

# Grappling with uncertainty in ecological projections: a case study using the migratory monarch butterfly

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**Abstract.** Projecting species' responses to future climate conditions is critical for anticipating conservation challenges and informing proactive policy and management decisions. However, best practices for choosing climate models for projection ensembles are currently in flux. We compared including a maximum number of models against trimming ensembles based on model validation. This was done within the emerging practice of ensemble building using an increasingly larger number of global climate models (GCMs) for future projections. We used recently reported estimates on primary drivers of population fluctuations for the migratory monarch butterfly (*Danaus plexippus*) to examine how multiple sources of uncertainty impact population forecasts for a well-studied species. We compared mean spring temperature and precipitation observed in Texas from 1980 to 2005 with predictions from 16 GCMs to determine which of the models performed best. We then built tailored climate projections accumulating both temperature (in the form of growing degree days) and rainfall using both "complete" (all 16) and "trimmed" (best-performing) ensembles based on three emission scenarios. We built the tailored projections of spring growing conditions to assess the range of possible climate outcomes and their potential impacts on monarch development. Results were similar when mean predictions were compared between trimmed and complete ensembles. However, when daily projections and uncertainty were accumulated over the entire spring season, we showed substantial differences between ensembles in terms of possible ecological outcomes. Ensembles that used all 16 GCMs included so much uncertainty that projections for future spring conditions ranged from being too cold to too hot for monarch development. GCMs based on best-performing metrics provided much more useful information, projecting higher spring temperatures for developing monarch larvae in the future which could lead to larger summer populations but also suggesting risk from excessive heat. When there is a strong basis for identifying mechanistic drivers of population dynamics, our results support using a smaller subset of validated GCMs to bracket a range of the most defensible future environmental conditions tailored to the species of interest. Yet understating uncertainty remains a risk, and we recommend clearly articulating the rationale and consequences of selecting GCMs for long-term projections.

**Key words:** climate projections; *Danaus plexippus*; global climate model ensembles; growing degree days; Lepidoptera; nonstationarity.

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## INTRODUCTION

Projecting species' responses to global change is critical in a world that is rapidly transforming (Araújo and New 2007, Petchey et al. 2015, Houlahan et al. 2017, Dietze et al. 2018). Ecological projections may inform conservation actions and influence far-reaching policy decisions (Buckley and Csörgő 2017, Triviño et al. 2018). Understanding where threats occur and how these threats may be affecting species differentially throughout their range is particularly challenging (Yates et al. 2018). Further, when making projections, multiple sources of uncertainty accumulate substantial error that can be difficult to quantify and interpret. Here, we use the term "projection" to mean predictions generated from ecological process models that are parameterized with future conditions generated from scenario-based global circulation models (GCMs). Although the purpose of our study is to assess ecological projections in relation to population dynamics, we focus specifically on the choice of atmosphere–ocean coupled GCMs as there has been little recent guidance on this within the ecological community.

To explore climate model selection and projection approaches, we place these topics within the larger framework of both accumulating uncertainty and also system nonstationarity. The problem of properly accumulating uncertainty within modeling frameworks is one that is complex, but familiar to most ecologists (Iles and Jenouvrier 2019, Zylstra and Zipkin 2021). Nonstationarity is a more novel framework and indicates nonlinear dynamics or complex interactions that are often not estimable within the boundaries of initial model-building space and can thus cause substantial divergence between projected and observed outcomes (Mouquet et al. 2015, Rollinson et al. 2021). Nonstationarity is often the primary culprit when models fail to transfer across time or space (Yates et al. 2018). For a spatial example, the relationship between species abundance and a covariate, such as precipitation, may vary throughout a species' range, as is the case for Northern cardinals across North America (Rollinson et al. 2021). However, if a model is parameterized solely in one ecoregion (e.g., temperate zones) and then projected to a new region where the timing or amount of precipitation is

fundamentally different (e.g., deserts), it is highly unlikely that the same model parameterization would transfer to this new region. A temporal example is the study of forest composition in the eastern United States that shows a decades-long shift from oak to maple dominance (McEwan et al. 2011). Research shows that this shift has been facilitated by several stressors that have been changing over time, including the loss of the chestnut tree, growth in deer browse, and trends in climate over the past century. Thus, predictive models of forest composition developed during any subset of decades may not transfer well across time because the dominant drivers have been consistently shifting (Rollinson et al. 2021). This issue can expand beyond changes in parameter estimates and ultimately be rooted in uncertainty related to the underlying structure of the model itself (e.g., does the model contain the relevant covariates and is the relationship correctly captured mathematically). Nonstationarity fundamentally calls into question our ability to ever account for all the unknown factors that may become important when making forecasts, but it also provides a framework for exploring when projections fail, even if models performed well during the validation phase. Despite all these sources of uncertainty (ecological, climate, and system nonstationarity), long-term forecasts are useful for considering future ecological conditions given our current understanding of a study system. Nevertheless, these challenges require clarity on the underlying model assumptions within the context of climate-based projections (Araújo and New 2007, Braunschweig et al. 2013, Sohl 2014, Yates et al. 2018).

