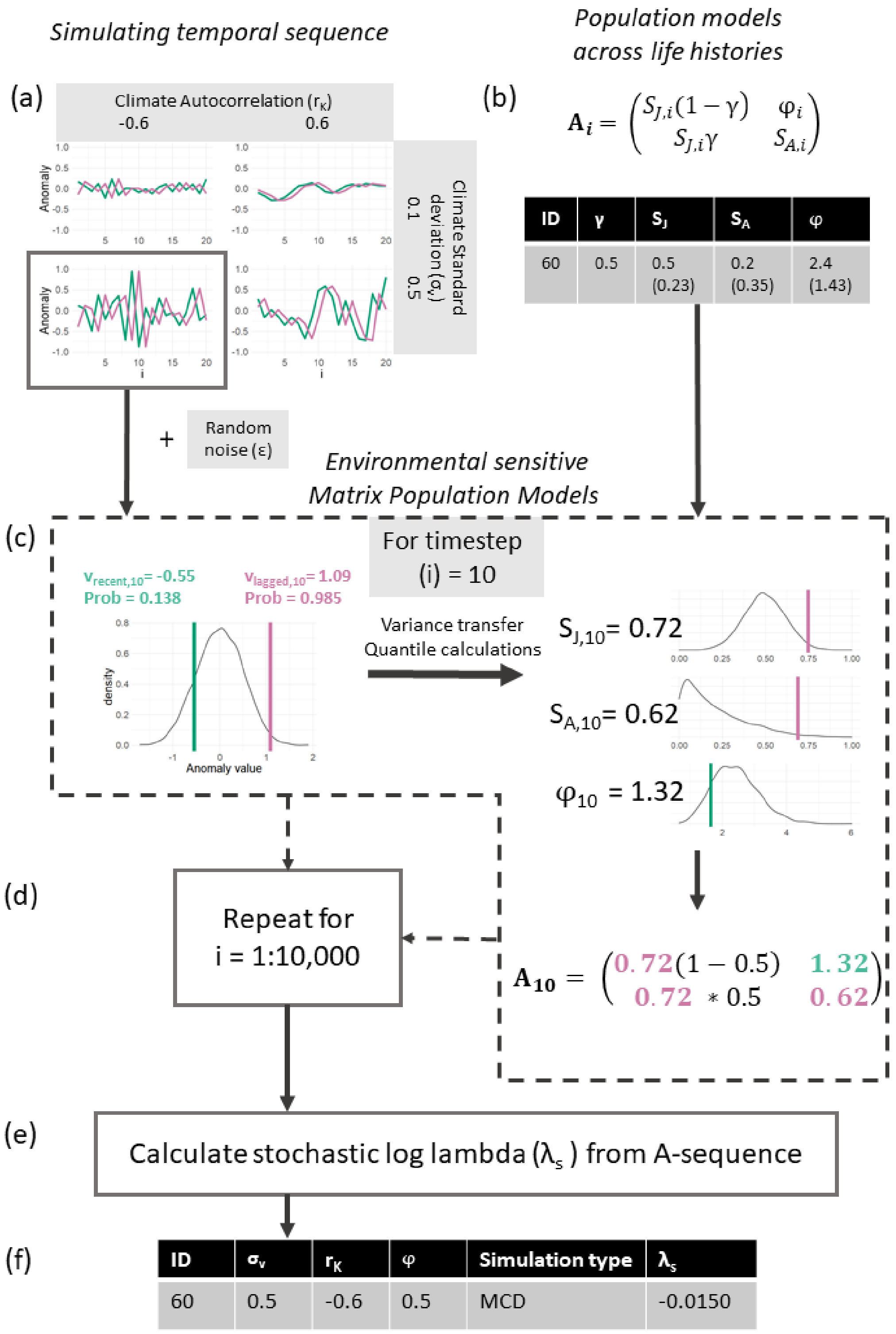

Figure 1. Workflow to simulate the effect of climate autocorrelation (r_K), climate variability (standard deviation of its distribution, σ_C), signal strength (p), and Temporally Variable Response (TVR), on the stochastic natural logarithm of population growth rate (λ_s). (a) create climate sequences of 10,000 steps, with different levels of autocorrelation and σ_c, and combine them with random noise into a environmental sequence (in this example 50% climate signal, 50% noise, signal strength = 0.5). (b) using a 2x2 MPM, create 147 different life histories, with different values for transition probability from juvenile to adult (γ), juvenile and adult survival (S_J and S_A), and with fecundity (φ) set so that matrix A produces a stable population (population growth rate = 1). As an example, one life history (ID) can be seen in the table, with vital rate means and standard deviations (in parentheses, for the three fluctuating vital rates). (c) for each time step, here as example i = 10,

calculate the quantile probability of the recent and 1-step lagged value from the normally distributed temporal sequence from (a), given a mean of 0 and standard deviation of σ_c*. Using this quantile probability, calculate the corresponding quantiles on the beta (for vital rates* S_J and S_A*) and gamma (for vital rate* φ*) distributions given the vital rates' respective mean and standard deviation defined in (b) to populate the* A_i *matrix. (d) repeat these calculations for all steps in the sequence. (e) calculate the* λ_s *using the sequence of A matrices. (f) create the result table with* λ_s *for each of the different life histories, autocorrelation, climate variability, signal strengths, and simulation type (TVR) as shown here, or control where* φ *also responds to recent climate (in green).*

The final step to produce the environmental sequences V, was to simulate random noise (ε), partition the variance of C and ε, and add them together. We included random noise in the temporal sequences to represent other factors that influence population dynamics in the real world, such as anthropogenic disturbances, biotic interactions, or other unknown climate drivers. We computed each individual value, *i,* of this temporal sequence, V, as

$$V_i = C_i * \theta_p + \varepsilon_i * \theta_{1-p} \qquad \text{Eq. 1}$$

where ε_i is the i^{th} individual random deviate from a normal distribution with mean 0 and standard deviation σ_V, C_i is the i^{th} random deviate from climate sequence described above with mean 0, standard deviation σ_C, and an autocorrelation level. We multiply each random deviate C and ε_i by parameters θ_p and θ_{1-p}, to, control the proportion (p) of variance in V that is explained by the climate driver C; p can also be seen as the signal strength of C, or the susceptibility of the vital rates to the climate driver C. Because our objective is to produce an environmental sequence V with standard deviation σ_V, summing up C and ε with untransformed variance σ_V^2, would produce a V with standard deviation $\sqrt{2\sigma_V^2}$. Multiplying each C_i and ε_i random deviate by θ_p and θ_{1-p}, respectively, shrinks their standard deviation to produce a V variable with the desired σ_V. For example, if the signal strength (p) is 0.5 and we aim to produce a random variable V with a standard deviation (σ_V) of 1, θ_p and θ_{1-p} are equal to approximately 0.7071**.** These values make intuitive sense on the variance scale: they produce two random variables C and E with standard deviation 0.7071 (and therefore variance 0.5), which sum to produce a variable V with standard deviation 1 (and therefore variance 1). We implemented 4 different p values (0.05, 0.25, 0.5 and 1). As such, we have temporal sequences where hardly any variance is explained by the climate driver, to sequences where the temporal sequence is fully driven by the climate driver. Our sequences thus encompass a range of temporal variance, autocorrelation, and of variance explained by the climate driver.

Population models for a range of life histories

In order to address how TVR (component 5) affects population demography, we used the Matrix Population Model (MPM) parameterization suggested by Neubert & Caswell (2000) (Figure 1b). This MPM has two stages, juvenile and adult, and yearly transitions are described by the following equations:

$$\mathbf{n_{t+1}} = \mathbf{n_t} * \mathbf{A}_t \qquad \text{Eq. 2}$$

$$\mathbf{A}_t = \begin{pmatrix} S_{J,t}(1-\gamma) & \varphi_t \\ S_{J,t}\gamma & S_{A,t} \end{pmatrix} \qquad \text{Eq. 3}$$

Where $\mathbf{n_t}$ and $\mathbf{n_{t+1}}$ are population size vectors at time *t* and *t+1* respectively, $\mathbf{A}_t$ is the transition matrix, γ is the probability of transitioning from juvenile to the adult stage if the individual survives to from *t* to *t+1*, $S_{J,t}$ and $S_{A,t}$ represent the survival probability of juveniles and adults respectively. Finally, φ_t is the number of offspring produced per surviving adult. This MPM can model a large range of life histories depending on the vital rate (γ, S_J, S_A and ρ) values (Neubert & Caswell, 2000). For example, changing adult survival so that it approaches 0 ($S_A \rightarrow 0$), changes the model species from iteroparous to semelparous (Neubert & Caswell, 2000). We recognize that to model the full range of life histories observed worldwide, we would need more realistic and complex MPMs. However, this simple life cycle can still span a wide range of life histories, and is sufficient to explore the relative effect of responding to different time windows on population dynamics across life histories.

To create MPMs that span a wide range of life histories, we followed Koons et al.'s (2016) method (Figure 1b). We set γ to either 0.2, 0.5 or 0.8 and set S_J and S_A from 0.05 to 0.95, in steps of 0.15. Then for every possible combination of γ, S_J and S_A, we calculated a value of φ such that Eq. 2 and Eq. 3 would result in a population growth rate (λ) of 1 (which equals a stable population). This resulted in 147 different life histories. Next, we calculated the standard deviation of S_J, S_A and φ to run stochastic simulations. Most of the existing literature assumes that in real world populations, these standard deviations evolve to inversely correlate to the elasticity of vital rates, a pattern known as "demographic buffering" (reviewed in Hilde et al., 2020). While evidence contrary to demographic buffering exists (e.g., Jäkäläniemi, Ramula, & Tuomi, 2013; McDonald et al., 2017), we decided to follow Koons et al. (2016) method in this as well, as it reflects the more common evidence on demographic buffering. To simulate these standard deviations, we used the elasticities (e) of S_J, S_A and φ to calculate a proportional measure of buffering: $\tau_i = (1 - e_i)/\max(e_{S_J}, e_{S_A}, e_{\varphi})$ where i is S_J, S_A or φ.

We calculated the standard deviation of survival rate, VR, as $\sigma_{VR} = \tau_i * 0.5 * CV_{max} * \overline{VR}$, where CV_{max} is the maximum coefficient of variation of a probability (Morris & Doak, 2004). Following Koons et al., (2016) we set CV_{max} to 1 for φ.

Finally, we calculated two life history traits (life expectancy and degree of iteroparity, Demetrius entropy) for our 147 life histories using the *popbio* (C. J. Stubben & Milligan, 2007) and *Rage* (Jones et al., 2022) R packages. To improve model fit, and facilitate comparisons of effect sizes, we transformed ln(life expectancy), and iteroparity into z-scores.

Environmental sensitive matrix population models

We then created an environmentally sensitive MPM to include the climate effect size (component 2) in our projections (Figure 1c). We kept γ fixed, but simulated variation in the other vital rates (S_J, S_A and φ) by mapping the normally distributed temporal sequence v (Eq. 1) in beta-distributed (for S_t) and gamma-distributed (for φ_t) values. To do so, we calculated the quantile of each V_i value given the distribution of V, and computed the value of that quantile for the beta and gamma distributions (Figure 1c). For example, if a value of V_i was the 98th percentile of its normal distribution, we drew the 98th percentile from the beta distribution for $S_{J,t}$ and $S_{A,t}$ (see S1.2). Note that while the means of these vital rates always remained the same, we scaled standard deviations by a factor σ_V (which ranged from 0.01 to 1).

Population projections

Using the MPMs and the environmental time series, V, we investigated the effect on populations when some of their vital rates respond to a recent climate driver, and others respond to lagged climate. Using these temporally varied responses to climate drivers (TVR) we projected the population dynamics over 10,000 time steps (Eq. 2-3, Fig. 1d) and calculated λs using the *popbio* package (Stubben, Milligan, & Maintainer, 2016) in R (R Core Team, 2021). We obtained a temporal sequence from Eq. 1 (hereafter, V_{recent}) and created the corresponding lagged temporal sequence by offsetting the C sequence of V_{recent} by one step, and a new ε sequence to create V_{lagged} (Fig. 1a). In the "control" simulations, S_J, S_A, and φ responded to the same C sequences, but different ε sequences. In the "TVR" simulations, the fecundity vital rate (φ) responded to V_{recent}, but the survival vital rates ($S_J$and S_A) responded to V_{lagged}. In these simulations, all vital rates respond in the same (positive) trend to the V sequences, thus creating positive covariance between the vital rates (component 3). Initial analysis showed that there was no difference in λs when fecundity instead of the survival responds to V_{lagged}; therefore, we only show the first.

Next, we repeated the simulations described above, but with the assumption of negative covariance (component 3) between the survival and fecundity vital rates in their response to C. Using similar calculations as described in the previous paragraph, we investigated the effect that responding to TVR could have, if the responses of the different vital rates to climate were negatively correlated. For this we re-ran the simulations in the previous paragraph, but multiplied C_i in Eq. 1 by -1 for the fecundity vital rate (φ).

In both simulations mentioned above, vital rates all respond equally strongly (p) to the climate driver. However, it is possible that stages respond with different intensity to a climate driver (e.g., Tredennick, Teller, Adler, Hooker, & Ellner, 2018). Therefore, as an additional analysis, we also picked one life history, and repeated the simulations with positive covariance. For each of the simulations we modified the response of S_J, S_A, or φ to the climate driver to be only half that of the other two vital rates. For example, in one simulation S_J and S_A would have a p = 0.5, and φ would have a p = 0.25. More details on the simulations can be found in S3.

Finally, to summarise the effect sizes of the different components (climate variance, signal strength, vital rate covariance, climate autocorrelation, and TVR) on λs we used linear mixed effect models for both the positive and negative vital rate covariance simulations. In these models, λs was the response variable, and the fixed effects were climate variance (σ_C; linear and quadratic), climate autocorrelation (r_K), signal strength (p), simulation type (TVR versus control), and the interaction of simulation type with $\sigma_{C,}$ autocorrelation and signal strength (p). For the random slope we used the effect of climate variance for each life history.

We first examine the outcome of simulations focusing on a single representative life history, and then use the linear mixed effect model to quantify the effects of fixed effects across our life histories. As our representative life history we choose a matrix model with S_J = 0.5, S_A = 0.2, γ = 0.5, and φ = 2.4, because this life history is relatively central in both longevity and iteroparity, and because it visually clearly shows the trends found across all life histories.

Correlation with life history traits

We investigated how mean ln(life expectancy) and degree of iteroparity correlated with our simulation results. We first calculated the log relative decrease in λ_s from $\sigma_c = 0.01$ to 1 for both the TVR and control simulations across the σ_c values. Specifically, we calculated relative decrease as

$$\text{relative decrease} = \ln\left(\frac{\lambda_{s,control,\sigma_C=1} - \lambda_{s,control,\sigma_C=0.1}}{\lambda_{s,TVR,\sigma_C=1} - \lambda_{s,TVR,\sigma_C=0.1}}\right). \qquad \textit{eq. 4}$$

Using this measure, values above zero meant that the TVR simulations had relatively lower decrease, and thus higher λ_s than control simulations. We then fit a linear mixed effect model, with the relative decrease as the response variable. The fixed effects were life expectancy, iteroparity, climate autocorrelation and signal strength, as well as the interaction between life expectancy and iteroparity with climate autocorrelation. The random effect was an intercept for each of our 147 different life histories.

Results

Simulations across life histories

The results for our representative life history (S_J = 0.5, S_A = 0.2, γ = 0.5, and φ = 2.4), show three main patterns in which TVR change λ_s. First, when vital rates respond in the same direction to climate, interannual variance in λ is lower (Figure 2), resulting in higher λ_s (Figure 3A). Second, these effect of TVR are amplified for larger values of σ_c and autocorrelation (Figure 3A). Regarding autocorrelation, its direct effect is minuscule when compared to its interaction with TVR (Figure 3A-B). Third, and importantly, in the case vital rates respond in opposite direction to climate, these two effects of TVR are reversed in sign, resulting in lower λ_s values (Figure 3B).

The linear mixed effect model shows that the above patterns hold across all life histories (see S2.4 for plots on the results for every life history), and it indicates two additional patterns. First, that signal strength (p) also amplifies the effects of TVR (Figure 4) with a magnitude similar to autocorrelation and σ_c. Second, it emphasizes that environmental variance σ_c remains the predominant force controlling λ_s (Figure S2.3).

Finally, we used the same life history as in Figure 3 (S_J = 0.5, S_A = 0.2, γ = 0.5 and φ = 2.4), to investigate the effect of different climate signal strengths across vital rates. When one vital rate experiences a climate signal (p) that is only half of the climate signal experienced by the other vital rates, the trends and relationships found in the main analysis remain (see S2.2).

Correlation with life history traits

The largest effects of TVR simulations on stochastic population growth rate (λ_s) occur for species with high life expectancy and, to a much lesser degree, species with low degree of iteroparity (Figure 5 and S2.4). Model estimates show that these effects of life history are amplified under negative autocorrelation (r_k) (Figure 6). As seen previously, the models confirm that the sign of vital rate correlation switches the effect of TVR on λ_s from beneficial (positive correlations) to detrimental (negative correlations, Figure 6). Figure S2.2 shows a graphical comparison of different life histories on the extremes of life expectancy and degree of iteroparity.

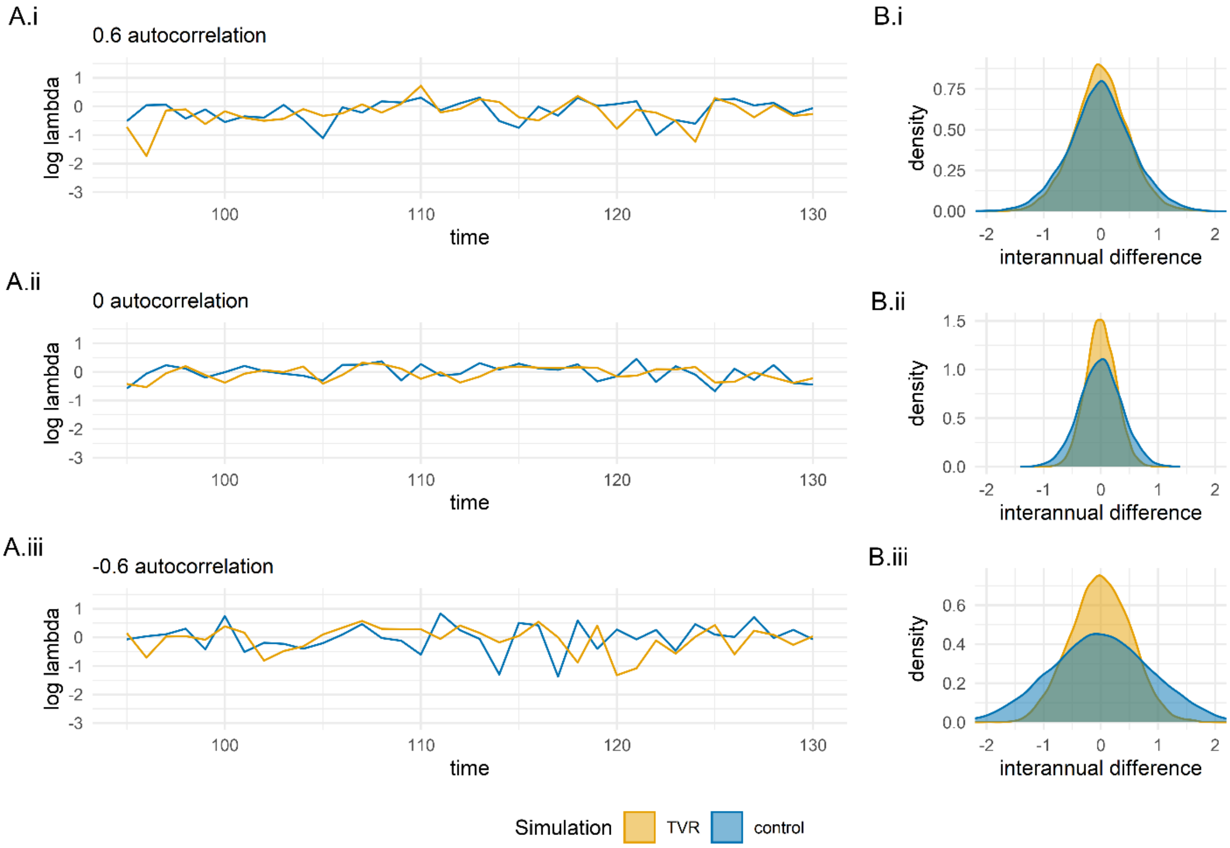

Figure 2. Under positive vital rate correlation, TVR simulations result in lower interannual variance in the natural logarithm of the population growth rate (log lambda) compared to the control simulation. A) log annual population growth rate (λ) across a 35-year time series (years 95-130 of 10,000 years) of stochastic matrix population model (MPM) projections where the MPMs vary according to a climate driver, and random noise. In this simulation, 50% of the variance was explained by a climate driver and 50% of the variance was random. In the "control" simulation all vital rate models respond to recent climate and in the temporally varied response (TVR) simulation, the survival vital rates (juvenile and adult survival) respond

to 1-year lagged climate, whereas the fecundity vital rate responds to recent climate. Simulations were done under (i) 0.6, (ii) 0 and (iii) -0.6 environmental autocorrelation in the climate driver. B) the density distribution of the interannual difference in λ for the whole 10,000-year sequence under (i) 0.6, (ii) 0 and (iii) -0.6 environmental autocorrelation in the climate driver.