Climate scenarios themselves are developed by a global network of climate centers that collectively create dozens of individual—albeit not independent—GCMs (reviewed for ecologists in Harris et al. 2014, Baker et al. 2017). Yet there is rarely one GCM that best captures a specific region's climate, and some GCMs perform particularly poorly in different regions or for specific metrics (Araújo and New 2007). This variability in model performance had led to the practice of choosing an ensemble of GCMs based on how well their projections into the past most closely match the observed climate (Knutti et al. 2010, Harris et al. 2014, Baker et al. 2017, Karmalkar et al. 2019). Choosing this ensemble impacts both

the specific projections and associated uncertainty, but formal guidelines for making these choices remain scarce (Gould et al. 2014, Baker et al. 2017, Harris et al. 2018, Iles and Jenouvrier 2019). This knowledge gap is problematic because comparison studies have found that determining GCM performance for individual systems is particularly sensitive to the specific “skill” (or training) metric used for GCM validation (Reichler and Kim 2008, Snover et al. 2013, Sofaer et al. 2017, Karmalkar et al. 2019). The choice of skill metric can have substantial impact on the projected scenarios even when compared skill metrics are highly correlated (Braunisch et al. 2013). The fact that these validation studies are extremely sensitive to the choice of skill metric has led to multiple, but varying recommendations for building ensembles, such as using multiple test metrics (Braunisch et al. 2013), focusing on spatial pattern reconstruction (Nashwan and Shahid 2019), developing ensembles based on capturing structural differences between models (Lutz et al. 2016), and emphasizing multiple runs of individual models (Kay et al. 2015), or a hybrid of these approaches (Farjad et al. 2019).

Exercises in validation and ensemble-building presume that models with the best hindcast performance will also produce the best forecasts, which is sometimes not the case (Araújo and New 2007, Yates et al. 2018). Ultimately, the validation that hindcasts were successful in making projections can only be achieved by waiting for the opportunity to make those validations in the future. Most studies are not long term enough to achieve this, although a new focus on iterative, short-term forecasting provides a framework for confronting this issue (Dietze et al. 2018). One arena that has been able to most fully track the connection between past and future performance is within the climate modeling community itself; comparisons of past forecasts to eventual outcomes have been presented within IPCC reports and model forecasts were shown to be well within the originally projected uncertainty bands (Stocker et al. 2013). While the potential disconnect between past and future performance makes any attempt to project models beyond the initial observation space challenging, we suggest that system nonstationarity provides the best framework to explore when past performance may not

be indicative of future performance (Rollinson et al. 2021).

Another substantial issue for ecologists when choosing GCMs is that the vast majority of studies where ecological dynamics are projected into the future rely on bioclimatic covariates that emerge from correlative species distribution models (SDMs) (Araújo and New 2007, Ehrlén and Morris 2015). These, also known as “niche” or “climate envelope” models, have a weak basis for inferring underlying mechanisms (Kearney and Porter 2009, Braunisch et al. 2013, Ehrlén and Morris 2015). Given that ensemble model validations are highly sensitive to the skill metric used, the recommendation to use a more inclusive set of GCMs when building ensembles makes sense, even though that may bias the resulting ensemble (Braunisch et al. 2013) and also increases the incorporated uncertainties (Cavanagh et al. 2017). Indeed, most recent studies making ecological projection have used ensembles of 10–30 GCMs (e.g., Hotta et al. 2019, Jakoby et al. 2019, Laskin et al. 2019, Svancara et al. 2019) where until the early 2010s, it was much more typical to use 4–5 (Fordham et al. 2011). Robust evidence of dominant drivers is derived only through mechanistic ecological studies (Braunisch et al. 2013, Sofaer et al. 2017), which are challenging to produce and are rarely available for most species or systems. Yet when this robust evidence is available, the argument for building ensembles using a smaller set of GCMs validated with well-supported skill metrics is that it increases the potential for reducing bias (Braunisch et al. 2013) and better characterizes the uncertainty in climate projections (Cavanagh et al. 2017).

The potential to use climate covariates that emerge from mechanistic studies as a basis for forward projections raises another, related challenge. Specifically, that the typical suite of climate variables that are packaged and released by global climate centers may not include the environmental variables identified by mechanistic research as being the most relevant drivers for a particular species. For example, daily or monthly rainfall is a commonly available variable in most climate projection products, but not a metric estimating long-term drought. When mechanistic studies identify climate covariates not typically available, it may be necessary to tailor the GCM

output via calculations on raw data to align projection covariates with the most relevant metrics (e.g., Cook et al. 2010, Terando et al. 2012, Baker et al. 2017, Jenouvrier et al. 2019, Laskin et al. 2019) rather than use packaged projections that are released to the public. Of the hundreds of papers published in the last thirty years that make ecological projections, relatively few specifically tailor their climate projections based on the primary climate factors emerging from the results of mechanistic studies (but see Jenouvrier et al. 2012, Renwick et al. 2018, Dorado-Liñán et al. 2019, Wang et al. 2019).

We use the eastern migratory monarch butterfly (*Danaus plexippus*) as a case study to examine the specific consequences of having a more restricted vs. inclusive approach to assembling GCMs for making ecological projections and on our ability to interpret those results. Understanding where threats occur at global scales and how these threats may be affecting species differentially throughout their range is particularly challenging for migratory species (Hostetler et al. 2015). We leveraged an extensive history of mechanistic studies to identify the dominant climate drivers of year-to-year variability and associated nonstationarity in annual monarch population sizes during summer. Because one of the climate metrics that best predicts monarch abundances, growing degree days (GDD, explained below), is not among the variables provided with most climate data products, we tailored our GCM forecasts to specifically quantify this metric. We then compared projected conditions using inclusive vs. restrictive rules for ensemble development based on specific skill metrics most relevant to monarch biology.

#### *The monarch butterfly as a model system for global change ecology*

Monarch butterflies are distributed around the globe, but their largest single population and the one that has received the most attention is the migratory population in eastern North America (Gustafsson et al. 2015). This population completes a yearly, multigenerational round-trip migration that takes it from a small set of mountaintops in central Mexico, where individuals overwinter in mass aggregations, to as far north as southern Canada (Appendix S1: Fig. S1). Individuals that had flown south to Mexico the

previous fall begin the journey back north in February and generally make it as far as Texas and the surrounding region by mid-March. There, they lay eggs on milkweeds (sub-family Asclepiadoideae) and when those eggs hatch, the developing caterpillars feed, pupate, and emerge as adults in mid-April. Those adults then continue the northward journey to the monarch's primary, summer breeding grounds, which encompasses a northern band from approximately 38 to 50 degrees latitude east of the 100th meridian (Appendix S1: Fig. S1). This northern breeding population produces an additional 2–3 generations over the course of the summer. Beginning in mid-August, the final generation of the year starts a southward migration back to the same region in central Mexico where their great (or great-great) grandparents spent the previous winter (Gustafsson et al. 2015).

The eastern migratory monarch is an ideal subject for global change research because it is so intensively monitored with multiple programs focused on adult migration, juvenile development, and adult abundance throughout its range. Just in 2011, hundreds of volunteers spent an estimated 72,000 h (the equivalent of ~35 full-time worker-years) collecting data throughout North America, with about half of those surveys focused solely on the monarch as opposed to on butterflies generally (Ries and Oberhauser 2015). This level of public engagement is partially due to the monarch being a cultural icon and a flagship species for both insects and migration (Gustafsson et al. 2015). The monarch is also widespread, highly detectable, and easy to identify making data collection by the public particularly tractable. This has led to an intense focus on the monarch, as both a subject of science monitoring by the public (Ries and Oberhauser 2015) and of conservation concern (Gustafsson et al. 2015). Public concern for the monarch escalated after declines were identified in the eastern population (Brower et al. 2012). The population remains well below its previous maximum-observed size (Thogmartin et al. 2020) and has recently been declared deserving of protection under the Endangered Species Act, although it was not listed so that other species could be prioritized for management (USFWS 2020). This means that continual monitoring and reassessment of the monarch will remain a critical need both to understand its dynamics but also to

provide the US Fish and Wildlife Service the information they require for their yearly deliberations. These studies reveal that many of the biggest drivers of global change on biodiversity, including climate, land use, and agricultural practices such as chemical spraying impact the monarch (Oberhauser et al. 2017, Malcolm 2018, Wilcox et al. 2019) but that those forces change over time (Saunders et al. 2018, Zylstra et al. 2021).

Over the last two decades, spring temperature and rainfall in Texas consistently account for the majority of year-to-year variability in the end-of-summer monarch population size in their Midwest breeding grounds (Zipkin et al. 2012, Saunders et al. 2016, 2018, Crewe et al. 2019, Zylstra et al. 2021). Saunders et al. (2016) showed that the combination of mean average rainfall and mean temperature across Texas, as measured via GDD during the spring breeding season, best explained variability in that year's summer monarch population size in the Midwest, which largely determines the size of the overwintering population (Flockhart et al. 2017, Saunders et al. 2019). Although spring GDD and precipitation were the best predictors of monarch population size, this relationship was strongest during "typical" springs. In other words, monarch summer population sizes were more difficult to predict when spring weather was unusually hot, cool, wet, or dry (Saunders et al. 2016), indicating nonstationarity in the underlying ecological processes.

These climate predictors of yearly monarch population size emerge from models based on a priori hypotheses built on years of mechanistic research (e.g., Zalucki 1982, Nail et al. 2015, Ries et al. 2015a, Flockhart et al. 2017, Agrawal 2019, Crewe et al. 2019). When underlying ecological mechanisms, including the dominant climate drivers, have strong support in empirical evidence, it is unclear if the emerging practice of using the most inclusive set of GCMs for climate projection ensembles is sound or if that unnecessarily inflates uncertainty (e.g., Cavanagh et al. 2017). Here, we explore the issues of GCM selection and projection uncertainty using the monarch butterfly as a case study to achieve the following objectives:

1. Evaluate and select the best GCMs from a suite of 16 models that are most often used for North America to produce tailored

environmental projections for the monarch butterfly based on spring climate (temperature and rainfall) in Texas.

2. Implement the ensemble of models chosen in objective 1 ("trimmed" ensemble) and compare climate projections to those from a full set ("complete" ensemble) using different emission scenarios calculated for three time periods (near-future, mid-future, and end-century).
3. Based on both sets of results, compare the projected climate change implications for monarch spring breeding under different emission scenarios at different time periods in the future, while accounting for both uncertainty and nonstationarity.