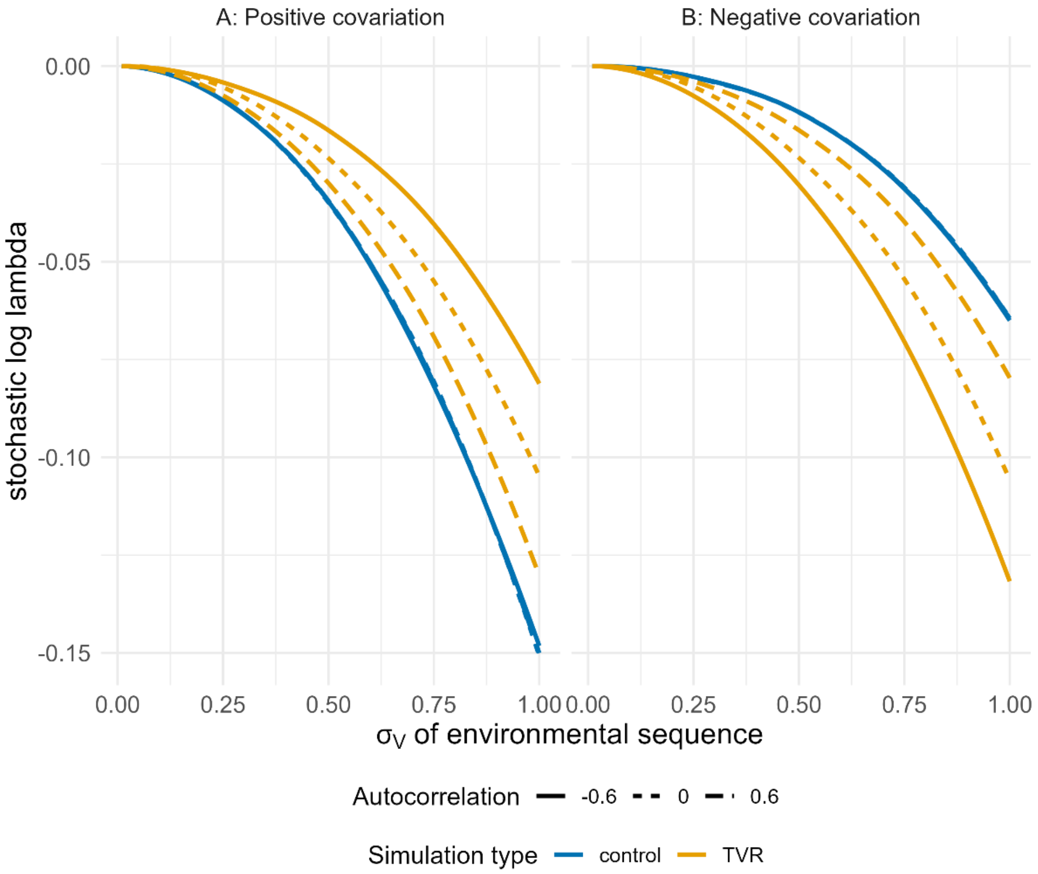

Figure 3. Responding to both lagged and recent climate (i.e., temporally varied responses – TVR) can either buffer or amplify the negative effect of increasing environmental standard deviation (σ_V). Projected stochastic population growth rates of a life history over a range of environmental variation and climate autocorrelations, using a 2-by-2 matrix population model. In this simulation, 50% of the variance was explained by a climate driver and 50% of the variance was random. We included two types of simulations, the control where all vital rates respond to the same (recent) climate, and the temporally varied response (TVR) simulations, where the vital rates in the somatic submatrix (survival) respond to climate that is one year lagged from that of the reproductive submatrix (fecundity). In A) all vital rates respond in a positive direction to the climate driver. In B) the reproductive submatrix responds to the climate driver in the opposite direction of the survival submatrix.

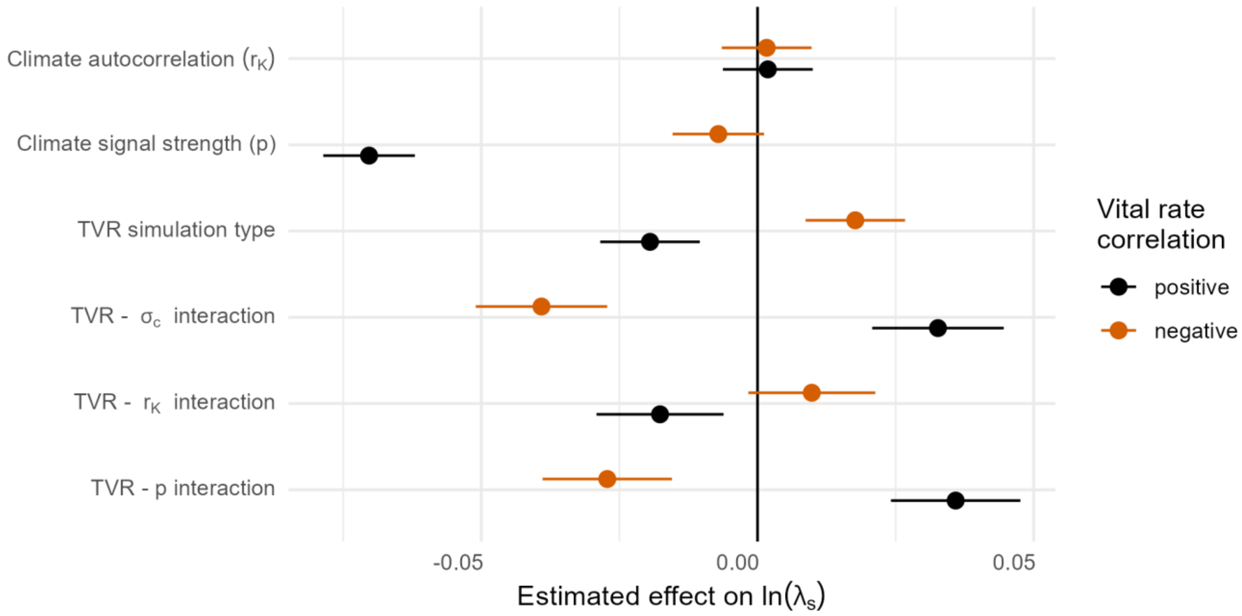

Figure 4. Selected coefficient estimates and 95% confidence interval of the two linear mixed effect models, relating the stochastic log lambda of population dynamic simulations to climate variables under either positive (in black) or negative (in red) correlation between the survival and fecundity vital rates. Climate autocorrelation (r_K) is the autocorrelation in the climate sequence used in the simulations, ranging from -0.6 to 0.6. Climate signal strength (p) is the relative importance of the climate sequence compared to random noise, ranging from 0.01 to 1. TVR simulation type is the difference between the Control and Temporally Varied Response simulations. Finally, the figure shows the estimates for the interaction effect of TVR with the climate standard deviation (σ_c), autocorrelation, and signal strength respectively. The coefficient of the linear mixed effect model not included in this graph are the intercept (positive; -0.045, -0.052:-0.038 CI; negative; -0.078, -0.085:-0.071 CI), and the linear (positive; 1.217, 1.195:1.239 CI, negative; 1.256, 1.233:1.278 CI) and quadratic (positive; -2.110, -2.664:-1.555 CI, negative; -2.077, -2.629:-1.524 CI) effect of σ_c.

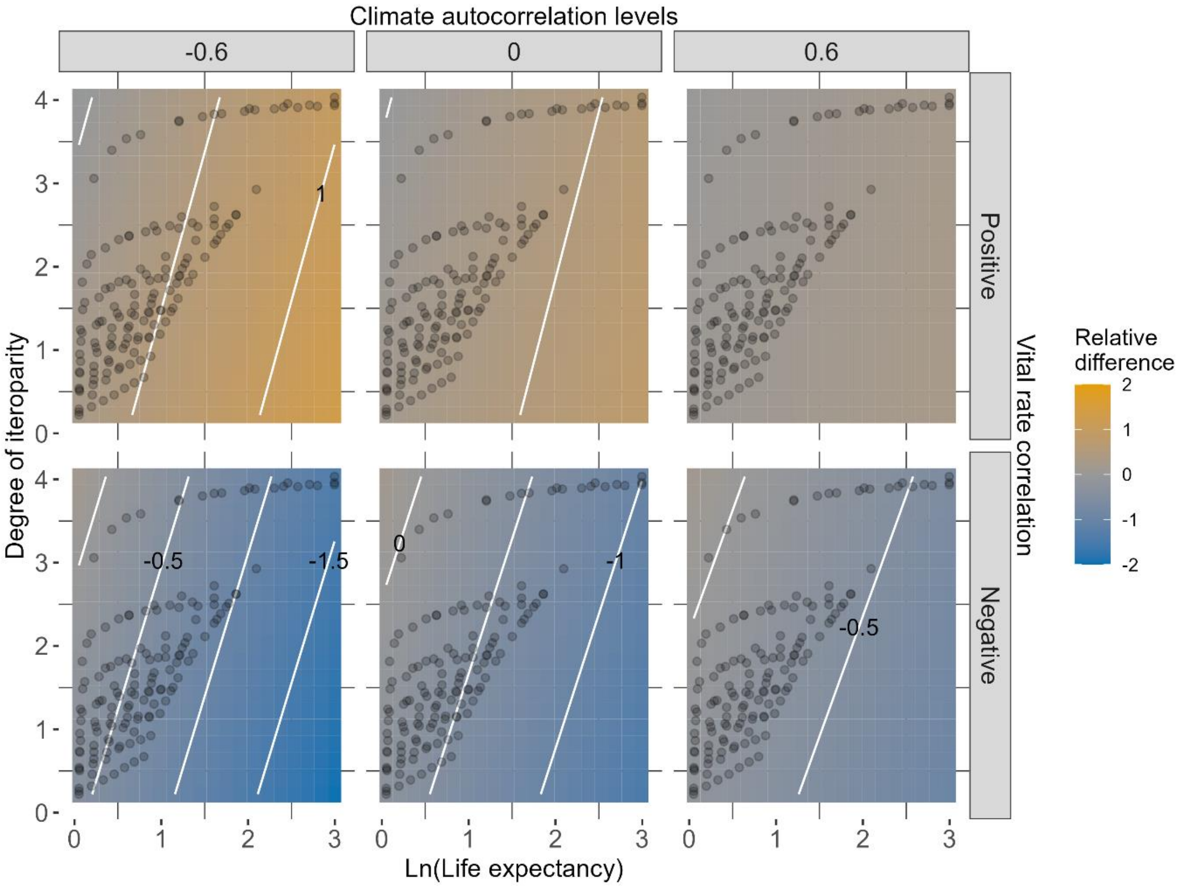

Figure 5. Slow life histories see the largest change in stochastic population growth rate (λ_s) in the presence of temporally varied responses (TVR). Relative difference in the decrease of stochastic population growth rate (λ_s) between simulations with TVR and control simulations, across a range of iteroparity and life expectancy. Colours show the predicted values of linear mixed effect models relating TVR to stochastic population growth rate (λ_s). Difference in λ_s was defined as the change in stochastic population growth rate from climate standard deviation of 0.1 to 1. The relative difference in λ_s was calculated by dividing the difference of the control simulations by the TVR simulations. Positive values indicate that TVR is beneficial for the population growth rate (i.e., has a lower decrease in λ_s compared to the control simulations), whereas negative values indicate that the responding with all vital rates to the same time window (control) is beneficial for the population growth rate. Each circle represents one of the 147 simulated life histories. In the TVR simulations, survival responds to climate that is one year lagged from that of fecundity; in the control simulations, all vital rates respond to the same (recent) climate. The results in the graphs refer to a climate signal strength of 0.5 (i.e., 50% of the vital rate's variance is driven by climate). Columns refer to three levels of autocorrelation (-0.6, 0, and 0.6). Rows refer to positive vital rate correlation (where all vital rates respond positively to the climate driver), or negative vital rate correlation (where the survival and fecundity vital rates respond in different directions to the climate driver).

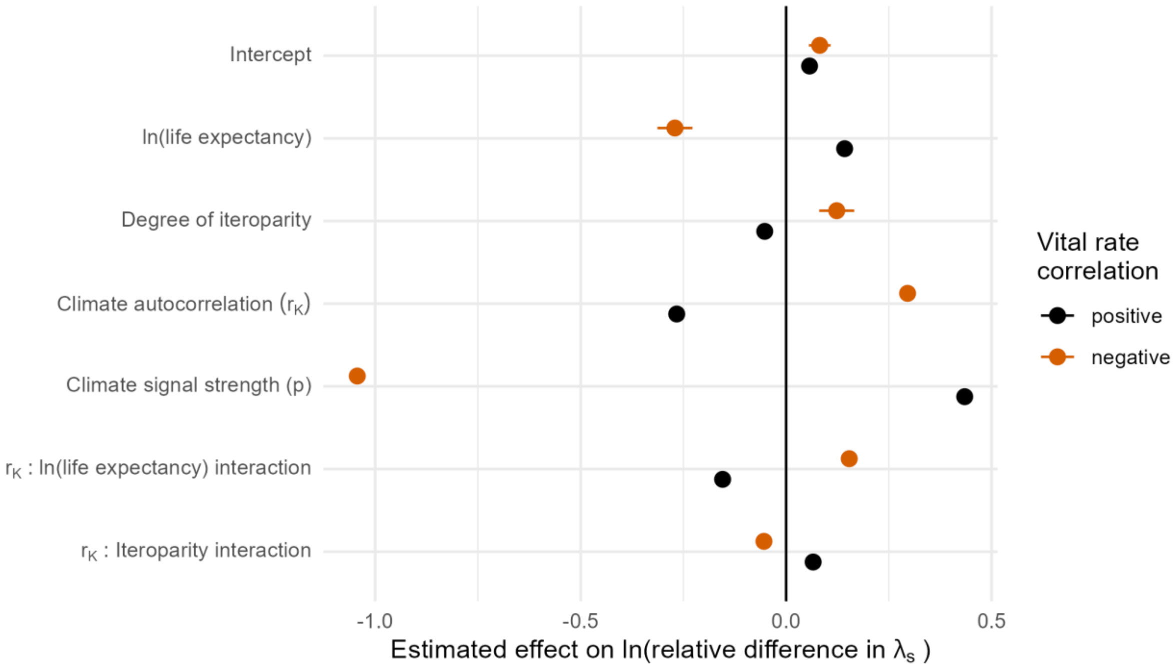

Figure 6. Coefficient estimates and 95% confidence interval of the two linear mixed effect models, relating the relative decrease in stochastic population growth rate to different life history and climate variables, and their interactions, under either positive (in black) or negative (in red) correlation between the survival and fecundity vital rates. ln(life expectancy) and degree of iteroparity are scaled variables for comparison. Climate autocorrelation (rK) is the autocorrelation in the climate sequence used in the simulations, ranging from -0.6 to 0.6. Climate signal strength (p) is the relative importance of the climate sequence compared to random noise, ranging from 0.01 to 1.

Discussion

There is concern that increased climate variance poses a threat to populations, which has motivated considerable interest in understanding this topic (e.g., Boyce et al., 2006; Vázquez, Gianoli, Morris, & Bozinovic, 2017). Here, we found that when vital rates of populations respond to climate with a mix of more recent and lagged climate driver timing (temporally variable response, TVR), this response buffers the populations from the effects of environmental variance on population growth. In particular, this buffering effect always occurs when the vital rates of a species respond to a climatic driver in the same direction (positive covariance). The magnitude of this buffering increases in inverse proportion to the temporal autocorrelation of climatic drivers. On the other hand, in the case of opposing responses of vital rates to the climate driver, TVR could actually exacerbate the effect of increasing climate variability. These results are relevant to population and conservation ecologists for two reasons. First, our results show that the direct effects of environmental autocorrelation on population dynamics are small with respect to their potential indirect effects mediated by TVR. Second, the conditions that lead to TVR buffering the effects of environmental variance are likely common in nature. Thus, our results encourage empirical studies to identify TVR, and to include them in population projection models.

Our results are perhaps the first to suggest that environmental autocorrelation might affect λs indirectly, by affecting vital rates covariation via TVRs. Previous studies found that environmental autocorrelation has relatively small direct effects on population growth rates (Eckhart et al., 2011; Paniw et al., 2018). As a result, many researchers currently investigate stochastic population dynamics under the assumption that no autocorrelation is present (e.g., Compagnoni et al., 2016; McDonald et al., 2017). Our simulations show that environmental autocorrelation can have up to ten times larger an effect on λ_s through interaction with TVR, compared to its direct effect. Temporal autocorrelation is expected to increase under climate change (Di Cecco & Gouhier, 2018), which would decrease the indirect buffering effect of TVR. However, significant regional variation in trends are also expected (Di Cecco & Gouhier, 2018), including regional decreases in autocorrelation, which would actually decrease their extinction risk.

We show that the presence of TVR reduces the annual variation in lambda and thus relatively increases λs under a wide range of scenarios that are likely to occur in nature. TVR increases λs when vital rates respond in the same direction to climate drivers. Climate drivers are usually thought to cause responses in vital rates that are similar in direction (e.g., Compagnoni, Pardini, & Knight, 2021; Hindle, Pilkington, Pemberton, & Childs, 2019). For example, drought typically harms multiple vital rates rather than harm some and benefit others. Examples of opposing trends in vital rate responses do exist (e.g., Dahlgren, Bengtsson, & Ehrlén, 2016; Noël et al., 2010), however, this opposing responses do not necessarily reflect direct responses to climate, but rather physiological tradeoffs that end up resulting in correlations of opposing sign (e.g., trade-offs in vital rates in response to limited resource availability rather than a direct response to the climate driver (Crone, Miller, & Sala, 2009; Tenhumberg et al., 2018). This benefit of TVR is highest in the presence of large, negative environmental autocorrelation. On the other hand, the benefit of TVR mostly disappears only in the presence of large, positive autocorrelation, or when the climate has a very weak effect on the temporal variance of vital rates. These conditions should also be uncommon in nature, as autocorrelations are not known to be so extreme as those considered in our simulations.

We find consistent results across life histories in the direction of the TVR effect on *λs*, suggesting that the effects of TVR on populations can likely be generalized to a variety of life histories. As expected, we find that the relative effects of TVR tend to be stronger in populations with high life expectancy and/or with low iteroparity. This is likely because high coefficients of variation are not possible for populations with low life expectancy (where juvenile survivorship is close to 0) or with high iteroparity (where adult survivorship is close to 1; Morris and Doak 2004). However, the relative decrease in *λs* under TVR was much more severe with changing life expectancy than with changing iteroparity. This could be because TVR effects on populations with different life expectancies act primarily through effects on juvenile survivorship, and effects on this young stage class can have a cascading effect on the entire life cycle.