## METHODS

### *Objective 1: Model evaluation and selection for "trimmed" ensemble*

To evaluate which GCMs should be retained in an ensemble of best-performing models, we compared observed climate in Texas to the projected hindcasts from a set of 16 GCMs acquired from the 5th iteration of the Coupled Model Intercomparison Project (CMIP5; see Appendix S1: Fig. S2 for a workflow). The CMIP project provides community access to consistent GCM implementations, including both hindcasts and future projections based on a set of shared scenarios of greenhouse gas emissions (Taylor et al. 2012). Most models produced under CMIP5 use GCMs calibrated from 1850 through 2005. Variability in the quality of historical climate products can also be a source of uncertainty when building and validating models (Baker et al. 2017), so we identified two sources of temperature and precipitation validation data for comparison. We used the Daymet dataset (Thornton et al. 2014) as one comparison source because it provides both daily temperature and precipitation products. In climate science, data are broadly categorized into two classes: observations and reanalyses. Observational data products, such as Daymet (Thornton et al. 2014), are solely modeled from ground-based measurements. On the other hand, reanalyses are also based on observational data but constrained by physical climate simulations. Here, we compared Daymet estimates to the

European Centre for Medium-Range Weather Forecasts' ERA-Interim reanalysis product (Dee et al. 2011) and CPC observations (Chen et al. 2008), reanalysis data for temperatures and rainfall, respectively. Results were nearly identical from both so we present only validation metrics from Daymet to obtain daily maximum and minimum temperatures and precipitation metrics from the same data products that are also independent of the GCMs themselves. These data are available at 1 km spatial resolution over North America from 1980 forward (Thornton et al. 2014) and so our validation period was set to 1980 (when Daymet starts) to 2005 (when CMIP5 GCM hindcasts end). Each GCM uses different spatial resolutions, and all datasets were harmonized to the coarsest GCM (Appendix S1: Fig. S2b). To evaluate model performance, we compared output from the 16 models for the temperature and precipitation variables to historical Daymet data during the monarch spring breeding period, from 22 March to 2 May (Ries et al. 2015a, Saunders et al. 2016). Our focal spring region is the entire state of Texas (Appendix S1: Fig. S1), the extent used for spring climate covariates in Saunders et al. (2016). We

selected GCMs based on minimizing deviations comparing Daymet observations to GCM predictions across the study region (Appendix S1: Fig. S2). We included all models for which the mean difference between model-simulated and observed values across all cells in the study extent during the 26-yr study period was no more than 1°C and 1 mm (for mean daily temperature and rainfall, respectively) with an estimated residual variance of no more than 2 standard deviations (SD) from the mean. We also included models that met these criteria for one of our climate metrics but not both, so long as the exceeding measure was no more than 2°C or 2 mm and had a measured variance of no more than 3 SD from the mean in the second variable (Table 1). We did not pre-specify how many GCMs should be included in the final ensemble.

**Objective 2: Model implementation to create “trimmed” and “complete” ensemble projections**

We selected three of the four future emission scenarios from the Representative Concentration Pathways (RCP) presented in the 5th IPCC report (2014): 2.6, 4.5, and 8.5 and made available to the modeling community within CMIP5.

Table 1. List of all candidate global climate models (GCMs), and performance metrics used to determine inclusion in our “trimmed” model ensemble.

GCM code	Spatial resolution	Origin	Temperature deviation (Model-Daymet)		Precipitation deviation (Model-Daymet)	
			Mean	SD	Mean	SD
<b>IPSL</b>	<b>3.7° × 1.8°</b>	<b>Institut Pierre-Simon Laplace; France</b>	<b>-0.38</b>	<b>2.06</b>	<b>-0.67</b>	<b>0.94</b>
<b>CMCC</b>	<b>0.75° × 0.75°</b>	<b>Centro Euro-Mediterraneo sui Cambiamenti Climatici Climate Model</b>	<b>-0.47</b>	<b>1.22</b>	<b>0.68</b>	<b>0.52</b>
<b>CCCMA</b>	<b>2.8° × 2.8°</b>	<b>Canadian Centre for Climate; Canada</b>	<b>2.0</b>	<b>1.62</b>	<b>0.71</b>	<b>0.89</b>
MIROC	1.4° × 1.4°	Atmosphere and Ocean Research Institute; Japan	1.11	1.58	1.1	0.56
BCC	1.1° × 1.1°	Beijing Climate Center; China	-1.4	1.65	1.13	0.95
MPI	1.8° × 1.8°	Max Planck Institute for Meteorology; Germany	0.54	2	1.4	0.78
<b>CSIROMK</b>	<b>1.8° × 1.8°</b>	<b>Commonwealth Scientific and Industrial Research; Australia</b>	<b>-0.72</b>	<b>1.78</b>	<b>1.45</b>	<b>0.83</b>
MRI	1.1° × 1.1°	Meteorological Research Institute; Japan	-1.86	1.33	1.8	0.42
<b>CCSM</b>	<b>1.1° × 1.1°</b>	<b>National Center for Atmospheric Research; USA</b>	<b>-0.55</b>	<b>1.62</b>	<b>1.98</b>	<b>0.95</b>
GFDL	2.5° × 2.0°	Geophysical Fluid Dynamics Laboratory; USA	-2.87	1.8	2.28	0.81
NCC	2.5° × 1.9°	Norwegian Climate Centre; Norway	-0.77	2.36	2.8	1.35
INM	2° × 1.5°	Institute for Numerical Mathematics; Russia	-2.28	2.48	2.82	1.01
CSIROBM	1.8° × 1.2°	Commonwealth Scientific and Industrial Research; Australia	1.31	1.8	2.86	1.35
CNRM	1.4° × 1.4°	Centre National de Recherches Meteorologiques; France	-1.68	1.83	3.21	1.33
HadCC	1.8° × 1.2°	Met Office Hadley Centre; UK (Center Coupled model)	-1.23	1.71	3.83	1.71
HadESM	1.8° × 1.2°	Met Office Hadley Centre; UK (Earth System Model)	-0.15	1.84	3.85	1.75

Notes: Boldface indicates selected models. All models listed are included in the “complete” ensemble.

Representative Concentration Pathways scenarios describe radiative forcing factors based on global greenhouse gas emissions that drive mean global temperatures (Van Vuuren et al. 2011, Taylor et al. 2012). The most pessimistic “business as usual” scenario is RCP 8.5, the projection if no action is taken to curb growth in emissions. The other extreme is RCP 2.6, the most optimistic of the emission scenarios and the one that most closely resembles the Paris targets (Sanderson et al. 2016, Jenouvrier et al. 2019). To explore the potential for nonlinear relationships between emissions and environmental outcomes, we also included RCP 4.5, an intermediate scenario. Some climate scenarios include an additional intermediate RCP (6.0), but since that was not available for all 16 GCMs, we did not include it among our scenarios.

We projected our two key climate variables into three future periods: early (2018–2038), middle (2040–2060), and end (2080–2100) of the 21st century. To do so, we created daily temperature and precipitation profiles during the monarch spring breeding season (22 March–2 May) as defined by Ries et al. (2015a) for each year of the three future time periods. For the precipitation profile, we accumulated spring rainfall (mm); for the temperature profile, we translated projected daily mean temperatures to GDD values and accumulated those during spring to develop a GDD profile for each year. GDD models convert daily temperature values into metrics relevant to ectothermic organismal growth rates (Ikemoto and Takai 2000). Specifically, thresholds are set at a minimum temperature where some growth is evident and a maximum where growth rates peak. One common way to calculate GDD is to simply subtract the lower threshold temperature from each day’s mean temperature or from the maximum developmental threshold, whichever is lower. For example, the lower and upper developmental thresholds for monarchs are 11.5°C and 33°C, respectively (Zalucki 1982). Thus, a day with an average temperature of 21°C adds 10.5°C to the accumulated GDD for a location (but an average temperature of 34°C would also add 21.5°C since 33°C is the upper threshold). Ectothermic organisms require a specific number of GDD to reach each developmental milestone. Monarchs must accumulate 323 GDDs in order to develop from an egg to an adult, and this usually occurs over a

period of 3–4 weeks (Zalucki 1982). GDD models rarely account for temperatures that become so hot that they inhibit growth, but laboratory studies show that daytime temperatures that peak above 38°C begin to have negative impacts on monarch development (Nail et al. 2015).

We present both trimmed and complete ensemble projections showing the mean and annual variability in temperature and precipitation during each of the three time periods for each emission scenario. Results in Saunders et al. (2016) and Zylstra et al. (2021) demonstrate that it is a combination of temperature and precipitation conditions that drives annual monarch population sizes, so we examine the bounding box of that combination of factors in two-dimensional space to capture projection variability.

## RESULTS

During the model evaluation period (1980–2005), the overall spatial patterns of temperature and, to a lesser extent, precipitation generally matched those projected by models (Figs. 1a, 2a respectively compared to Figs. 1b–q, 2b–q). The observed temperatures across Texas showed a latitudinal gradient ranging from ~28°C in the south to ~8°C in the north (Fig. 1a). All 16 GCMs captured this north-south gradient in temperatures (Fig. 1b–q), although most temperatures predicted by the model were cooler (by up to 6°C) than actual observations (Fig. 1d, e, p, q; Table 1). In contrast, precipitation followed a more variable gradient along both latitude and longitudinal bands with wetter conditions in the east (often more northeast) and drier conditions in the west (often further south). Most models also captured the rainfall gradient (Fig. 2a, but see Fig. 2j). There were larger discrepancies between observed and simulated precipitation values compared to temperature (Fig. 2). Most models over-predicted precipitation (with rates up to 8 mm/d greater than in Daymet, as in Fig. 2i), while only one model under-predicted (with rates up to 2 mm/d lower than in Daymet, Fig. 2c).

Five out of the 16 candidate models were selected to generate future climate predictions for monarch spring breeding in our trimmed ensemble based on our selection criteria (Table 1). Although we did not set the number of GCMs to include in our final ensemble, five is a