Based on physiological principles, we expect that many natural populations have TVR. For example, many plant species are known to have preformation of leaves and/or inflorescences more than 12 months before emergence (e.g., Diggle, 1997; Inouye, 1986). Thus, the vital rates associated with growth and/or fecundity will respond to climate drivers in this same timeframe as the preformation (e.g., Evers et al., 2021). In combination with possible frost damage that has rapid demographic consequences (e.g., Iler et al., 2019), alpine species could be a prime example of species with TVR. The presence of belowground rhizomes is another physiological characteristic that has been linked to lagged climate drivers in *Heliconia acuminata* (Scott, Uriarte, & Bruna, 2021). For this species, more immediate climate responses have been observed as well (Westerband & Horvitz, 2017). Even if species only exhibit immediate physiological responses to climate drivers, indirect climate effects can still lead to TVR. For example, the presence of nurse plants positively influenced seedling recruitment (e.g., Flores-Torres & Montaña, 2012), and any delayed effect of climate on the nurse plant would thus translate to the seedling as well.

Studies have shown that vital rates (growth, survival, and reproduction) correlate with climate drivers in unique ways that reflect different biological mechanisms (Bogdziewicz et al., 2020; Fritts, 2012; Trugman et al., 2021). Therefore, it is plausible that the link between vital rates and climatic drivers is complex in nature. Currently, few empirical studies have tested for the presence of TVR. However, previous studies searching for TVR have found evidence for them (Evers et al., 2021; Scott et al., 2021; Tenhumberg et al., 2018), suggesting that TVR might be common. Our recent study (Evers et al. 2021) conducted a review of literature published between 1997 and 2017 and found that most demographic studies consider only a single climate timeframe: typically, the first 12 months prior to vital rate responses. However, among the eight studies that tested for the presence of lagged effects in multiple vital rates, seven found evidence of TVR (Evers et al., 2021).

Our results bolster the nascent research agenda focused on the importance of TVR on population dynamics. This research agenda can advance via both empirical investigations and population modeling studies. Empirically, there are still too few studies that test for the existence of TVR, perhaps because such studies require long-term data (van de Pol et al., 2016, Tenhumberg et al. , 2018; Evers et al. 2021; Scott et al. 2021). Thus, we encourage researchers with long-term demographic data to explicitly test for TVR. A large literature on TVR would provide a better understanding of their prevalence and underlying mechanisms. Further, our results are relevant to conservation research aimed at understanding and accurately forecasting the dynamics of populations known to be threatened by climate change, (e.g., Compagnoni et al., 2021; Lindell, Ehrlén, & Dahlgren, 2022). In the case of species particularly sensitive to climatic variation, explicit modeling of TVR could substantially change forecasts by correctly accounting for the indirect effects of climatic autocorrelation.

We have shown that populations that respond to a mix of temporal climate drivers can be buffered from increasing climate variance. We have also shown that climatic temporal autocorrelation, often acknowledged but unmodelled, can either increase or dampen the effect of variability when driven by mixed temporal climate drivers. Thus, explicitly accounting for mixed temporal climatic drivers might be an overlooked avenue to improve our understanding of population responses to future climatic change.

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Author contribution

S.M.E. conceived the research question and wrote the first draft of the manuscript. All authors contributed to the conceptual framework. Simulations were done by S.M.E., with input from A.C. All authors contributed to the finalization of the text and approved this submission.

Data Availability Statement

All code used for the analyses of this paper can be found on https://github.com/SanneE1/TVR_ population_dynamics

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Supplementary materials

S1 Method details

S1.1 Simulating temporal sequences

First, we simulated the normally distributed climate driver, C, by creating an autocorrelated sequence using the following equations:

$$C_i = c_{i-1} * r_K + \epsilon \tag{1}$$

$$\epsilon \sim Norm(0,1) \tag{2}$$

$$C = \frac{C - \bar{C}}{\sigma_{\bar{C}}} * \sigma_C \sim Norm(0, \sigma_C) \tag{3}$$

where i ranges from 1 to 10,000, r_K is the autocorrelation value. $\bar{C}$ and $\sigma_{\bar{C}}$ are the mean and standard deviation of the sequence created in Eq. (1) and so $\frac{C-\bar{C}}{\sigma_{\bar{C}}}$ scales the sequence to a $\sim Norm(0,1)$ distribution. σ_C is the standard deviation of the desired climate simulation. We used normally distributed processes because it is straightforward to partition their variance.

Second, we combined the climate sequence C with random noise to create a single temporal sequence. We computed each random deviate i of the temporal sequence V as:

$$V_i = C_i * \theta_p + \epsilon_i * \theta_{1-p} with i = 1, 2, ..., 10000 \tag{4}$$

$$C_i \sim Normal(0, \sigma_V) \tag{5}$$

$$\epsilon \sim Normal(0, \sigma_V) \tag{6}$$

where i ranges from 1 to 10,000, ϵ_i is the random noise but always had an autocorrelation equal to zero. We included random noise in the temporal sequences to represent other factors that influence population dynamics in the real world, such as anthropogenic disturbances, biotic interactions or other unknown climate drivers. θ_p and θ_{1-p} control the proportion (p) of variance in V that is explained by C. p can also be seen as the proportion to which C contributes to V, or the susceptibility of the vital rates to C.

Note that summing two independent random variables with mean 0, produces a new random variable whose variance is equal to the sum of the variances of the two summed random variables. Hence, to have a random variable with variance 1, and assuming a p = 0.5, both C and ϵ should have variance 0.5. Translating this example using standard deviation, the C and ϵ variables will have standard deviation ~0.71 which summed will produce a variable V with standard deviation 1. As such to ensure that the standard deviation of C and ϵ are equal to that of V, and because partitioning occurs on the variance scale, we calculate θ_p and θ_{1-p} as $\theta_p = \frac{\sqrt{\sigma_c^2 * p}}{\sigma_c}$ and $\theta_{1-p} = \frac{\sqrt{\sigma_c^2 * (1-p)}}{\sigma_c}$. In other words, we transform the standard deviation (σ_V) into variance, and back-transform it to a standard deviation after multiplying it by p and 1-p, respectively.

We considered 4 different p values (0.05, 0.25, 0.5 and 1). As such, we have temporal sequences where hardly any variance is explained by the climate driver, to sequences where the temporal sequence is fully driven by the climate driver. Our sequences thus encompass a range of temporal variance, autocorrelation, and of variance explained by the climate driver.

S1.2 Calculating vital rate distributions

Using the method of moments, we can use the mean and standard deviation of the survival probabilities, to calculate the shape parameters of the S vital rate distributions in Eq. 3 of the main manuscript as:

$$S \sim Beta(\alpha_S, \beta_S) \tag{7}$$

$$\alpha_S = (\frac{\mu_S * (1-\mu_S)}{(\sigma_S * \sigma_c)^2} - 1) * \mu_S \tag{8}$$

$$\beta_S = (\frac{\mu_S * (1-\mu_S)}{(\sigma_S * \sigma_c)^2} - 1) * (1-\mu_S) \tag{9}$$

Where α_S and β_S are the shape parameters of the beta distributions and μ_S and σ_S are the mean and standard deviation of S. σ_c is the standard deviation of the temporal sequence (V). Multiplying σ_S by σ_c scaled the observed standard deviations, as σ_c varied between 0.01 and 1.

The ϕ vital rate distribution is defined as:

$$\phi \sim Gamma(\alpha_\phi, \beta_\phi) \tag{10}$$

$$\alpha_\phi = \frac{\mu_\phi^2}{(\sigma_\phi * \sigma_c)^2} \tag{11}$$

$$\beta_\phi = \frac{\mu_\phi}{(\sigma_\phi * \sigma_c)^2} \tag{12}$$

Where α_ϕ and β_ϕ are, respectively, the shape and scale parameters of the gamma distributions, and μ_ϕ and σ_c are the expected value and standard deviation of ϕ.

S2 Additional results

S2.1 Life history trait distributions and responses

Below Figure S2.1 shows the trait distribution of our 147 simulated life histories. It also shows the locations of the life history 60, of which the simulation results are shown in figure 1 of the manuscript.

Of other four life histories labelled here, nr. 92 and 144, have similar degree of iteroparity, but a low (92) and high (144) life expectancy. Nr 111 and 44 have similar life expectancy but low (111) and high (44) degree of iteroparity. The results of the simulations for the latter four life histories can be seen in the next figure.

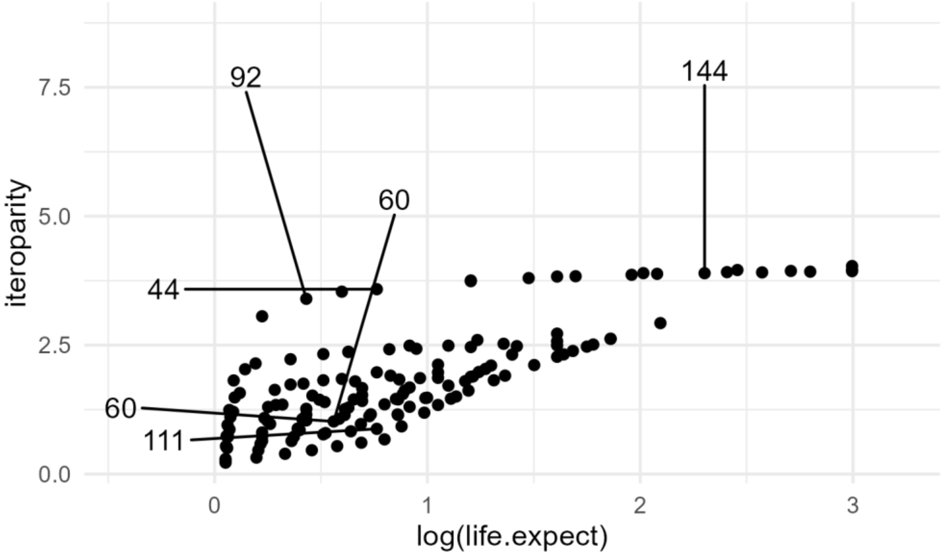


Figure S2.1: Life history trait distribution of the 147 life histories used in the simulations. log(Life expectancy) on the x-axis and degree of iteroparity on the y-axis. Number 60 is the life history shown in the main manuscript. Nr. 92 and 144 are life histories with low and high life expectency, but similar degree of iteroparity. Nr. 111 and 44 are life histories with low and high degree of iteroparity, but with similar life expectancies.

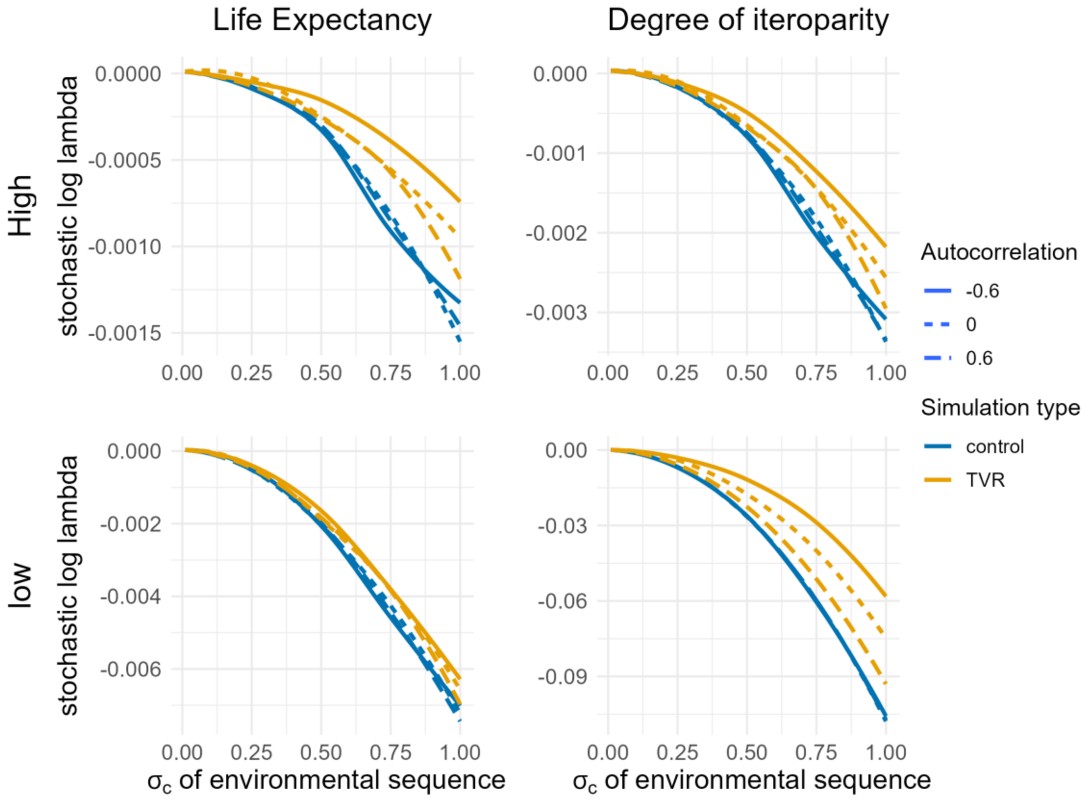


Figure S2.2: Simulation results for 4 different life histories. Low and high life expectancy (92 and 144) have similar degrees of iteroparity, low and high degree of iteroparity (111 and 44) have similar life expectancy. Each panel shows projected stochastic population growth rates of the life history over a range of environmental variation and climate autocorrelations, using a 2-by-2 matrix population model. In these simulations, 50% of the variance was explained by a climate driver and 50% of the variance was random. We included two types of simulations, the control where all vital rates respond to the same (recent) climate, and the Temporally Varied Response (TVR) simulations, where the vital rates in the somatic submatrix (survival) respond to climate that is one year lagged from that of the reproductive submatrix (fecundity). All vital rates respond in the same direction to the environmental sequence (i.e., positive covariance in the vital rates)

S2.2 Different climate signal strengths between vital rates

In the simulations of the main manuscript, all 3 vital rates (S_J, S_A} and ϕ) respond with the same strength to the climate driver. In other words, although the standard deviation of the vital rates differ, the responses have the same relative deviation from the mean, or same probability given the mean and std. dev. In the main manuscript we investigate how different directional responses of the vital rates to the climate can influence the effect of Temporally Varied Response. One additional option is the possibility of certain vital rates responding with different strengths to climate driver. One classic example is the survival probability of seedlings/saplings being more strongly influenced by climate than the survival probability of adults/larger individuals.

Here we repeated the simulations presented in the main manuscript, with one addition. We incorporated the presence of a “weak” vital rate. For this vital rate, the signal strength was only half of that of the other vital rates. We used the same life history and signal strength as highlighted in the main manuscript whose mean vital rate values are S_J = 0.5, S_A = 0.2, γ = 0.5 and ϕ = 2.4 and signal strength of 0.5. This means that the “weak” vital rate, had a signal strength of 0.25. These simulations were done under positive vital rate covariance. Thus, the upper left panel of the figure below (“all equal”) is thus an exact replicate of Figure 2A.

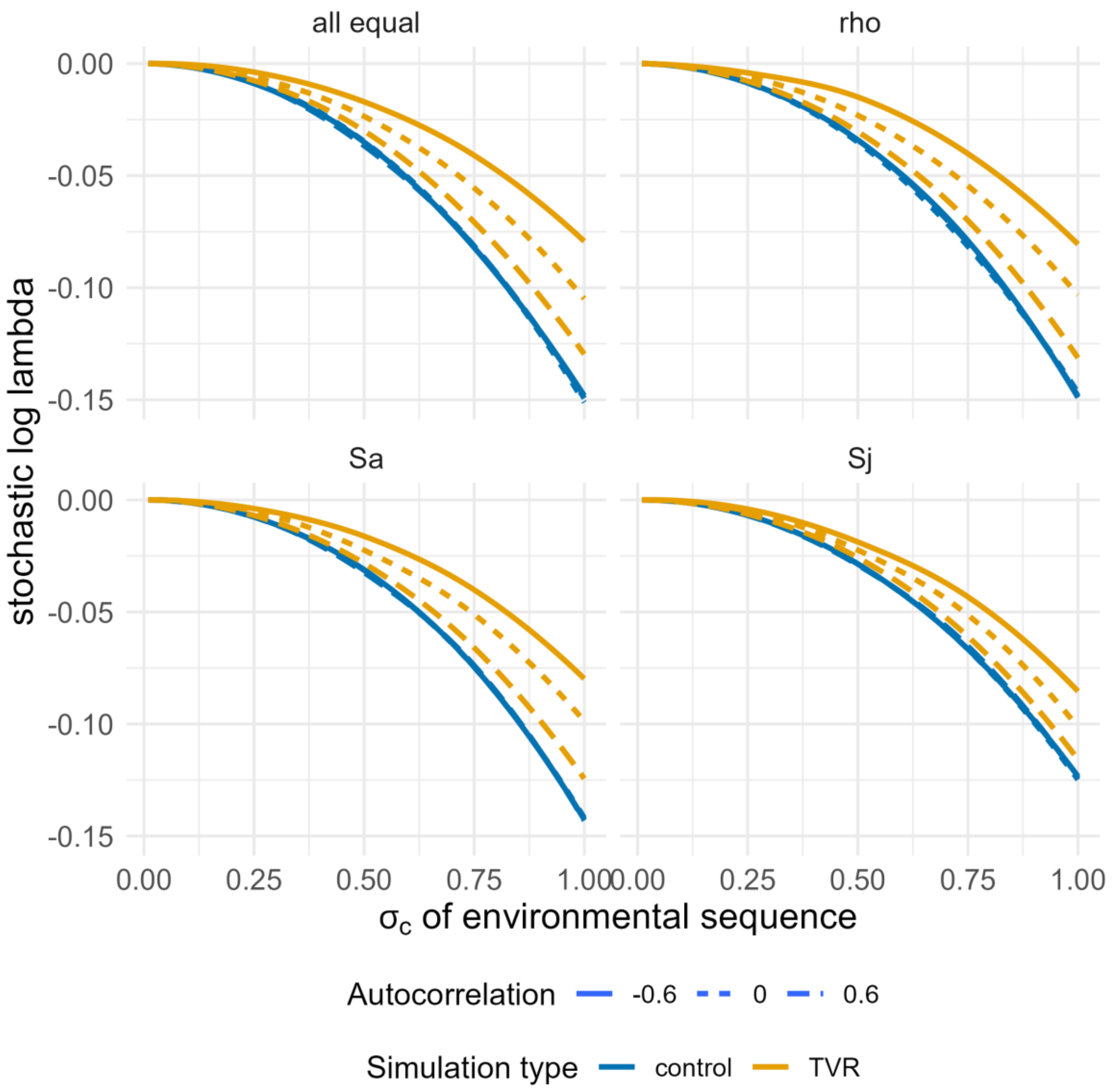


Figure S2.3: Projected stochastic population growth rates of a life history over a range of environmental variation and climate autocorrelations, using a 2-by-2 matrix population model. We included two types of simulations, the control where all vital rates respond to the same (recent) climate, and the Temporally Varied Response (TVR) simulations, where the vital rates in the somatic submatrix (survival and growth) respond to climate that is one year lagged from that of the reproductive submatrix (fecundity). All vital rates respond in a positive direction to the climate driver. In these simulation, we used a signal strength of 0.5 for the normal response. In other words 50% of the variance was explained by a climate driver and 50% of the variance was explained by a random variable. In the simulation similar to those analysed in the main manuscript (labelled "all equal"), all climate sensitive vital rates respond with a signal strength of 0.5. The other three panels show simulations where two of the three vital rates respond with a signal strength of 0.5. The third vital rate (named in the panel label), a weak response to climate was modelled with a signal strength of 0.25. i.e., by having 25% of the variance explained by the climate driver, and 75% by a random variable.

S2.3 Regression summaries

Below is the summary of the regression, correlating the stochastic log lambda with environmental and simulation covariates and the full graphical representation of the coefficient estimates (i.e., the full version of Figure 4 in the main manuscript).

```
## [1] "Possitive vital rate correlation"
```

```
## Linear mixed model fit by REML ['lmerMod']
## Formula: lambda ~ clim_sd + I(clim_sd^2) + clim_auto + sig.strength +
##     lag_type + lag_type:clim_sd + lag_type:clim_auto + lag_type:sig.stre
ngth +
##     (I(clim_sd^2) - 1 | lh_id)
##    Data: df %>% filter(vr_cov == "positive")
##
## REML criterion at convergence: 3912009
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -34.309  -0.138  -0.090   0.072  15.023
##
## Random effects:
##  Groups   Name         Variance Std.Dev.
##  lh_id    I(clim_sd^2) 11.669   3.416
##  Residual               1.393   1.180
## Number of obs: 1233731, groups:  lh_id, 147
##
## Fixed effects:
##                               Estimate Std. Error t value
## (Intercept)                  -0.045280   0.003531 -12.824
## clim_sd                       1.217261   0.011318 107.550
## I(clim_sd^2)                 -2.109637   0.281940  -7.483
## clim_auto                     0.001867   0.004150   0.450
## sig.strength                 -0.070317   0.004230 -16.622
## lag_typeUmatrix              -0.019460   0.004601  -4.230
## clim_sd:lag_typeUmatrix       0.032664   0.006075   5.377
## clim_auto:lag_typeUmatrix    -0.017649   0.005869  -3.007
## sig.strength:lag_typeUmatrix  0.035868   0.005983   5.995
##
## Correlation of Fixed Effects:
##             (Intr) clm_sd I(_^2) clim_t sg.str lg_tyU clm_s:_U clm_t:_U
## clim_sd     -0.593
## I(clm_sd^2)  0.014 -0.034
## clim_auto    0.000  0.000  0.000
## sig.strngth -0.539  0.000  0.000  0.000
## lg_typUmtrx -0.652  0.179  0.000  0.000  0.414
## clm_sd:lg_U  0.434 -0.268  0.000  0.000  0.000 -0.667
## clm_t:lg_tU  0.000  0.000  0.000 -0.707  0.000  0.000  0.000
## sg.strng:_U  0.381  0.000  0.000  0.000 -0.707 -0.585  0.001    0.000
```

```
## [1] "Negative vital rate correlation"
```

```
## Linear mixed model fit by REML ['lmerMod']
## Formula: lambda ~ clim_sd + I(clim_sd^2) + clim_auto + sig.strength +
##     lag_type + lag_type:clim_sd + lag_type:clim_auto + lag_type:sig.stre
ngth +
##     (I(clim_sd^2) - 1 | lh_id)
##    Data: df %>% filter(vr_cov == "negative")
##
## REML criterion at convergence: 3909731
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -34.112  -0.133  -0.090   0.062  15.020
##
## Random effects:
##  Groups   Name         Variance Std.Dev.
##  lh_id    I(clim_sd^2) 11.609   3.407
##  Residual               1.391   1.179
## Number of obs: 1233727, groups:  lh_id, 147
##
## Fixed effects:
##                               Estimate Std. Error t value
## (Intercept)                  -0.078090   0.003528 -22.137
## clim_sd                       1.255544   0.011308 111.035
## I(clim_sd^2)                 -2.076572   0.281216  -7.384
## clim_auto                     0.001659   0.004146   0.400
## sig.strength                 -0.007093   0.004227  -1.678
## lag_typeUmatrix               0.017698   0.004597   3.850
## clim_sd:lag_typeUmatrix      -0.039113   0.006070  -6.444
## clim_auto:lag_typeUmatrix     0.009824   0.005863   1.676
## sig.strength:lag_typeUmatrix -0.027198   0.005977  -4.550
##
## Correlation of Fixed Effects:
##             (Intr) clm_sd I(_^2) clim_t sg.str lg_tyU clm_s:_U clm_t:_U
## clim_sd     -0.593
## I(clm_sd^2)  0.014 -0.034
## clim_auto    0.000  0.000  0.000
## sig.strngth -0.539  0.000  0.000  0.000
## lg_typUmtrx -0.652  0.179  0.000  0.000  0.414
## clm_sd:lg_U  0.434 -0.268  0.000  0.000  0.000 -0.667
## clm_t:lg_tU  0.000  0.000  0.000 -0.707  0.000  0.000  0.000
## sg.strng:_U  0.381  0.000  0.000  0.000 -0.707 -0.585  0.001    0.000
```

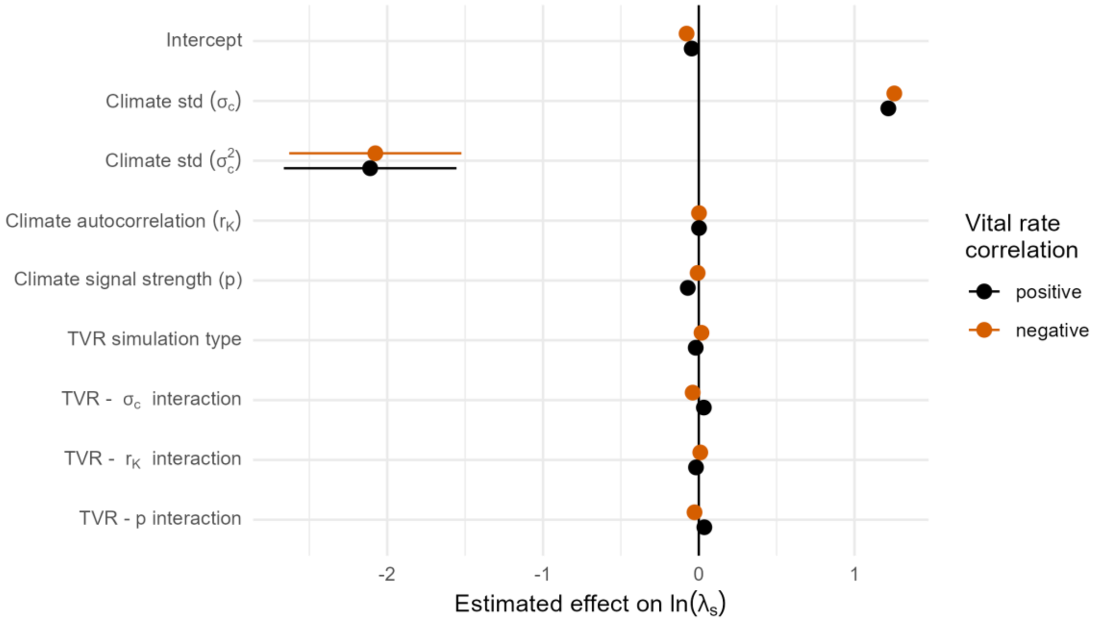


Figure S2.4: Coefficient estimates and 95% confidence interval of the two linear mixed effect models, relating the stochastic log lambda of population dynamic simulations to climate variables under either positive (in black) or negative (in red) correlation between the survival and fecundity vital rates. Climate standard deviation ranges from 0.01 to 1, cliamte autocorrelation (rK) is the autocorrelation in the climate sequence used in the simulations, ranging from -0.6 to 0.6. Climate signal strength (p) is the relative importance of the climate sequence compared to random noise, ranging from 0.01 to 1. TVR simulation type is the difference between the Control and Temporally Varied Response simulations. Finally, it shows the estimates for the interaction effect of TVR with the climate standard deviation (σc), autocorrelation and signal strength respectively.

Next is the model summary of the regression that correlates the relative decrease in stochastic log lambda with environmental covariates and life history traits. Relative decrease is defined as follows;

$$RelativeDifference = ln(\frac{\lambda_{s,TVR,\sigma_{c=0.1}} - \lambda_{s,TVR,\sigma_{c=1}}}{\lambda_{s,control,\sigma_{c=0.1}} - \lambda_{s,control,\sigma_{c=1}}}) \qquad (13)$$

As such, a relative difference below 0 means less decrease for the TVR simulations, and a value above 0 means less decrease for the control simulations. Below is also a graphical representation of the model coefficients estimates and 95% confidence interval.

```
## [1] "Possitive vital rate correlation"

## Linear mixed model fit by REML ['lmerMod']
## Formula:
## log(rel_decrease) ~ life.expect + iteroparity + auto_cat + sig.strength
+
##     auto_cat:life.expect + auto_cat:iteroparity + (1 | lh_id)
##    Data: df2 %>% filter(vr_cov == "positive")
##
```

```
## REML criterion at convergence: 80797.5
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -28.0830  -0.3263   0.0004   0.2989  25.5452
##
## Random effects:
##  Groups   Name        Variance Std.Dev.
##  lh_id    (Intercept) 0.004695 0.06852
##  Residual             0.114537 0.33843
## Number of obs: 119553, groups:  lh_id, 147
##
## Fixed effects:
##                       Estimate Std. Error t value
## (Intercept)           0.057029   0.005869   9.716
## life.expect           0.142359   0.009336  15.249
## iteroparity          -0.052122   0.009330  -5.587
## auto_cat             -0.266256   0.002682 -99.273
## sig.strength          0.434511   0.002755 157.699
## life.expect:auto_cat -0.154542   0.004401 -35.113
## iteroparity:auto_cat  0.065698   0.004350  15.103
##
## Correlation of Fixed Effects:
##             (Intr) lf.xpc itrprt aut_ct sg.str lf.x:_
## life.expect  0.000
## iteroparity  0.000 -0.789
## auto_cat    -0.001 -0.001  0.000
## sig.strngth -0.211 -0.002  0.000  0.000
## lf.xpct:t_c -0.001 -0.002  0.000  0.004  0.000
## itrprty:t_c  0.000  0.000 -0.001  0.006  0.000 -0.781
```

```
## [1] "Negative vital rate correlation"
```

```
## Linear mixed model fit by REML ['lmerMod']
## Formula:
## log(rel_decrease) ~ life.expect + iteroparity + auto_cat + sig.strength
+
##     auto_cat:life.expect + auto_cat:iteroparity + (1 | lh_id)
##    Data: df2 %>% filter(vr_cov == "negative")
##
## REML criterion at convergence: 166989.7
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -14.5100  -0.3818   0.0167   0.4330  15.0367
##
## Random effects:
##  Groups   Name        Variance Std.Dev.
##  lh_id    (Intercept) 0.02623  0.162
##  Residual             0.23815  0.488
## Number of obs: 118516, groups:  lh_id, 147
##
## Fixed effects:
##                       Estimate Std. Error  t value
## (Intercept)           0.081716   0.013553    6.029
```

```
## life.expect          -0.270612   0.021859  -12.380
## iteroparity           0.123097   0.021852    5.633
## auto_cat              0.295557   0.003889   76.003
## sig.strength         -1.043687   0.003999 -260.957
## life.expect:auto_cat  0.153595   0.006423   23.912
## iteroparity:auto_cat -0.054012   0.006301   -8.572
##
## Correlation of Fixed Effects:
##             (Intr) lf.xpc itrprt aut_ct sg.str lf.x:_
## life.expect  0.000
## iteroparity  0.000 -0.789
## auto_cat     0.000  0.000  0.000
## sig.strngth -0.132  0.000  0.000 -0.001
## lf.xpct:t_c  0.000  0.000  0.000  0.016  0.000
## itrprty:t_c  0.000  0.000  0.000  0.010 -0.001 -0.773
```

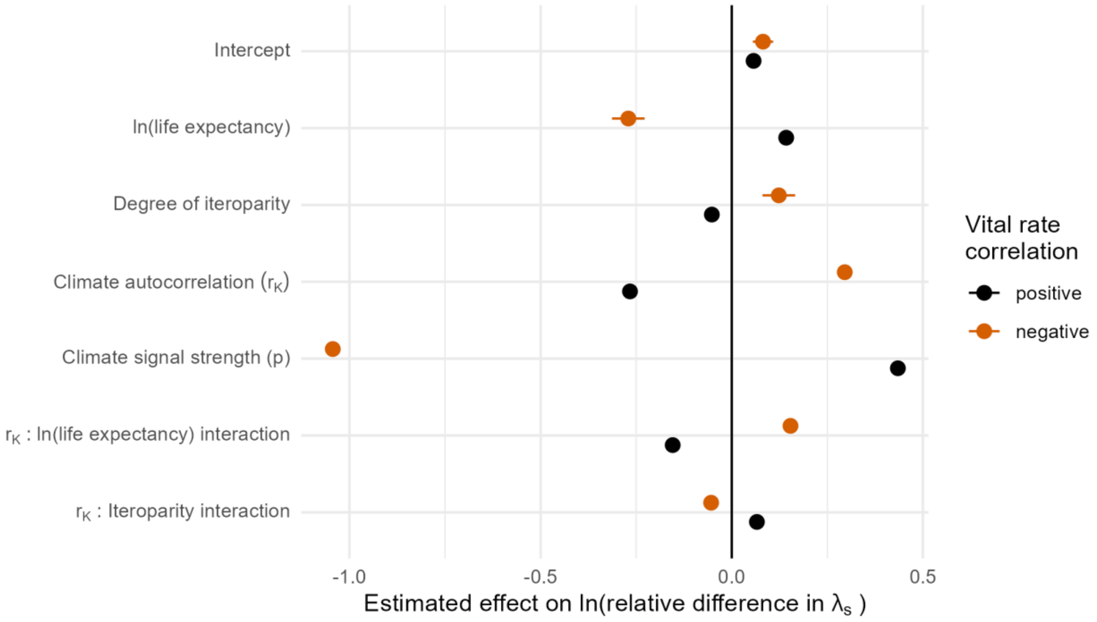


Figure 2.5: Coefficient estimates and 95% confidence interval of the two linear mixed effect models, relating the relative decrease in stochastic population growth rate to different life history and climate variables, and their interactions, under either positive (in black) or negative (in red) correlation between the survival and fecundity vital rates. ln(life expectancy) and degree of iteroparity are scaled variables for comparison. Climate autocorrelation (rK) is the autocorrelation in the climate sequence used in the simulations, ranging from -0.6 to 0.6. Climate signal strength (p) is the relative importance of the climate sequence compared to random noise, ranging from 0.01 to 1.

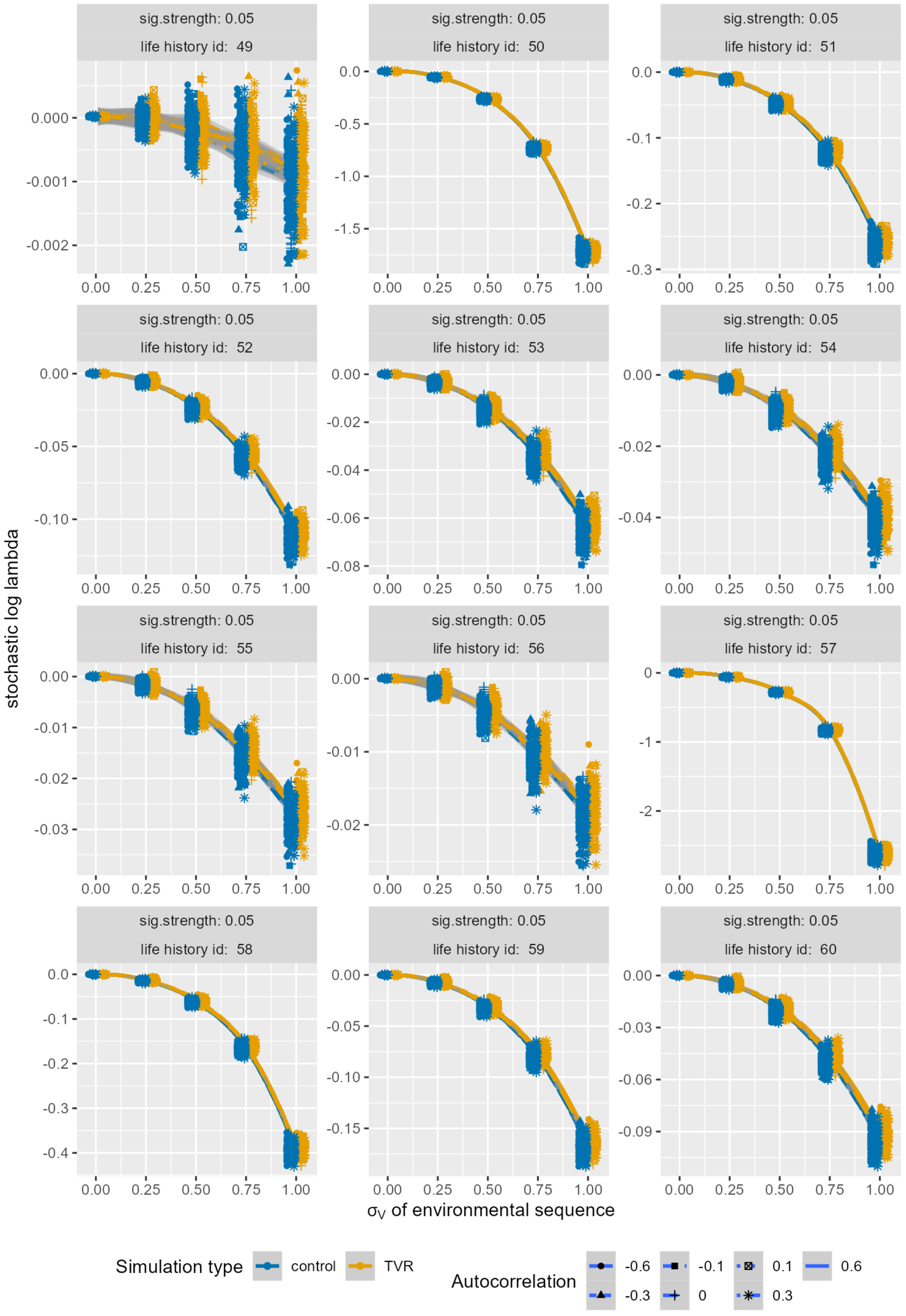
S2.4 Individual life histories results

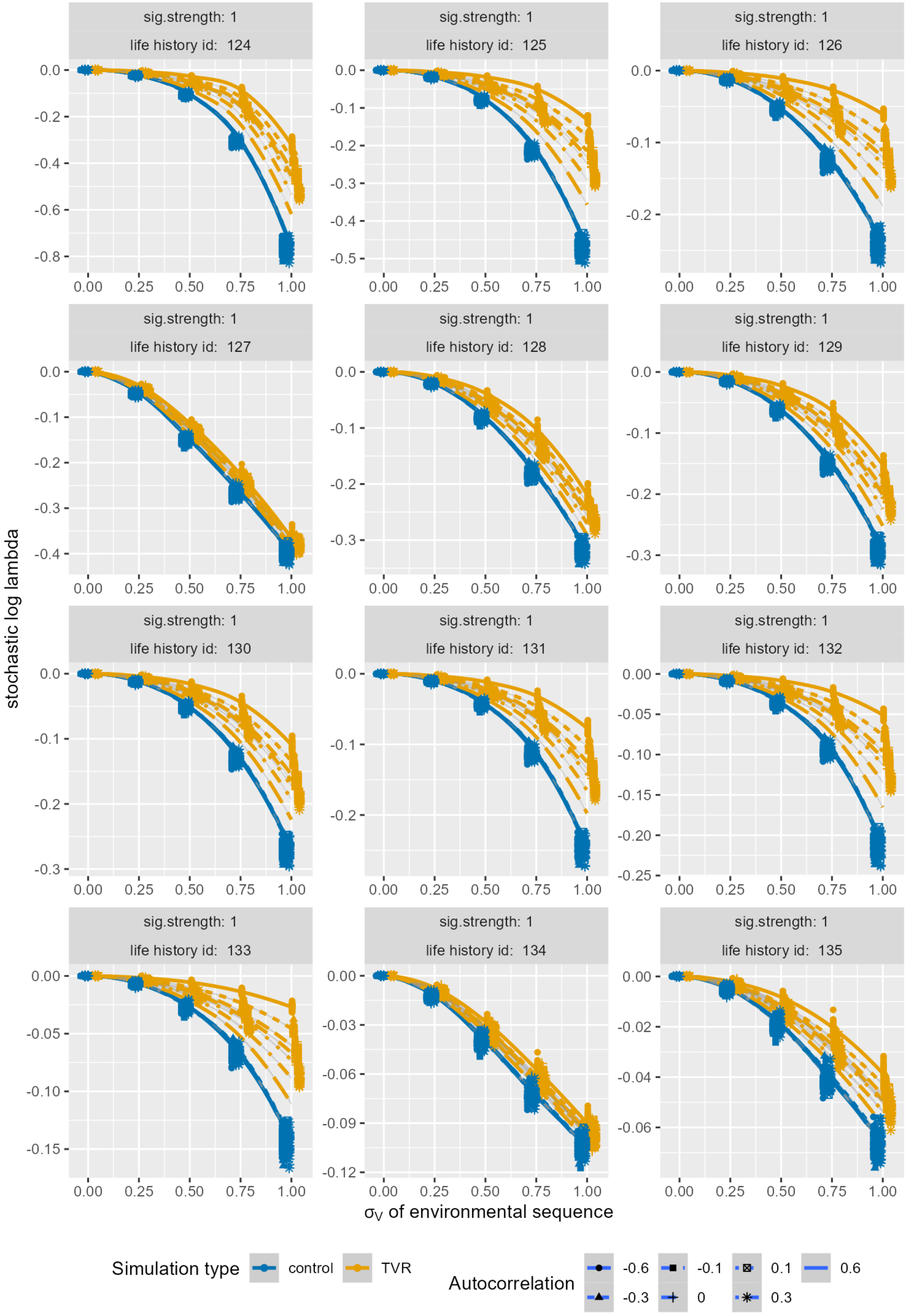
Please not that this section has been slimmed down in this dissertation compared to the version currently in revision in Journal of Ecology. There this section consists of 98 pages. Here, I have selected 4 random pages.