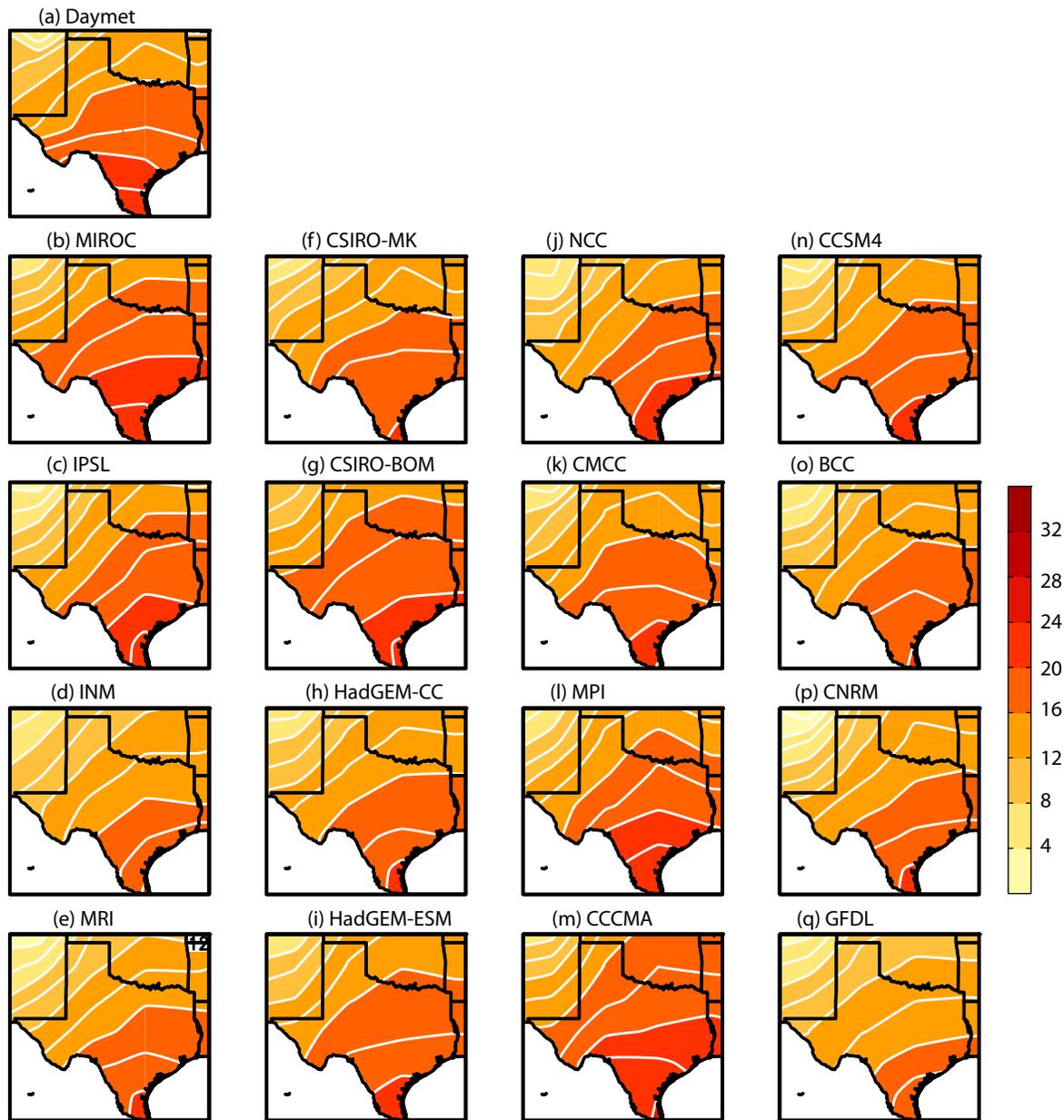


Fig. 1. Surface temperature (°C) averaged over 22 March–2 May from 1980 to 2005 from the (a) Daymet observations, and 16 atmosphere–ocean general circulation models (b)–(r), which are described in Table 1. Contours denote 2°C intervals.

number that is consistent with recommendations for achieving a reasonable balance between allowing a small number of models to dominate and swamping out differences between models by choosing too many (Fordham et al. 2011). To examine the variability in model performance,

we mapped the differences between observed and projected metrics across the study region for all 16 GCMs for both temperature (Appendix S1: Fig. S3) and precipitation (Appendix S1: Fig. S4).

To demonstrate how both temperature (measured in GDD) and accumulated precipitation