In the graphs below, points of the control and TVR simulations are slightly dodged to make sure both are visible. They are however, at the same climate standard deviation (i.e., although the climate std. looks like 0.95 for and 1.05, all have a value of 1)

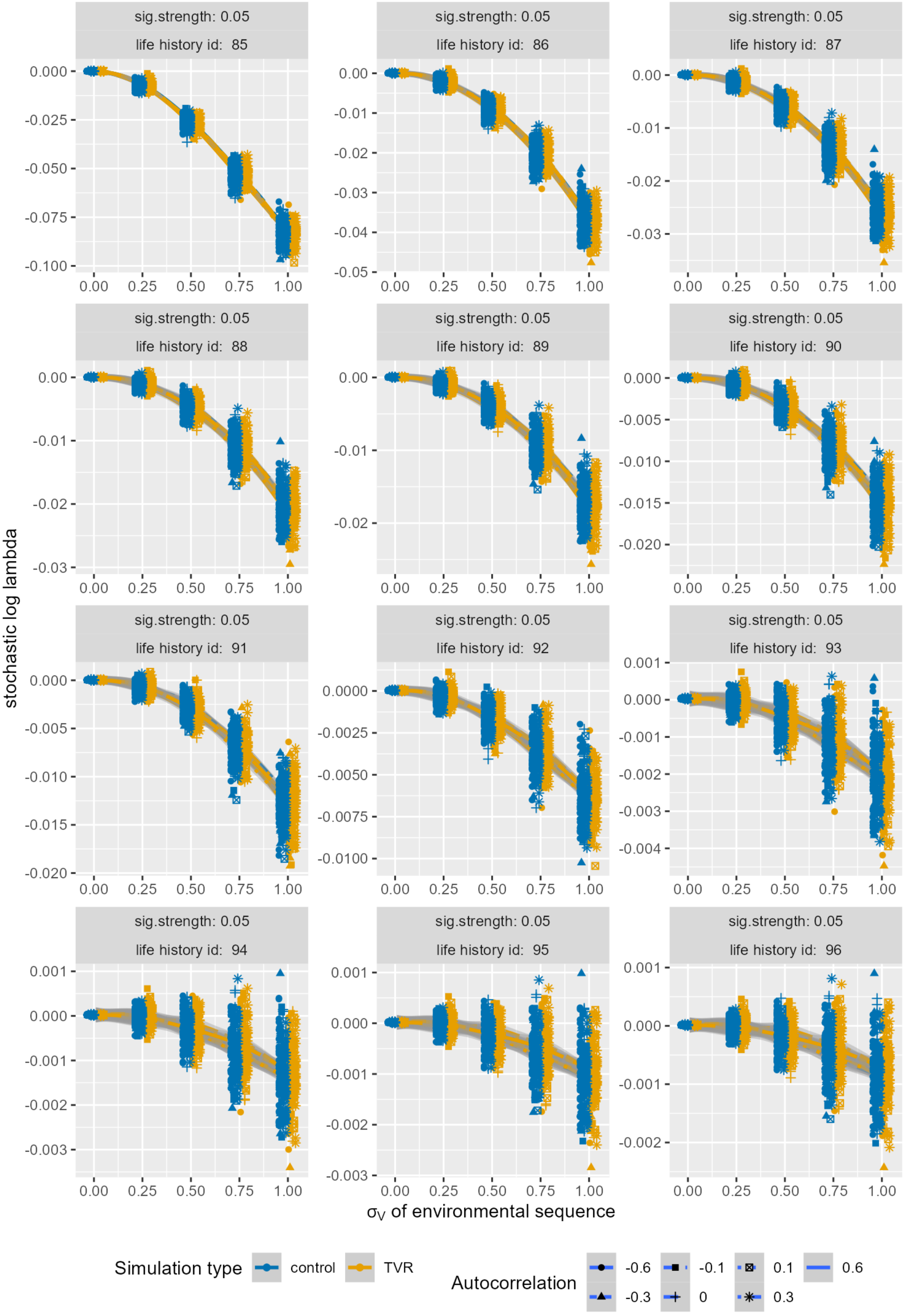
In the graphs below, individual lines are drawn using splines (in the ggplot2::geom_smooth() function). This formula does not match the functional form of the models in S2.3 and are therefore only for illustration purpose.

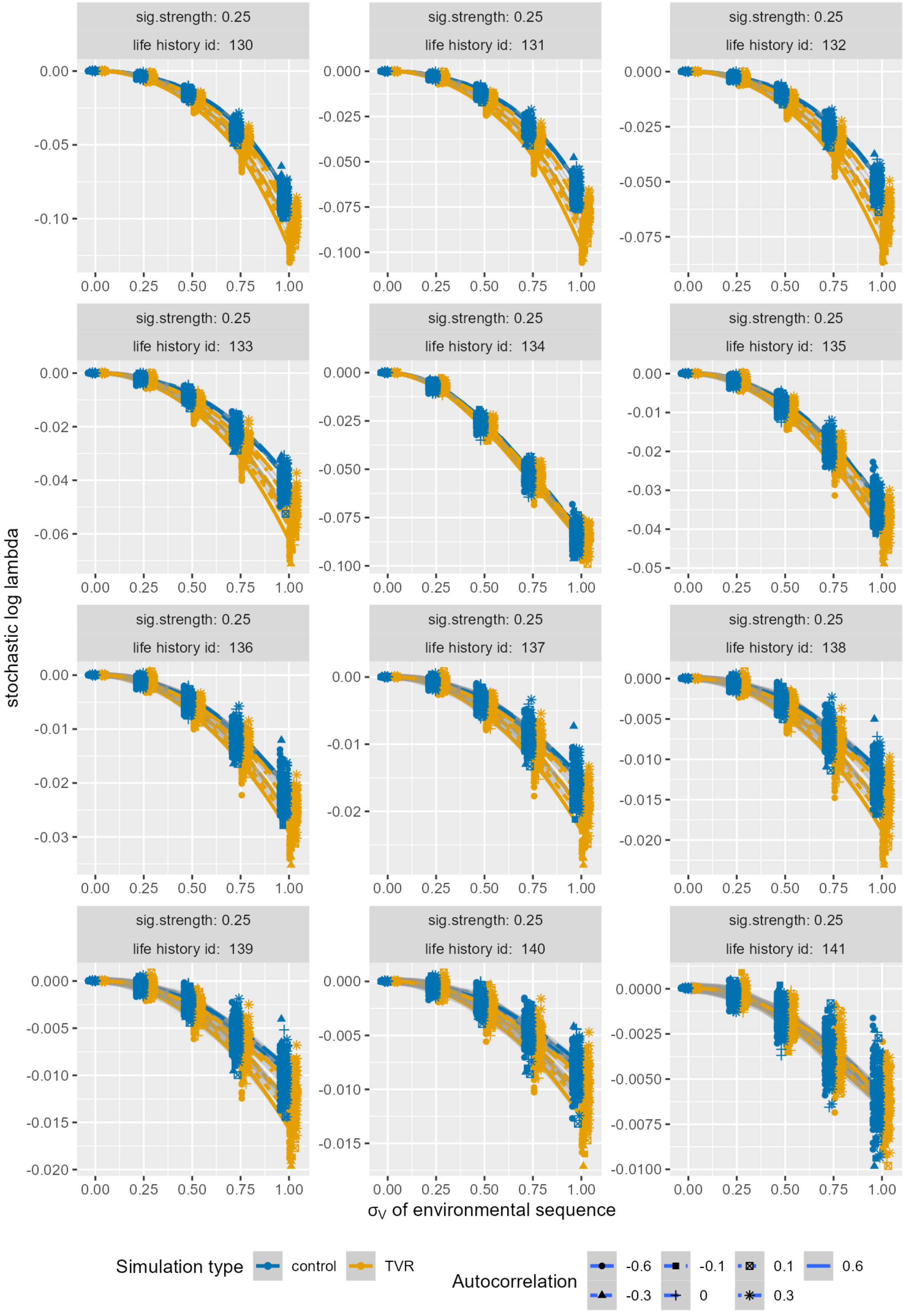
Positive vital rate covariation




sig.strength: 1
life history id: 124
life history id: 125
life history id: 126
life history id: 127
life history id: 128
life history id: 129
life history id: 130
life history id: 131
life history id: 132
life history id: 133
life history id: 134
life history id: 135
0.0
-0.2
-0.4
-0.6
-0.8
-0.1
-0.3
-0.5
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.03
-0.06
-0.09
-0.12
-0.02
-0.04
0.00
0.25
0.50
0.75
1.00
stochastic log lambda
σ$_V$ of environmental sequence
Simulation type
control
TVR
Autocorrelation
-0.6
-0.3
-0.1
0
0.1
0.3
0.6

Negative vital rate covariation




sig.strength: 0.25
life history id: 130
0.00
-0.05
-0.10
sig.strength: 0.25
life history id: 131
0.000
-0.025
-0.050
-0.075
-0.100
sig.strength: 0.25
life history id: 132
0.000
-0.025
-0.050
-0.075
sig.strength: 0.25
life history id: 133
0.00
-0.02
-0.04
-0.06
sig.strength: 0.25
life history id: 134
0.000
-0.025
-0.050
-0.075
-0.100
sig.strength: 0.25
life history id: 135
0.00
-0.01
-0.02
-0.03
-0.04
-0.05
sig.strength: 0.25
life history id: 136
0.00
-0.01
-0.02
-0.03
sig.strength: 0.25
life history id: 137
0.00
-0.01
-0.02
sig.strength: 0.25
life history id: 138
0.000
-0.005
-0.010
-0.015
-0.020
sig.strength: 0.25
life history id: 139
0.000
-0.005
-0.010
-0.015
-0.020
sig.strength: 0.25
life history id: 140
0.000
-0.005
-0.010
-0.015
sig.strength: 0.25
life history id: 141
0.0000
-0.0025
-0.0050
-0.0075
-0.0100
0.00
0.25
0.50
0.75
1.00
stochastic log lambda
σV of environmental sequence
Simulation type
control
TVR
Autocorrelation
-0.6
-0.3
-0.1
0
0.1
0.3
0.6

Chapter 4

Herb and shrub shading could buffer the negative effects of future climate on the endangered *Dracocephalum austriacum*

Sanne M. Evers[1,2], Zuzana Münzbergová[3,4] & Tomáš Dostálek[3]

Affiliations

[1] Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle (Saale), Germany

[2] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[3] Department of Population Ecology, Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic

[4] Department of Botany, Faculty of Science, Charles University, Prague, Czech Republic

Abstract

The relationship between population dynamics and climate is a complex question that is becoming increasingly important due to climate change. The effects of climate variables can be unpredictable and change through time, and understanding how they interact with other biotic and abiotic factors is crucial for conservation efforts. Here we analysed a 20-year dataset of four populations of the endangered plant species, *Dracocephalum austriacum*, to investigate the effects of climate and possible climate-interactions on vital rates, such as survival, flower probability and seed production, and population growth rate.

We found that models with potential evapotranspiration by shading interactions were the best predictive models for survival probability, flower probability and number of seeds produced. For growth and seed production probability, the best models included precipitation by shading interactions. We also found that climate sensitivity was higher under low and high shading levels for survival and number of seeds respectively. Higher shading levels also result in a higher stochastic population growth rate, and can buffer the effect of future climate change, although under most climate scenarios, the populations will still go extinct. The results suggest that shading is important for the long-term persistence of these plant populations in the face of climate change.

The study emphasizes the importance of long-term studies to properly understand population dynamics and the impact of climate change on populations. The results of this study suggest that despite being a species of open habitats, localities with heterogenous microhabitats with different levels of shading are important for the long-term persistence of these plant populations in the face of climate change. The study provides valuable insights for conservation efforts and underscores the need for continued research in this area.

Introduction

Investigating the effect of climate on population dynamics is a long running topic (e.g., Lewontin & Cohen, 1969), and is only becoming more salient (Sutherland et al., 2013; Urban, 2015). It has become increasingly clear that the relationship between population dynamics and climate can be much more complex than is usually modelled. First, the timing of the most relevant climate is often outside *a-priori* expectations (Evers et al., 2021). Second, it is possible for the effect of a climate variable to vary through time (Tenhumberg, Crone, Ramula, & Tyre, 2018). Finally, the relationship between climate and vital rates can also depend on other (a)biotic factors (e.g., Bütof et al., 2012; Tye, Menges, Weekley, Quintana-Ascencio, & Salguero-Gómez, 2016). Including the right climate timeframe and relationship in our analysis is crucial as climate change is already causing previously unobserved climate values and changes in historical (auto)correlations (Di Cecco & Gouhier, 2018; IPCC, 2014). Fortunately, our understanding of complex climate driver timing has been steadily improving thanks to the development of useful tools and methods (e.g., Bailey & van de Pol, 2016; Gasparrini, Scheipl, Armstrong, & Kenward, 2017; Teller, Adler, Edwards, Hooker, & Ellner, 2016). On the other hand, including more complex climate relationships will often require more data than the most studies have (Salguero-Gómez et al., 2015; Teller et al., 2016). Simulations show that exclusion of these complexities could have significant effects on population level inferences (Evers, Knight, & Compagnoni, *in revision*).

Being able to understand how climate interacts with other (a)biotic factors can be incredibly useful in conservation efforts, when these (a)biotic factors can be manipulated in conservation efforts (e.g., Martorell, 2007). For example, non-targeted species can be removed to decrease light competition (Canham et al., 1990). However, when removing other species, especially trees and shrubs, other functions, such as soil-moisture retention (Rickard, 1967), will be lost. Unfortunately, the effect of climate on plant vital rates is a data intensive question requiring a minimum of 20 years for multiple sites (Tenhumberg et al., 2018) and investigating interaction effects will increase the required amount of data. With the median length of plant demographic studies well below the required length, at 5 years (Salguero-Gómez et al., 2015), it is vital that we thoroughly explore the climate effects and interactions in the few datasets that have the required length and try to find trends that can be applied to other species with less data available (e.g., Evers et al., 2021)

Dracocephalum austriacum is a prime example of a species with sufficient data available to investigate the effects and interactions of climate. *Dracocephalum austriacum* is an endangered species of open rocky outcrops, and conservation efforts have focused on removing encroaching shrub and tree species at these localities. The aim of removing the encroaching individuals was to decrease the level of shading experienced by *D. austriacum* individuals. However, after several drought years, survival of individuals appeared to be significantly higher in areas with more encroachment and shading (*personal obs. T. Dostalek*). Other efforts to conserve the species also include population reinforcement by transplants pre-cultivated in controlled conditions. A previous study of eight years on seven populations in the French alps, has shown that the effect of temperature can depend on the slope of the locality (Nicolè, Dahlgren, Vivat, Till-Bottraud, & Ehrlén, 2011).

In this manuscript, we analyse 16 years of a long-term dataset of four populations of *D. austriacum* in the Czech Republic. This dataset has been previously analysed when four yearly transitions were available (Dostálek & Münzbergová, 2013), but the populations have been continuously monitored since then. Here we will take advantage of this increased dataset and new methods developed. We investigate the effect of climate and several (a)biotic factors (shading, slope, soil depth and rock presence) on the vital rates and population growth rate of the four *D. austriacum* populations. Finally, we forecast the development of the populations under several future climate scenarios, investigating what effects these different factors and future climate will have on the monitored populations.

Method

Species

Dracocephalum austriacum (Lamiaceae) is a long-lived perennial species growing on rocky steppes with a range from North-East Spain to central Europe and to Turkey (IUCN 2021). Although as of 2011 *D. austriacum* was classified by the IUCN as data deficiency, it is clear that populations are scarce throughout its range and these populations are mostly small and declining (Bilz, 2011). This species was suggested to form persistent seed bank (Dostálek & Münzbergová, 2013) eventhough its importance for population dynamics has not been fully understood yet (Andrello et al., 2012; Dostálek & Münzbergová, 2013). In the Czech Republic, open rocky habitats with characteristic species (including *D. austriacum*) are being threatened by shrub and tree encroachment. In an effort to protect the species, several populations have been put under active management. This management consists of regular removal of shrubs and trees, such as *Swida sanguinea*, *Rosa sp.* and *Fraxinus excelsior* that encroach upon *D. austriacum* populations.

Data collection

Individual level data for *D. austriacum* have been recorded in May/June from 2003 until the present in four population in the Bohemian Karst in Central Europe (Dostálek & Münzbergová, 2013). In this study we will analyse data ranging from 2003-2019 These populations were; Haknovec (Hk), Císařská rokle (Cr), Kodská stěna (Ks) and Radotínské údolí (Ru). Exact coordinates are withheld for the protection of the populations. Measurements taken during data collection include number of vegetative stems, flowering stems, length of the longest stem, traits related to seed production on 2 randomly chosen flowering stems (length of flowering stem, inflorescence length, number of calices, number of seeds). Each year localities were also searched for newly emerged seedlings which were defined as new plants with one thin stem up to 10 cm long. In addition to the yearly census, experiments were performed to understand the species seedbank dynamics. We estimated the percentage of viable seeds produced by cutting 100 seeds and visually checking if the embryo was developed. This resulted in assumption that 45% of the sown seeds were viable. Next, to estimate survival of the seeds in the seed bank, we buried a total of 9 nylon bags at Hk locality, each containing 50 seeds in autumn 2015. Specifically, we buried 3 bags, at 3 different locations at Hk. Next, we excavated three seed bags (one at each site) in the following three years (May 2017, 2018, 2019) and checked seed viability by cutting and visually checking embryo as before. On average, 8.9% and 5.9% seeds survived after two and three years, respectively. After three years, there were no viable seeds found.

Data on herb and shrub encroachment (hereafter shading), soil depth, slope and rock presence has been recorded on the individual plant level. Herb and shrub encroachment were estimated on a scale from 0 to 10, where 0 was characterized as no other plants present within 20 cm and 10 as very dense herb and/or shrub vegetation, with the *D. austriacum* individual completely overgrown. Soil depth was determined for each individual using a nail pushed into the soil in three random places within 5 cm of the individual. Slope was estimated on a microsite of 20x20 cm with the *D. austriacum* individual in the center. Finally, rock presence was estimated as proportion in % of rock or larger stones on the same 20x20cm microsite.

Climate data

Climate data and future climate projections used in our analyses were obtained from CHELSA. We retrieved historical monthly climate values from 2001 to June 2019 of mean daily air temperature (tas) and precipitation (pr) from CHELSA V.2.1 (Karger et al., 2017, 2018). We also retrieved monthly tas and pr projections from the cmip5 time series (Karger, Schmatz, Dettling, & Zimmermann, 2019, 2020) for 2022 to 2100. Next we calculated the potential evapotranspiration (PET) for both the historical climate and the future projections using the SPEI package (Beguería & Vicente-Serrano, 2017) in R (R Core Team, 2021). We include PET in our analysis as this variable combines temperature and precipitation to reflect the potential water lost to the plants. Although PET is available for the historical data from CHELSA, we used our calculated PET values for consistency across the historical and future climate (correlation between calculated PET, and PET available from CHELSA =0.92). Finally, we calculated the mean and standard deviation of the historical tas, pr and PET. We used these values to transform the historical and future climate values into climate anomalies (Z-scores).

We also created two ARIMA (Autoregressive Integrated Moving Average) models without drift based on 30 years (World Meteorological Organization, 2017) of climate data. Using ARIMA models, we are able to simulate monthly climate values, with the same autocorrelations as in the climate data. The first set of ARIMA models (historical ARIMA hereafter) was created using historical tas, pr and PET from 1989-2018. This time period was chosen as the most historical period, that still included all the census years of *D. austriacum* and the most recent year with complete CHELSA data available. The second set of ARIMA models (future ARIMA hereafter) were based on forecasted monthly values of tas, pr and PET, from 2071-2100, which are the last 30-years of the future projections. As these models will be used to run long-term simulations (10,000 time-steps), we did not include drifts in the ARIMA models. As such, these models represent "stable" historical and future climate.

Vital rate models

We modelled five vital rates as being size dependent on the (log transformed) number of stems. These vital rates were: survival probability (s), change in size (g, hereafter growth, although shrinkage is also possible), flowering probability (f_p), seed production probability (a_p) and number of seeds produced ($seed_n$). We used Functional Linear Models (FLM) to investigate which of the environmental and climate covariates had the best predictive power (Teller et al., 2016). We included a range of two years of past data (details next paragraph) for each of the climate variables (tas, pr and pet) separately, as well as the other recorded environmental variables (shading, slope, rockiness and soil depth). Finally, we also considered interactions between the climate and environmental variables. All models include population (Hk, Cr, Ks and Ru) as fixed effect, and year as random effect. Climate data was monthly data, shading was used as a yearly value and slope, rockiness and soil depth were available as one value per individual. To test if a climate variable, environmental variable, or an interaction between climate and environment had the best predictive power, we used AIC to select the best model.

Functional Linear Models (Ramsay & Silverman, 2005) are a great tool to link climate drivers to demography, and are excellently explained by Teller and colleagues (2016) in this context. However, in short, these FLMs are models that include (in our case) 2 years of monthly climate effects, using a smooth function in a gam model, using the mgcv package (Wood, 2017) in R (R Core Team, 2021). With this method, the autocorrelation within the time range considered is accounted for. To test for interactions between climate and environmental drivers, we included climate interactions with the environmental covariates as tensor products. Because we included these interactions, we were not able to use 24 knots (i.e. one knot per month as done in Teller et al. (2016)). Instead, we used 8 knots for the s and g models and 5 knots for the f_p, a_p and $\underline{seed_n}$ models resulting in knots every 3-, or 5-months rather than one for every month.

Using the results of the seed experiments, we calculated the proportion of seeds produced in time t that were viable at the census in $t + 1$ ($seed_{s1}$). We also calculated the probability of seeds surviving in the seedbank from $t + 1$ to $t + 2$ ($seed_{s2}$) and from $t + 2$ to $t + 3$ ($seeds_{s3}$). Then, using these survival probabilities, the observed number of seeds produced in the years from $t - 2$ to t and the number of new seedlings observed in year $t+1$ we estimated the germination probability. Finally, we estimated the size distribution in $t+1$ of seedlings in t that transfer to the adult stage (sdl_d).

Population model

To investigate the long-term population level effects, we created an Integral Projection Model (IPM) using *ipmr* (Levin et al., 2021). This IPM consist of 3 discrete stages (Seedbank year 1 (B_1) and year 2 (B_2) and Seedlings (Sdl)) and 1 continuous stage (plants (n)). Transition probabilities and sub-kernels were based on the vital rate models described in "Vital rate models" above. The full IPM equation looks as follows;

$$B_{1,t+1} = \int_L^U [F(z)]\, n(z,t)dz * (1 - germ) \qquad \textit{eq. 1}$$

$$B_{2,t+1} = seed_{s2} * B_{1,t} * (1 - germ) \qquad \textit{eq. 2}$$

$$SDL_{t+1} = \left[\int_L^U [F(z',z)]\, n(z,t)dz + \; seed_{s3} * \; B_{2,t} + \; seed_{s2} * \; B_{1,t}\right] * germ \qquad \textit{eq. 3}$$

$$n(z',t+1) = \int_L^U [P(z',z)]n(z,t)dz + sdl_s * \; sdl_d(z') * \; SDL_t \qquad \textit{eq. 4}$$

Where $germ$ is the germination probability of a seed, $seed_{s2}$ and $seed_{s3}$ are seed survival probabilities in the second and third year respectively, sdl_s is the average seedling survival probability and $sdl_d(z')$ is the size distribution of seedlings that enter the continuous plant stage (n). U and L are the upper and lower limits of integral (ln(size) = 0 and 4.121 resp.). These limits correspond to the smallest size possible and 120% of the largest observed log-transformed size (stems = 31). We integrated this IPM using the midpoint rule, and 100 mesh-points and we corrected for unintentional eviction using a truncated distribution.

Finally, $F(z',z)$ and $P(z',z)$ are the fecundity and survival/growth sub-kernels defined as:

$$F(z) = \; f_p(z) * a_p(z) * seed_n(z) * seed_{s1} \qquad \textit{eq. 5}$$

$$P(z',z) = s(z) * g(z',z) \qquad \textit{eq. 6}$$

Where $f_p(z)$, $a_p(z)$, $seed_n(z)$, $s(z)$ and $g(z',z)$ are the flowering probability, seed production probability of a flowering individual, number of seeds produced by a seed producing individual, survival probability and growth, described above in the "Vital rate models" section. To prevent extreme values, $seed_n(z)$ was limited to 515 which is about 3.8 times the maximum observed (=137).

To create long-term population growth rate for our populations, we iterated our IPMs several times for 10,000 timesteps. We used either the historical or future ARIMA models to create climate sequences. We also ran the IPMs for four different levels of shading (0, 2, 4, and 6). We did not include slope, soil depth or rockiness in our IPM simulations as our analyses of the vital rate models found that of the environmental covariates, only shading was included in the best models.

Next, we used an Individual Based Model (IBM) to investigate the short-term extinction probability for our populations. The structure of our IBM followed the structure of the IPM and vital rate models. We set our extinction threshold to 10 adult individuals as this is the minimal population size able to survive for longer time (T. Dostálek, pers. obs.). Using the forecasted climate anomalies from CHELSA, we forecasted population numbers from 2022 to 2100. To analyse if and how much climate change is speeding up extinction probability, we also forecasted the populations for an equal amount of time, using climate sequences simulated from the historical ARIMA models described above.

Results

Vital rate models

For all the vital rates (survival, growth, flower probability, seed probability and number of seeds) the model with the lowest AIC score included a climate-by-shading interaction. As such we show the results using poisson distributions with lambdas of 0, 2, 4 and 6 to simulate shading levels. These values symbolise a range of decrease, stable and increase in the shading level experienced by the populations, whose shading distribution during monitoring had a lambda ranging from 2.2 to 3.6 (Figure S1A).

For survival, flowering probability and number of seeds the selected climate variable was potential evapotranspiration (PET), whereas for growth and seed probability, the selected climate variable was precipitation. Shading had very small effect on the effect of climate on growth (Figure 1B). For flowering probability, and the probability to produce seeds higher shading levels increase the effect of climate, but we see no large difference of effect of climate across the two years before census considered in the analyses (Figure 1C&D). We do see changes of the effect of climate through the two years of climate before census in survival and number of seeds produced (Figure 1A&E). We see that PET can have a positive and negative effect on survival and seed number, depending on when it is. Moreover, we see that lower and higher shading levels lead to more variability in the response to PET in survival and seed number respectively. The full model summaries for the vital rates can be found in Supplement S3.

Our long term IPM shows that higher levels of shading results in higher stochastic population growth rate, λ_s (Figure 2). We also see that the effect of shading is a larger under most of the future climate models. However, under the RCP 4.5 scenario (Figure 2) three of the four climate models show significantly larger decreases in λ_s compared to the historical climate. Under the RCP 8.5 scenario this is true for all models (Figure S2).

In our short-term (until 2100) forecasts using individual based models, we see that almost all populations will drop below the extinction threshold (10 adult plants) before 2100 if there is no, or low shading. Here we present the results of our analyse using historical climate and the projected climate from the CMCC model. We choose to show the CMCC model projections, as our IPM analyses indicates this to be the second best for *D. austriacum*, in terms of population growth rate. The results of the other models, can be found in the Supplement (S5). Moreover, extinction will most likely occur faster due to predicted climate change (Figure 3). Ks will most likely go extinct, regardless of shading level or future climate scenario. Our IBM also shows that this would have been the case, even without climate change (Figure S5). Cr and Ru might be able to persist until 2100 under a shading level of 6. However, we only see persistence with the CMCC climate model for both populations (Figure 3), and MIROC5 for Cr (Figure S5). We also see stronger effects of shading for Hk, compared to the other populations (Figure S5).

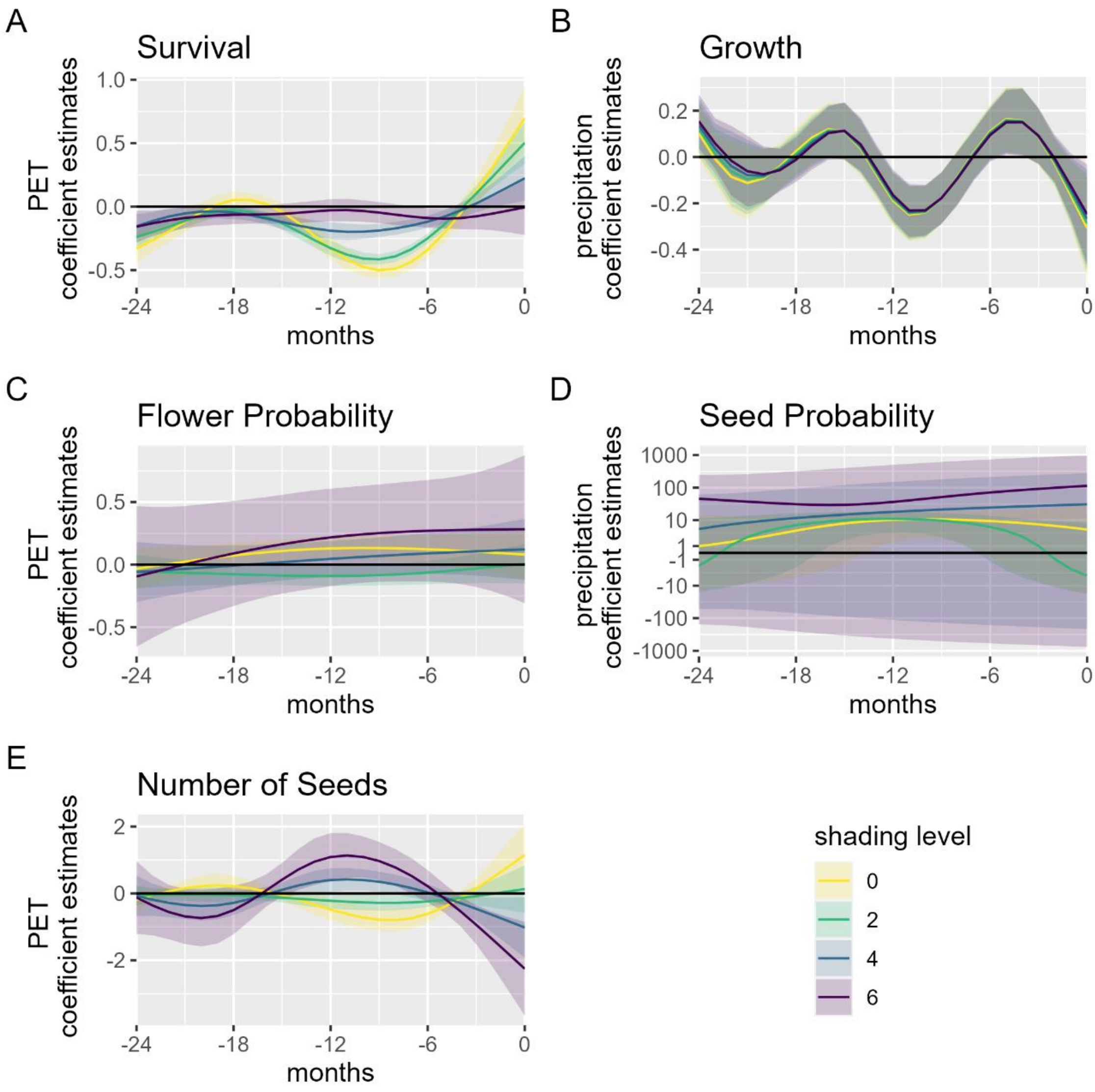


Figure 1. Effect of Potential Evapotranspiration (A,C,E) and precipitation (B,D) in the Functional Linear Models for survival (A), growth (B), Flowering probability (C), Probability of producing seeds for a flowering individual (D) and the number of seeds per seed-producing individual (E) for Dracocephalum austriacum.

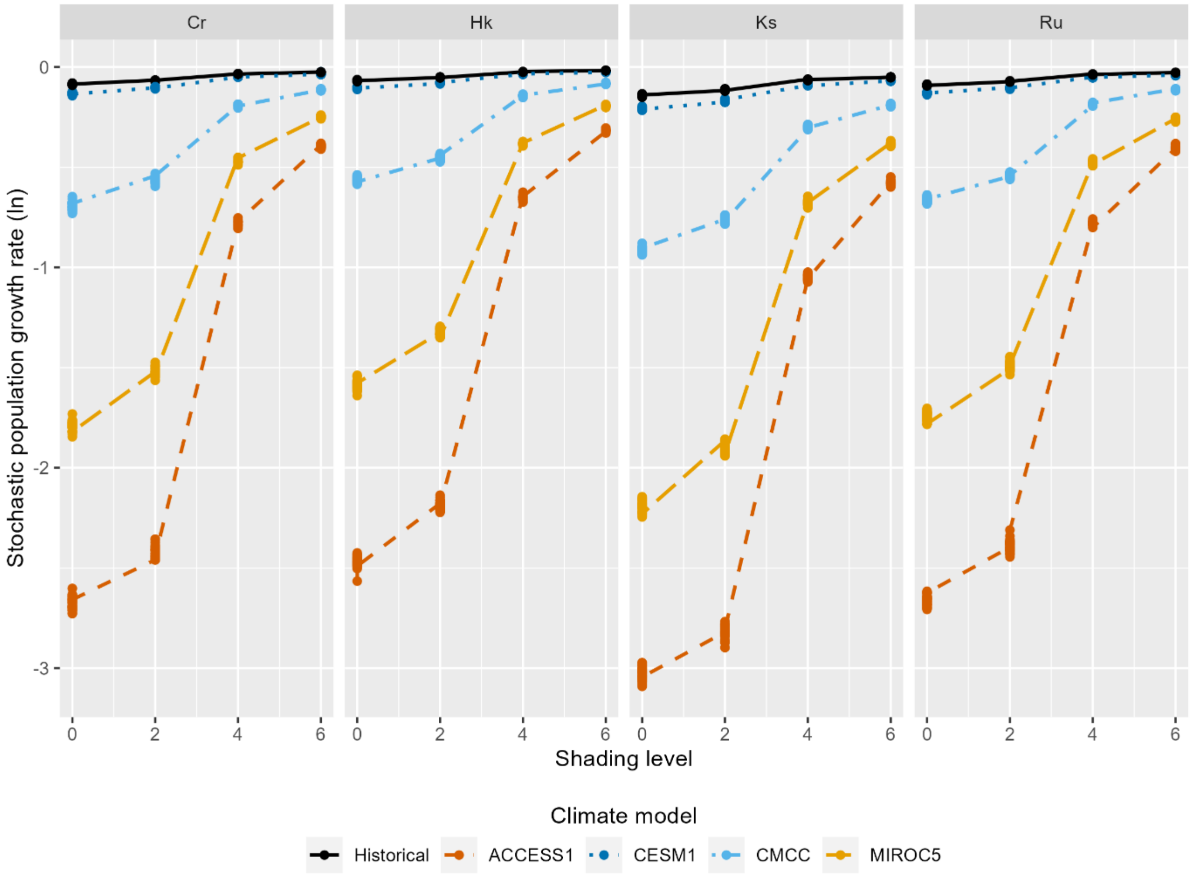


Figure 2. Long-term population growth rates of Dracocephalum austriacum predict large decreases of population sizes, but significantly less decrease under higher levels of shading. Stochastic population rates, calculated using long running integral projection models, and ARIMA models of the historical climate and 4 future climate projections under Representative Concentration Pathway scenario 4.5.

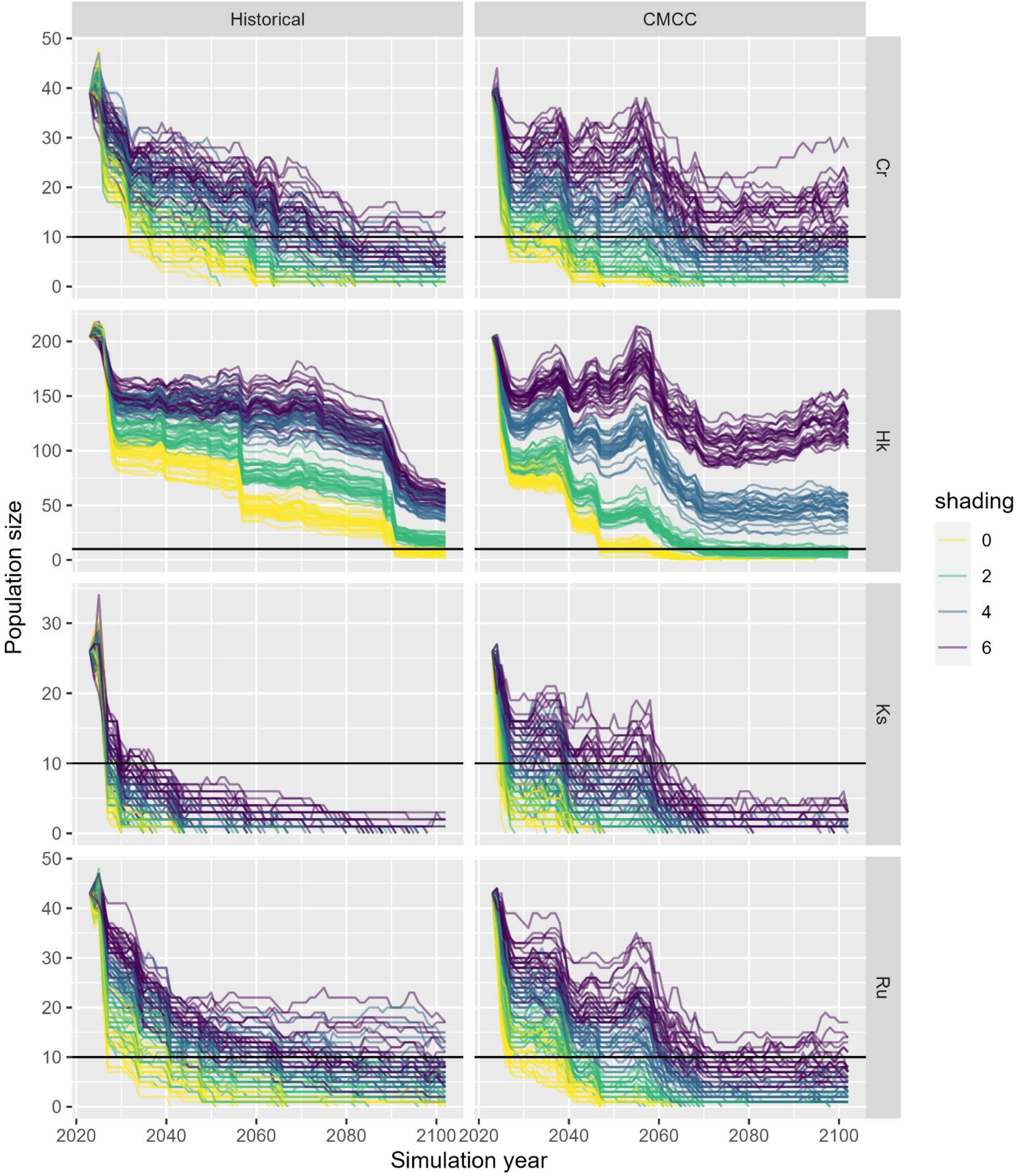


Figure 3. Most populations of Dracocephalum austriacum *are predicted to drop below extinction threshold (<10 individuals) faster under future climate, and with lower shading levels. Simulations were run from 2023 to 2100, using climate simulated from a historical ARIMA model or forecasted climate by the CMCC circulation model. Population simulations were done under different shading levels, using an Individual Based Model. Each line represents a separate simulation run (n=30 per shading level/locality/climate model).*

Discussion

With an increase in endangered and at-risk populations as well as species due to climate change (IPCC, 2014; Urban, 2015), the need for conservation actions has increased. However, it is important that we assess conservation actions, in the light of the projected changes in climate. Here we analysed a long-term dataset of four *Dracocephalum austriacum* populations. We investigated both the effect of climate and of several other (a)biotic factors on the populations. These populations have been under active management through the removal of encroaching interspecific individuals to reduce shading. We found vital rates with clear long-lasting climate effects. All vital rate models included an interaction of climate with herb and shrub shading. These outperformed all other vital rate modes with or without interactions. Contrary to the aim of conservation actions already in place, we found that higher levels of shading are actually beneficial for all the populations. This is true under current climate, but especially obvious for our projections under future climate. Nevertheless, almost all projections using forecasted climate show drastic decrease in population growth rate and earlier extinction.