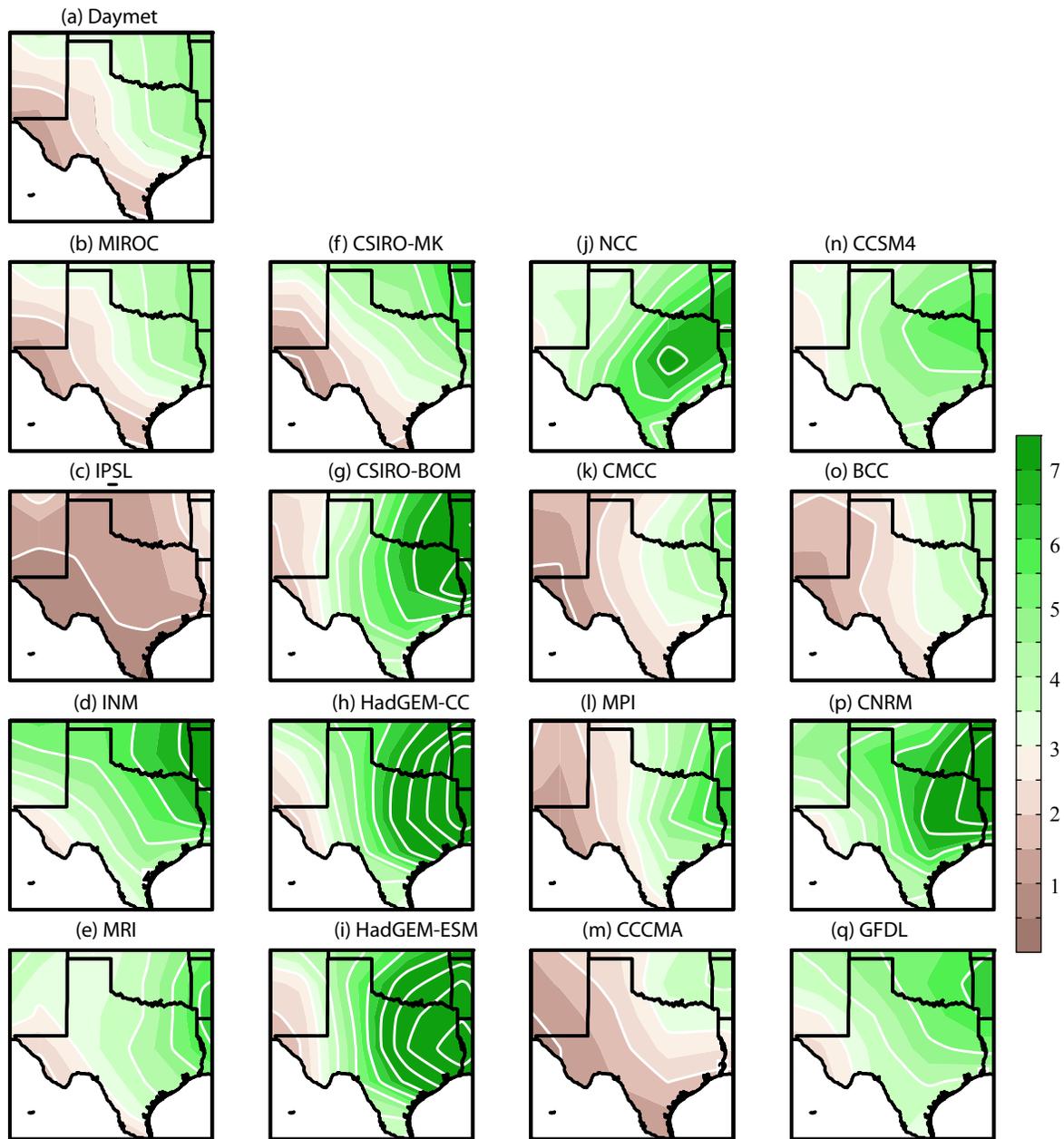


Fig. 2. Precipitation rate (mm/d) averaged over 22 March–2 May from 1980 to 2005 from the Daymet observations (a) and 16 atmosphere–ocean general circulation models (b)–(r) which are described in Table 1. Contours denote 1 mm/d intervals.

varied among the 16 models for each evaluation year (1980–2005), we present those along with observed values (Fig. 3). Given that our focal environmental covariates were cumulative over the season (i.e., both rainfall and GDD are summed from daily values across the spring

season), there were substantial discrepancies among model projections that accumulate over time (Fig. 3) even though the differences were minor when assessing mean daily values (Figs. 1, 2, Appendix S1: S3, S4). Observed yearly values (open, black circles in Fig. 3) overlap predicted

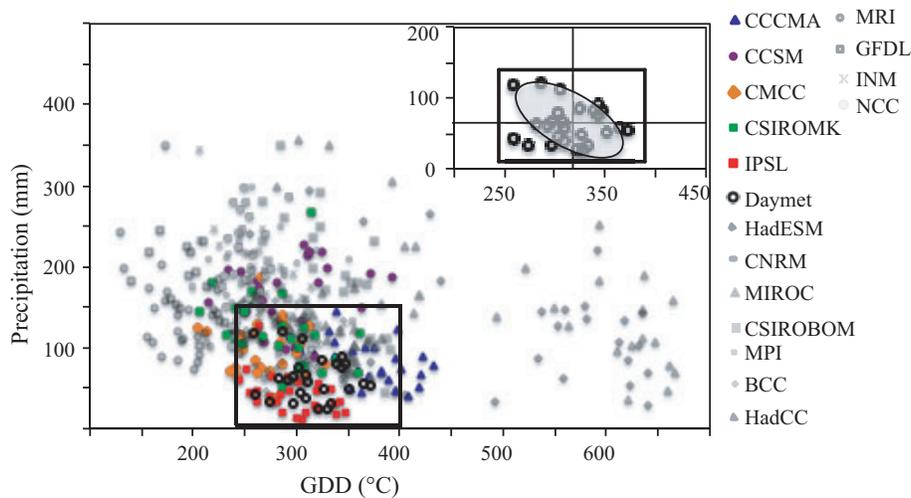


Fig. 3. Average springtime GDD (°C) and precipitation (mm) in Texas from 1980 to 2005 estimated by Daymet (open, black circles) and for 16 GCMs. Five selected GCMs (CCCMA, CSIROMK, CCSM, CMCC, and IPSL) are displayed in colored symbols, excluded GCMs are in gray. Inset also displays 1980–2005 observed GDD and precipitation (Daymet), the cross hairs indicate the 26-yr mean for GDD and precipitation. The oval shaded region encloses the climate space where the year-specific predictive accuracy of monarch counts in Illinois is high, based on Saunders et al. (2016). A box duplicating the bounding box of the inset is also shown on the main figure for reference.

values much more from our trimmed ensemble (colored symbols in Fig. 3) compared to the 11 models that were excluded (gray symbols in Fig. 3).

Mean projections for temperature and precipitation are similar for trimmed and complete ensembles across scenarios and timeframes (Fig. 4), but substantial differences accumulate through time, especially when uncertainty is integrated into the projections (Fig. 5). Generally, mean projected changes were similar between ensembles, although mean projections from the complete ensemble tended to show slightly lower than average temperatures (Fig. 4a–i) and drier conditions (Fig. 4j–r) compared to the trimmed ensemble. Our trimmed ensemble predicted that temperatures will become, on average, warmer (by 1–6°C) across Texas, depending on the scenario and projection period (Fig. 4a–i). However, the most substantial increase in projections was isolated to the late 21st century under the most extreme (RCP 8.5) scenario (Fig. 4i). Predicted changes in precipitation patterns were minor, but indicated slightly wetter futures in the near-term and the middle of the 21st century under mild and moderate emission scenarios.