Our results show that survival probability and number of produced seeds are mostly likely sensitive to two different consequences of herb and shrub encroachment. Specifically, these two vital rates show large differences in their sensitivity to climate, based on the level of shading. For survival probability, lower shading levels result in more variability, whereas number of seeds shows more susceptibility to climate with higher shading levels. Such climate and habitat interactions, leading to opposing trends in sensitivity and directional responses have been found in the literature before (Fernandes, Máguas, & Correia, 2017). We suspect that these opposing responses of survival and seed production in *D. austriacum* are being driven by two opposing consequences of encroachment. Conservation efforts for *D. austriacum* have focused on the removal of encroaching individuals to reduce the light competition (e.g., Dormann et al., 2020; Funk & McDaniel, 2010). However, shrubs also assist in soil moisture retention (Rickard, 1967), and removal will most likely decrease the water available to *D. austriacum* individuals. Our results indicate that the number of seeds produced is most likely limited by light availability, as under higher shading levels, the number of seeds produced becomes more sensitive to potential evapotranspiration (PET). On the other hand, survival is more sensitive to climate under lower levels of shading. This suggests that survival benefits from the presence of other herbs and shrubs, because of higher water availability. This hypothesis is supported also by personal observations during drought years, where most of the surviving individuals were located in more shaded and wetter areas.

The fact that both our long-, and short-term forecasts show a clear benefit of higher shading levels, despite contrasting effects of shading on the vital rate level, can most likely be explained by the difference in sensitivity of the population growth rate to the vital rates (Salguero-Gómez et al., 2016). Long-lived perennials are usually most sensitive to variation in survival. Survival varies less under higher levels of shading, which is beneficial to the stochastic population growth rate (Tuljapurkar, 1990) and thus results in better forecasts for the populations under higher shading levels.

Our study is also a great example of the importance of long-term studies in properly understanding population dynamics. In this study, we analysed a 20-year dataset of *D. austriacum*. This same dataset has been previously analysed, however, at that time, only four years of data were collected (Dostálek & Münzbergová, 2013). These four years, did not include very dry years, and as such no serious effects on plant survival were found and the variability in climate effects on vital rates was very small. Moreover, overestimation of seedbank dynamics resulted in inaccurate buffering of many (climate) effects (Dostálek & Münzbergová, 2013).

Although we did not find significant effects of pollen supplement on population growth rate in our previous study (Castro, Dostálek, van der Meer, Oostermeijer, & Münzbergová, 2015), there were significant effects on seed production. As this was done using models with our short term data with overestimated seedbank (Dostálek & Münzbergová, 2013), it might be possible that future climate changes might also affect pollinator communities and consequently *D. austriacum* population dynamics. More research will be needed to determine if these changes will be positive or detrimental for our populations.

Another study on *D. austriacum* population dynamics also found strong effects of climate on population dynamics and vital rates. Nicolè and colleagues (Nicolè et al., 2011) found effects of temperature and slope of the population on survival probability. However, they did not consider precipitation or PET, which our result show results in models with better predictive power than temperature. Moreover, the populations analysed by Nicolè et al. (2011) were located between 1300 and 2000 m asl (Bonin, Nicole, Pompanon, Miaud, & Taberlet, 2007), which is significantly higher than our populations (240-350 m asl). This makes direct comparison slightly more complicated. However, Nicolè et al. (2011) observed that *D. austriacum* occurs in patches with low competition, and speculate that shrubs and trees might have a detrimental effect on the populations. This is contrary to our findings, however, it is not uncommon to find contrasting climate effects across elevation (e.g., Dolezal et al., 2021).

Finally, our study also has implications for the conservation efforts of this species and possibly other species. Current conservation efforts of *D. austriacum* are focused on the removal of encroaching individuals that provide shading, under the assumption lower shading levels to be beneficial for the populations. This is in sharp contrast with our results, that indicate that low levels of shading will be detrimental for the perseverance of the populations. That we find such a contrast between current management strategies, and our results, suggests similar analyses might be needed for other species currently under management. For *D. austriacum*, we do not have many observations of high (>8) shading levels, despite our extensive dataset. Rather than removal of (almost) all encroaching individuals we therefore suggest more heterogeneous approach. We suggest that this approach focusses on preventing full encroachment, and strategic removal of encroaching individuals so patches of high shading remain as a refuge in cases of drought.

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Data availability

All the R-code used in the analyses in this article can be found here; https://github.com/SanneE1/Dracocephalum_pop_analysis. Data supporting this study are available at the authors upon reasonable request.

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Supplement

S1 Shading distribution

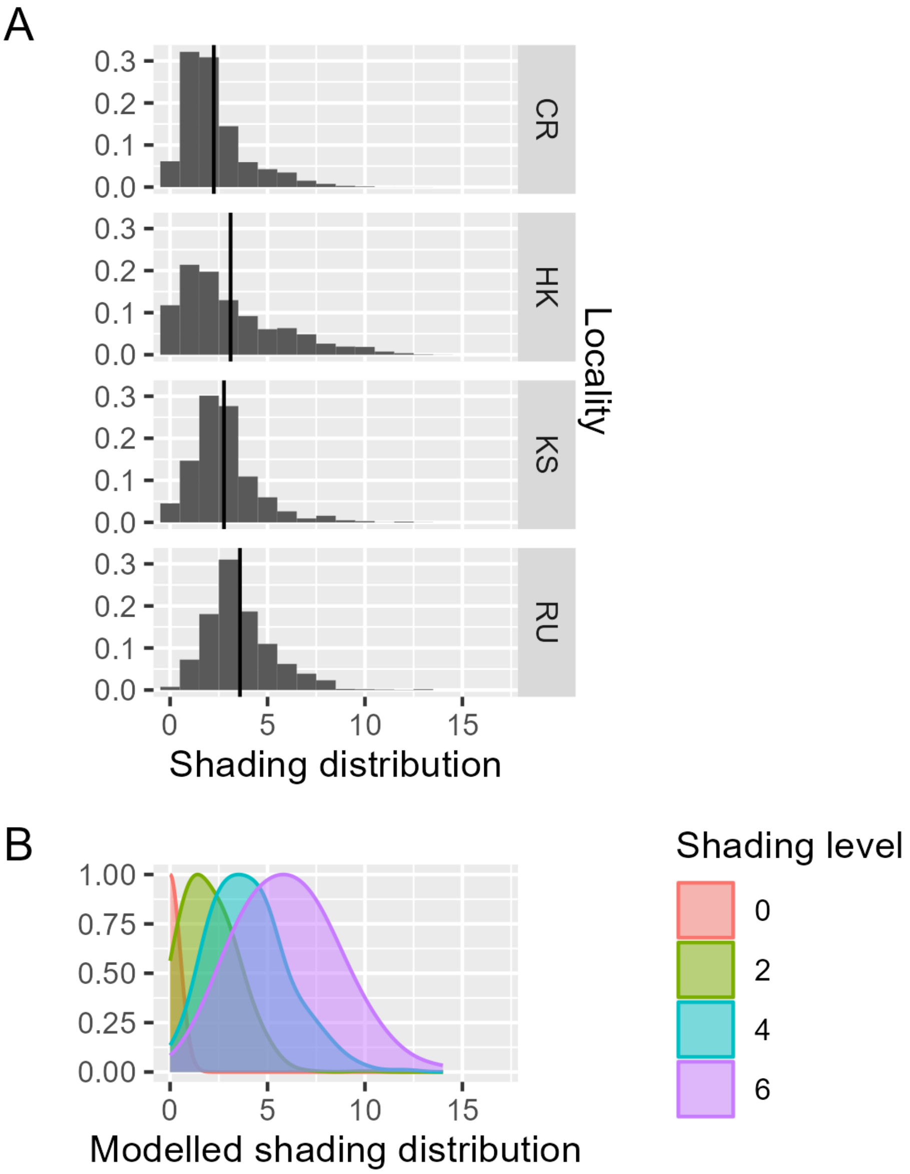

Figure S1. The shading distribution of the different localities is close to a poisson distribution with lambda of 2-4. A shows the shading distribution observed in the four different localities (Císařská rokle (Cr), Haknovec (Hk), Kodská stěna (Ks) and Radotínské údolí (Ru) during monitoring. B shows the distributions of the different shading levels used in the individual based model in the main manuscript.

S2 Climate model distributions

PET

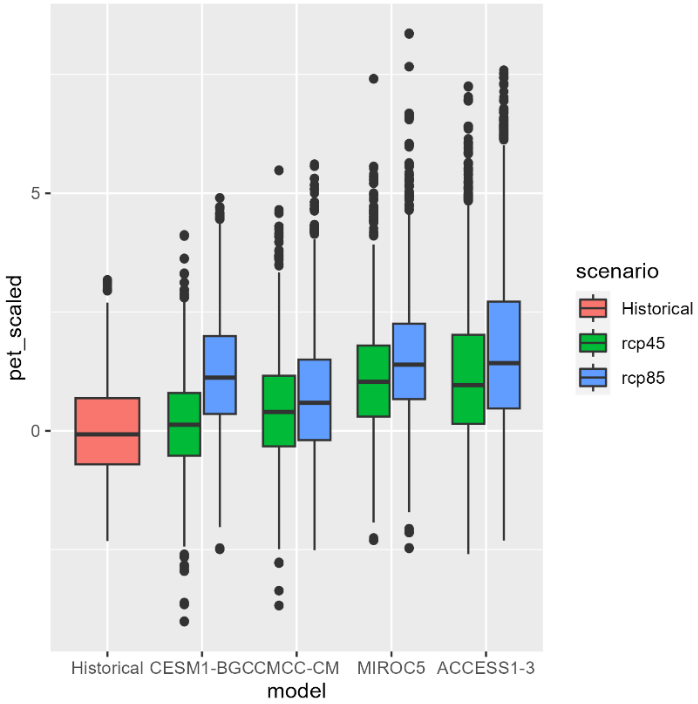

Figure S2. Mean and standard deviation of Potential Evapotranspiration anomalies show different increases from historical climate, in both the RCP 4.5 and 8.5 scenario.

Precipitation

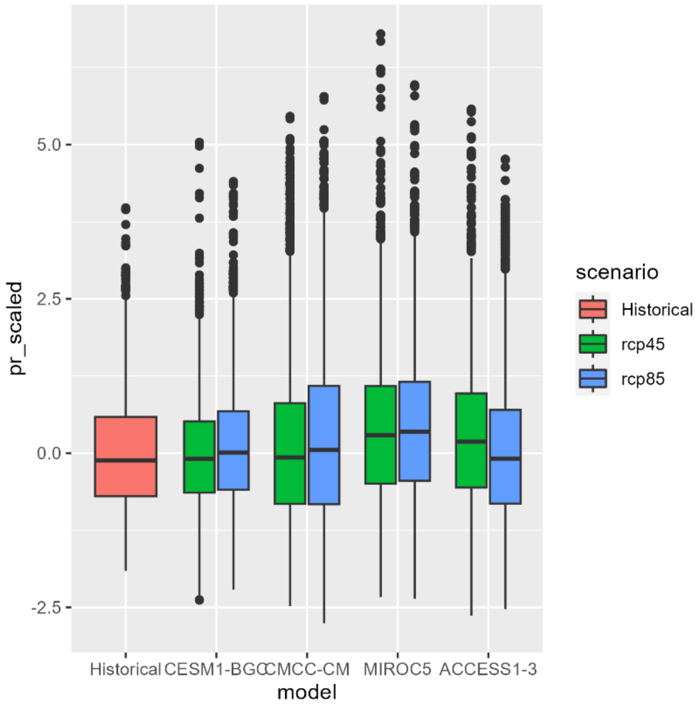

Figure S3. Mean and standard deviation of Precipitation anomalies show different increases from historical climate, in both the RCP 4.5 and 8.5 scenario.

S3 Vital rate models summaries

Survival

```
##
## Family: binomial
## Link function: logit
##
## Formula:
## survival_t1 ~ ln_stems_t0 + population + s(year_t0, bs = "re") +
##     te(lags, tot_shading_m, k = lag/3, by = pet_scaledcovar)
##
## Parametric coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)   1.84174    0.17323  10.632  < 2e-16 ***
## ln_stems_t0   0.95183    0.09532   9.986  < 2e-16 ***
## populationHK  0.42493    0.21702   1.958  0.05023 .
## populationKS -0.57463    0.20587  -2.791  0.00525 **
## populationRU  0.33272    0.27250   1.221  0.22209
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                            edf Ref.df  Chi.sq p-value
## s(year_t0)                               1.453  10.00   2.965  0.0295 *
## te(lags,tot_shading_m):pet_scaledcovar 13.546  17.01 168.594  <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.313   Deviance explained = 32.9%
## UBRE = -0.49772  Scale est. = 1         n = 2375
```

Growth

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## ln_stems_t1 ~ ln_stems_t0 + population + s(year_t0, bs = "re") +
##     te(lags, tot_shading_m, k = lag/3, by = pr_scaledcovar)
##
## Parametric coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)   0.37550    0.34855   1.077   0.2815
## ln_stems_t0   0.85774    0.01092  78.530   <2e-16 ***
## populationHK -0.01159    0.02821  -0.411   0.6812
## populationKS -0.03906    0.02848  -1.371   0.1704
## populationRU -0.10857    0.06527  -1.663   0.0964 .
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                           edf Ref.df     F p-value
## s(year_t0)                              7.802  10.00 7.832 < 2e-16 ***
## te(lags,tot_shading_m):pr_scaledcovar 14.868  15.34 2.144 0.00535 **
```

```
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.762   Deviance explained = 76.5%
## GCV = 0.22615  Scale est. = 0.22198   n = 2099
```

Flower probability

```
##
## Family: binomial
## Link function: logit
##
## Formula:
## flower_p_t0 ~ ln_stems_t0 + population + s(year_t0, bs = "re") +
##     te(lags, tot_shading_m, k = lag/5, by = pet_scaledcovar)
##
## Parametric coefficients:
##               Estimate Std. Error z value Pr(>|z|)
## (Intercept)   -1.7306     0.5162  -3.353 0.000801 ***
## ln_stems_t0    1.3681     0.2152   6.357 2.06e-10 ***
## populationHK   0.5443     0.4269   1.275 0.202341
## populationKS   0.7380     0.4678   1.578 0.114680
## populationRU  -0.0909     0.7974  -0.114 0.909246
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                     edf Ref.df Chi.sq  p-value
## s(year_t0)                        5.201  9.000 17.615 0.000763 ***
## te(lags,tot_shading_m):pet_scaledcovar 6.668  8.258  6.872 0.599962
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.353   Deviance explained = 33.4%
## UBRE = 0.086963  Scale est. = 1         n = 235
```

Abortion probability

```
##
## Family: binomial
## Link function: logit
##
## Formula:
## seed_p_t0 ~ ln_stems_t0 + population + s(year_t0, bs = "re") +
##     te(lags, tot_shading_m, k = lag/5, by = pr_scaledcovar)
##
## Parametric coefficients:
##               Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -21.9761    42.0983  -0.522   0.6017
## ln_stems_t0   -0.3525     0.3679  -0.958   0.3381
## populationHK   3.6370     1.5012   2.423   0.0154 *
## populationKS   0.3990     1.3283   0.300   0.7639
## populationRU   7.8611    39.8630   0.197   0.8437
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
```

```
## Approximate significance of smooth terms:
##                                        edf Ref.df Chi.sq p-value
## s(year_t0)                           5.419   9.00  5.271   0.114
## te(lags,tot_shading_m):pr_scaledcovar 16.108  17.06 11.111   0.853
##
## R-sq.(adj) =  0.516   Deviance explained = 59.7%
## UBRE = -0.0083258  Scale est. = 1         n = 131
```

Number of seeds

```
##
## Family: Gamma
## Link function: log
##
## Formula:
## est_seed_n_t0 ~ ln_stems_t0 + population + s(year_t0, bs = "re") +
##     te(lags, tot_shading_m, k = lag/5, by = pet_scaledcovar)
##
## Parametric coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)    0.4927     0.6492   0.759    0.455
## ln_stems_t0    0.8365     0.1427   5.861 3.46e-06 ***
## populationHK  -0.2914     0.4155  -0.701    0.489
## populationKS   0.2220     0.3923   0.566    0.576
## populationRU  -0.7187     2.1244  -0.338    0.738
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                        edf Ref.df     F p-value
## s(year_t0)                           1.044   5.00 0.806  0.0147 *
## te(lags,tot_shading_m):pet_scaledcovar 9.827  11.08 1.085  0.4066
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.652   Deviance explained = 77.2%
## GCV = 1.4211  Scale est. = 0.55483   n = 42
```

S4 Long term population growth rate

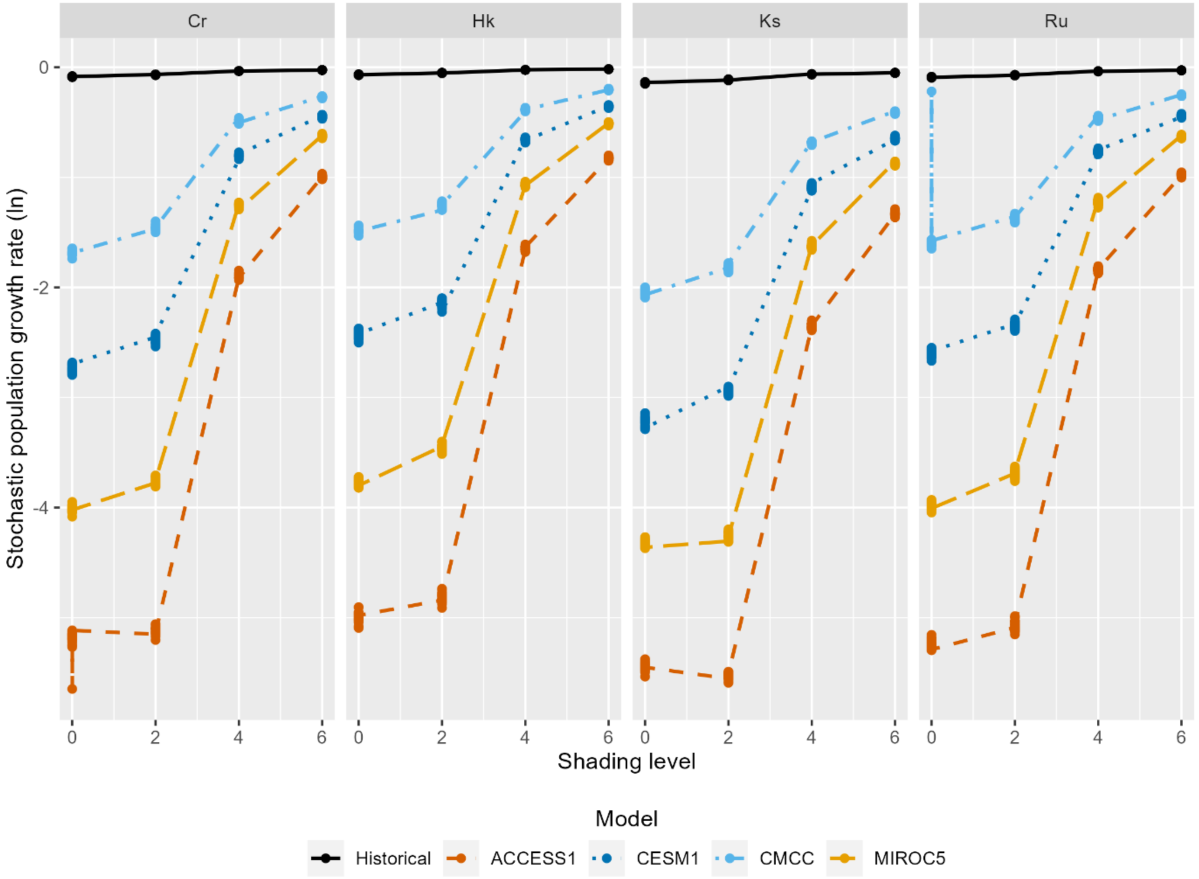

Figure S4. Long-term population growth rates of Dracocephalum austriacum predict large decreases of population sizes, but significantly less decrease under higher levels of shading. Stochastic population rates, calculated using long running integral projection models, and ARIMA models of the historical climate and 4 future climate projections under Representative Concentration Pathway scenario 8.5.

S5 Short term population projections

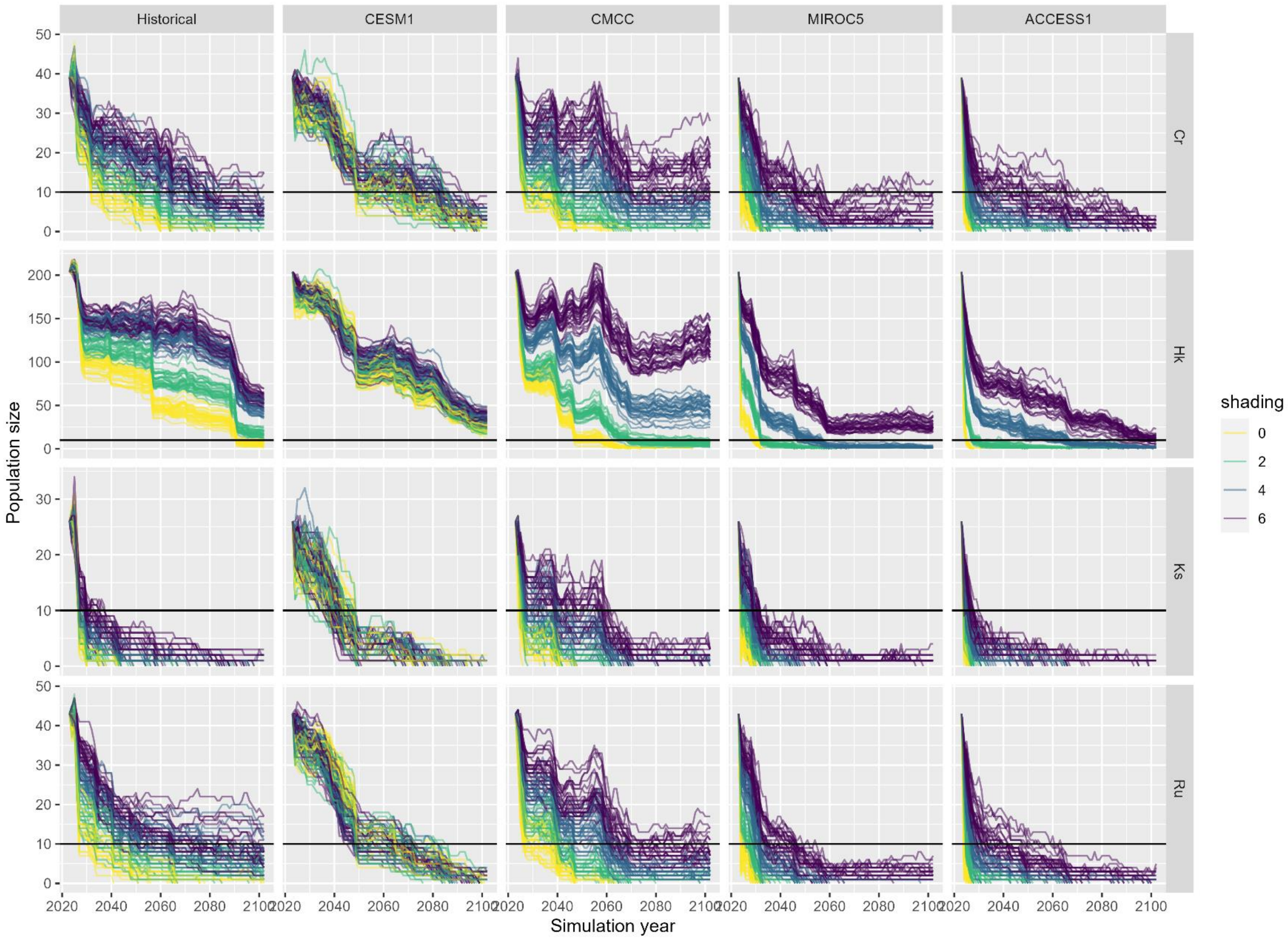

Figure S5. Most populations of Dracocephalum austriacum *are predicted to drop below extinction threshold (<10 individuals) faster under future climate, and with lower shading levels. Simulations were run from 2023 to 2100, using climate simulated from a historical ARIMA model or forecasted climate by the CESM1, CMCC, MIROC5 and ACCESS1 circulation models. Population simulations were done under different shading levels, using an Individual Based Model. Each line represents a separate simulation run (n=30 per shading level/locality/climate model).*

Chapter 5

Synthesis

Population models are a fundamental tool for ecologist to investigate the effects of climate on population dynamics. As these models are built upon vital rate regressions, it is important to use models that are as accurate as possible. This is a considerable challenge as the relationship between climate and vital rates is complex. Although much research has been done on the correlation between climate and vital rates, research in this dissertation shows that the timing of climate drivers is a component often overlooked or wrongly modelled. Considering the ongoing climate change and its threat to plant populations (Urban, 2015), it is important that we improve our understanding of climate and vital rate correlations and thus population dynamic forecasts.

Main findings

In chapter 2 I found a clear discrepancy between the timeframe of climate drivers considered in the literature, and those that best predict the vital rates of the four plant species I analysed. There is a clear preference in the literature to select recent (<12 months of census) climate drivers, in particular climate drivers during the most recent growing season. It was therefore surprising that the models with the best predictive power for the vital rates of my species had timeframes mostly located in the dormant season, and had longer lags (> 12 months before census). While the selection method used in my analyses requires more data than is usually available, I was able to link several climate driver time frames to physiological processes that can assist future research to select better timeframes.

Having shown that current literature uses mostly similar time frames, but model selection methods select more diverse timeframes, I investigated the effect on population level inferences when more diverse timeframes were included. I found that although the directional effects are dependent on many factors, the inclusion of temporally varied responses (TVRs) could significantly influence population growth rate. Interestingly I found that the effect of autocorrelation mediated through TVR was about 10x bigger than the direct effects of autocorrelation on population growth rate.

Finally, in chapter 4 I used a long-term dataset to investigate the effect of climate on four *Dracocephalum austriacum* populations. In the analyses I incorporate many of the suggestions from the previous two chapters. I show that the sensitivity of two vital rates to climate depends on the shading level, but that the most sensitive shading level is reversed for these two vital rates, indicating opposing mechanisms. I also show that under most climate scenarios the population growth rate of *D. austriacum* is significantly lower than under historical climate, resulting in earlier projected extinction.

Discussion

In Chapter 1 I briefly discussed the development of population models, and how ecologist have continuously tried to improve existing methods by implementing increasingly realistic assumptions. Trying to link climate to variation observed in population dynamics and models, has been an equally long process (Andrewartha & Birch, 1954; Sutherland et al., 2013). Early attempts focused on linking population level inferences (such as population growth rate) to *a priori* selected climate drivers (e.g., Aanes et al., 2002). These analyses were necessarily limited to population-level patterns and a small number of climate drivers, as tools and computational power were not available for more in-depth analyses. It is interesting though, that the development of more complicated models and analyses have been well received by population ecologists, but at the same time, researchers appear to have stuck to the same *a priori* selection of climate drivers, despite evidence pointing to other possibilities (Dalgleish, Koons, Hooten, Moffet, & Adler, 2011; Fox, Ribeiro, Brown, Masters, & Clarke, 1999; Groffman et al., 2001; Hacket-Pain et al., 2018).

It has mostly been recently that studies have started including climate drivers with more diverse timing (e.g., Scott, Uriarte, & Bruna, 2021; Shryock, Esque, & Lee Hughes, 2014). The development of several model selection methods and packages have played a great part in this trend (Bailey & van de Pol, 2016; Gasparrini, Scheipl, Armstrong, & Kenward, 2017; Ramsay & Silverman, 2005). Together, these methods and packages have helped develop our understanding that often, the *a priori* selected climate drivers are not necessarily the ones with the best predictive power. However, the research my co-authors and I have done in chapter 2 is the first that explicitly challenges the expectation that climate drivers in the most recent growing season drive the vital rates of herbaceous plants. Moreover, chapter 3 is the first in combining the topic of timing with the many other components that influence long-term population dynamics.

Being able to improve the predictive power of our vital rate models is always a goal we should be aiming for. However, as ecologists, discovering the actual mechanisms through which climate influences population dynamics is equally important. Including the possibility of long lagged climate drivers, as done in chapter 2, can increase the difficulty in finding these mechanisms. Lagged climate drivers can be caused through several mechanisms, many of which can be hard to decipher (e.g., resource depletion; Crone, Miller, & Sala, 2009; Tenhumberg, Crone, Ramula, & Tyre, 2018). However, lagged climate drivers caused by processes like leaf pre-formation (e.g., Diggle, 1997), are most likely easier to link. It is worth noting that being able to link the selected time frames in *Frasera speciosa* to leaf pre-formation, was only possible by the fundamental biological research done by one of my co-authors (Inouye, 1986). This highlights the importance of such hands-on biological research in the time of rapid methodical and technological advances in ecology (e.g., Marzluff, Knick, & Millspaugh, 2001; Palumbi, Gaines, Leslie, & Warner, 2003; Tay, Erfmeier, & Kalwij, 2018).

With climate change already influencing plant population dynamics in present day (IPCC, 2014), it is vital that we make the best of already existing datasets. In chapter 2 and 3 I show how we can improve our predictions, but in Chapter 4 I show how research into population dynamics can look like in a real dataset, when incorporating the conclusions of the two previous chapters. Moreover, I have shown that doing so, can allow us to tease apart complex climate relationships, with applicable implications in conservation. Unfortunately, for many species there will simply not be enough time to gather the required amount of data (10-20 years; Tenhumberg et al., 2018; van de Pol et al., 2016) for these type of climate analyses (Salguero-Gómez et al., 2015). Fortunately, there is a possibility that an increased reliance on spatial replication can decrease the required monitoring years (Compagnoni, Evers, & Knight, 2022). Although this method could reduce the number of years required, it requires a high time and resource investment in a very short time.

Whether we re-analyse old, long-term datasets, planned short-term datasets with enough spatial replication, or anything in between, using the correct climate drivers is still vital. Using less optimal climate drivers will results in less accurate population forecasts, especially when historical existing climate (auto)correlations changing under climate change (Di Cecco & Gouhier, 2018; IPCC, 2014).

Future directions

Next, I would like to share some of my thoughts on the areas of further research and new questions prompted by this dissertation.

First, although I have been able to link certain physiological processes to lagged climate drivers, other processes or mechanisms can be a lot harder to detect. It would require a lot of demographic and physiological research which might not be possible for every species. As such it would be interesting to investigate if there are proxies, such as life history traits, that can be used to predict appropriate timeframes. It would not be unexpected to find a correlation with traits in the fast-slow continuum (Salguero-Gómez et al., 2016). I have already started this effort through the supervision of a master thesis, but much work still needs to be done.

We have also now gained a thorough understanding of how temporally varied responses can influence population growth rates, thanks to the simulations in chapter 3. The strength of simulation studies is in the simplification, which allows us to thoroughly study the aspects of interest, without other complexities convoluting the mechanisms. However, this simplification also means that in real examples, the conclusions of the simulations are less clear. It would therefore also be interesting to further explore how population growth rates change using empirical examples. These will present different timings of climate drivers, and different forecasted climate sequences.

For the population analysis of *Dracocephalum austriacum*, there are still some interesting questions to address. It is clear that this species will suffer from climate change, and that current conservation actions will probably not be enough to save the populations from extinction. Previous efforts have been made to transplant small individuals from botanical gardens into the monitored, and unmonitored populations. If these efforts are to be repeated (*pers. comm.*, T. Dostálek), the population model build for chapter 4 could be used to investigate how many and how often transplants are needed to save the populations from extinction. Alternatively, it might be possible to use seed addition rather than transplants. This would require less effort, but a significant, yet to be investigated, amount of seeds would be needed.

Conclusion

We need to start considering different timeframes. Not doing so, might not only result in VR regressions with lower predictive power, but it could also lead to different population level conclusions. More complex vital rate regression models (Chapter 3) can also point us to different processes through which climate influences population dynamics. In the end, this dissertation has shown that climate driver timing can be complex and alter population dynamics, but it is absolutely possible and necessary to include these complexities in our research.

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Appendices

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Despite the fact that it’s only my name on the cover, this dissertation has never been the work of a single person. The role the people around me have played in getting this work completed is too big to put on a single page, but I am going to try anyway.

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Finally, I think it is right that I end with where it all started; thank you Mom, for your friendship and support. Thank you for always encouraging of a toddler’s whiney why’s, a teenager’s dreams and an adult’s hopes.

Authors’ contributions

Chapter 2

Evers, S. M., Knight, T. M., Inouye, D. W., Miller, T. E., Salguero-Gómez, R., Iler, A. M., & Compagnoni, A. (2021). Lagged and dormant season climate better predict plant vital rates than climate during the growing season. *Global Change Biology*, *27*(9), 1927-1941. doi: 10.1111/gcb.15519

Conception: 50%

Statistical analysis: 90%

Writing: 60%

Chapter 3

Evers, S. M., Knight, T. M., & Compagnoni, A. (*in revision*). The inclusion of immediate and lagged climate responses amplifies the effect of climate autocorrelation on long-term growth rate of populations. *Journal of Ecology*.

Conception: 50%

Statistical analysis: 90%

Writing: 70%

Chapter 4

Evers, S. M., Münzbergová, Z., Dostálek, T., (*in prep.*) Herb and shrub shading could delay extinction of the endangered *Dracocephalum austriacum.*

Conception: 33%

Statistical analysis: 100%

Writing: 80%

Publications and conference participations

Publications

Evers, S. M., Knight, T. M., & Compagnoni, A. (*in revision*). The inclusion of immediate and lagged climate responses amplifies the effect of climate autocorrelation on long-term growth rate of populations. *Journal of Ecology*.

Levin, S. C., **Evers, S.**, Potter, T., Guerrero, M. P., Childs, D. Z., Compagnoni, A., ... & Salguero-Gómez, R. (2022). Rpadrino: An R package to access and use PADRINO, an open access database of Integral Projection Models. *Methods in Ecology and Evolution*, *13*(9), 1923-1929. doi: 10.1111/2041-210X.13910

Compagnoni, A., **Evers, S.**, & Knight, T. (*under review*). Spatial replication can best advance our understanding of population responses to climate. *Ecography.* doi: 10.1101/2022.06.24.497542

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Levin, S. C., Childs, D. Z., Compagnoni, A., **Evers, S.**, Knight, T. M., & Salguero-Gómez, R. (2021). ipmr: Flexible implementation of Integral Projection Models in R. *Methods in Ecology and Evolution*, *12*(10), 1826-1834. doi: 10.1111/2041-210X.13683

Conference participation

2023

Oral presentation | 8th meeting of the Evolutionary Demography Society
"Including different timeframes for climate drivers, and why it matters for population dynamics"

Workshop co-organizer | 8th meeting of the Evolutionary Demography Society
"Analysis and interpretation of stage-structured population models via RCOMPADRE, Rage, and ipmr."

2022

Workshop organizer | SFE2-GfÖ-EEF joint meeting

"An introduction to modeling and synthesizing Integral Projection Models using the R packages ipmr and Rpadrino"

Poster presentation | SFE2-GfÖ-EEF joint meeting

"Immediate and lagged responses to climate can benefit or hinder populations"

Poster presentation | iDiv internal conference

"Immediate and lagged responses to climate can benefit or hinder populations" – Student poster prize – 1st place

2021

Recorded oral presentation | Ecological Society of America Annual Meeting

"Vital rates responding to different temporal climatic windows provide buffering for populations in an increasingly variable world"

Workshop co-organizer | Ecological Society of America Annual Meeting

"ipmr: An R Package for Easy and Flexible Construction and Interpretation of Integral Projection Models"

Workshop co-organizer | British Ecological Society Annual Meeting

"Analysis and interpretation of stage-structured population models via RCOMPADRE, Rage, and ipmr."

2020

Recorded oral presentation | British Ecological Society Annual Meeting

"Are we timing it right? Lagged and dormant season climate predicts vital rates in perennial plants better than growing season climate." – Student presentation prize, Runner-up

Curriculum vitae

Sanne M. Evers

Doctoral Researcher

ORCID: orcid.org/0000-0002-8002-1658

Education

PhD. in Ecology
Aug. 2019 – Present

Helmholtz Centre for Environmental Research (UFZ),
Martin-Luther-University Halle-Wittenberg &
German Centre for Integrative Biodiversity Research (iDiv)
Supervisors: Tiffany Knight & Aldo Compagnoni
Dissertation: *Exploring the complexities of climate driver timing: Insights at the levels of vital rates and population dynamics.*

MSc Biology
Feb. 2015 – Aug. 2017

Wageningen University & Research
Specialization: *Conservation and Systems Ecology*
Thesis: *"The correlation between primary production and predator-prey ratios"*
Internship: *"Mammal Inventory and habitat use in Ntchisi Forest Reserve, Malawi"*

BSc Biology
Sept. 2011 – Feb. 2015

Wageningen University & Research
Major: Ecology and Biodiversity
Minor: Wildlife Biodiversity

Research Experience

Guest Researcher
April-July 2022

Czech Academy of Science
The effect of climate and encroachment on the population dynamics of the endangered *Dracocephalum austriacum*

- Funded by the ConservePlants action of the European Cooperation in Science and Technology
- Assisted in the yearly census of multiple population *D. austriacum*

Research Assistant
2013-2017

Martin-Luther-University Halle-Wittenberg & German Centre for Integrative Biodiversity Research
Spatial interaction Ecology

- Digitizing published matrix population models into COMAPDRE
- Digitizing published integral projection models into PADRINO
- Using QGIS to enter individual level information (like size) on *carpobrotus spp.* populations from pictures

Supervision experience

Supervisor
2022-2023

MSc thesis
Titled: "The prevalence and duration of lagged climate effects across different plant histories"

Co-supervisor
2020-2022

3 MSc internships
6-week internships in the Spatial Interaction Ecology group at the German Centre for Integrative Biodiversity Research (iDiv)

Other Activities

Main organizer Nov. 2022	**“An introduction to modeling and synthesizing Integral Projection Models using the R packages ipmr and Rpadrino” workshop** • Writing workshop proposal • Organizing and leading a 4-hour pre-conference workshop at the SFE^2-GfÖ-EEF joint meeting. • Presenting on integral projection model theory and two R-packages • Writing tutorials
Co-organizer 2021-2023	**Several workshops that introduce the “ipmr” R package** Tasks; • present theory and packages Conferences; • Annual meeting of the Ecological Society of America, 2021 • Annual meeting of the British Ecological Society, 2021 • 8th meeting of the Evolutionary Demography Society, 2023
Phd representative March 2021 – March 202	**yDiv board** • Peer elected PhD representative at the iDiv graduate school advisory board. • Communication with the yDiv board and graduate students on current topics. • Sharing opinion and raising relevant topics as a PhD to the advisory board.

Languages & Program Skills

Dutch	Native speaker	**R**	Expert
English	Fluent in reading, writing and speech	**Git**	Advanced
German	Advanced in reading, writing and speech	**QGIS**	Basic

Declaration of independence / Eigenständigkeitserklärung

I hereby declare that I have written this doctoral thesis entitled "*Exploring the complexities of climate driver timing: Insights at the levels of vital rates and population dynamics*" independently and without outside help and that I have not used any sources or aids other than those indicated in the text. Text passages that have been taken over verbatim or in terms of content from works used have been marked as such by me. I further declare that I have never applied for a doctoral degree before. This doctoral thesis has not been submitted to the Faculty of Natural Sciences I - Life Sciences of the Martin Luther University Halle-Wittenberg or to any other scientific institution for the purpose of obtaining a doctorate.

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „*Exploring the complexities of climate driver timing: Insights at the levels of vital rates and population dynamics*“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Sanne Maria Evers, Halle (Saale), 13.04.2023