However, under the extreme emission scenario, minor drying occurred in the near-term and middle of the century (Fig. 4j–o). Later in the century, a stronger gradient is projected to develop, with wetter conditions in the northeast portion of Texas and drier conditions in the southwest (Fig. 4p–r). While average projections across Texas were roughly similar for trimmed and complete ensembles (Fig. 4), the projected uncertainty was substantially greater using the complete ensemble when compared to our trimmed ensemble (Fig. 5).

## DISCUSSION

Projecting the climatic conditions that developing monarch larvae may experience in their current spring breeding range over the next several decades rests on several assumptions. These include the specific emission scenarios considered and the appropriateness of the underlying climate model structure used to make those projections. By considering the full spectrum of global climate emission scenarios, using both complete and trimmed GCM ensembles, we identified a range of potential outcomes relative

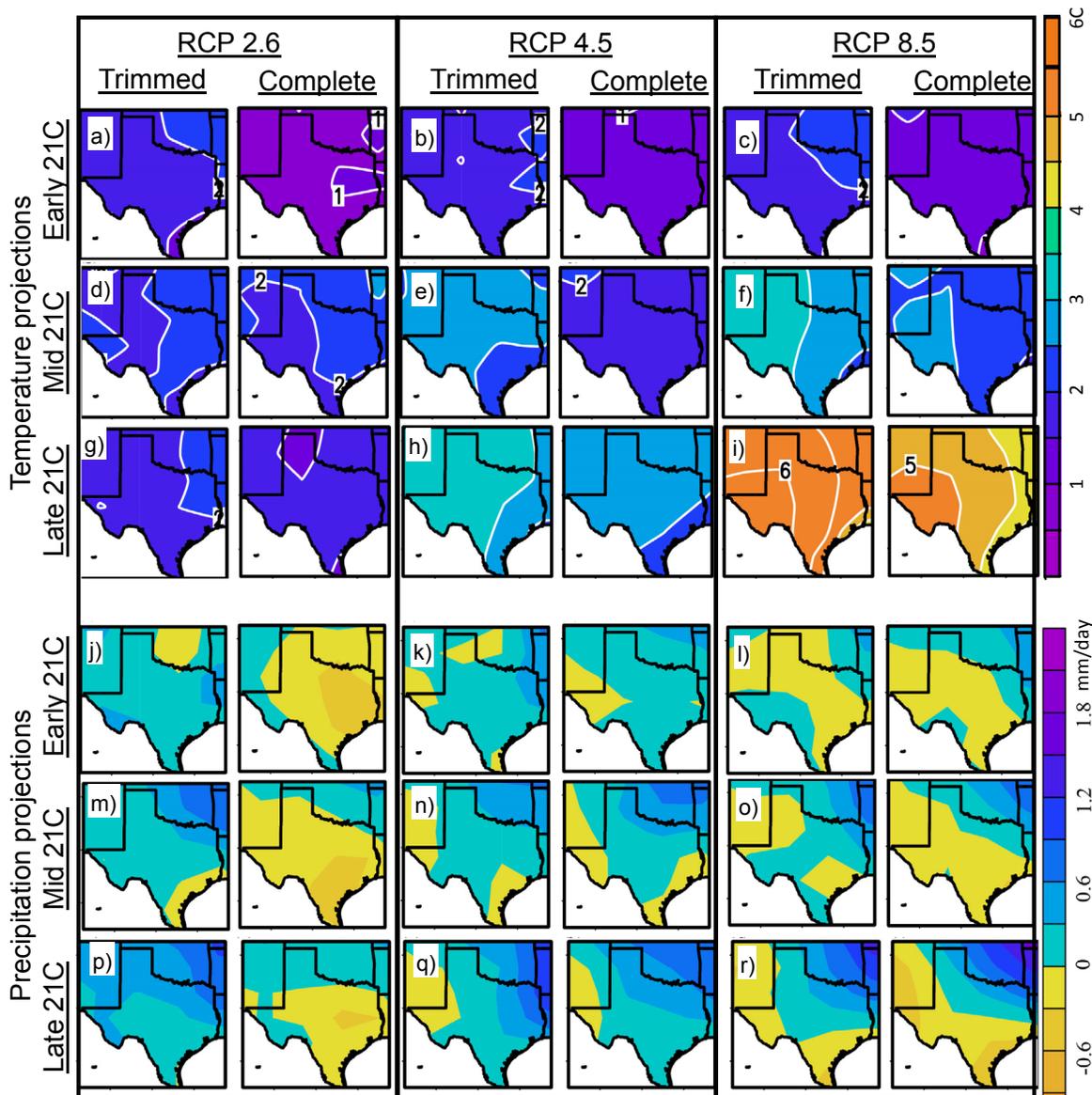


Fig. 4. Predictions for changes in mean springtime surface temperature (a–i) in °C and mean springtime precipitation (j–r) in mm/d for different project periods (rows). Results are shown for different emission scenarios (columns) and also with “trimmed” (5-model) and “complete” (16-model) side-by-side for comparison (left side and right side, respectively).

to future developmental conditions for monarch larvae during the critical spring breeding phase of their annual migratory cycle (Appendix S1: Fig. S1). As expected, the average for both trimmed and complete-model outcomes showed a gradual and similar increase in overall mean temperature and an increased variability in

precipitation, with the pessimistic RCP 8.5 “business-as-usual” scenario causing the most extreme changes by the end of the century (Fig. 4). Yet presenting uncertainty estimates around the overall means paints a much starker picture of differences between projections emerging from the complete and trimmed ensembles

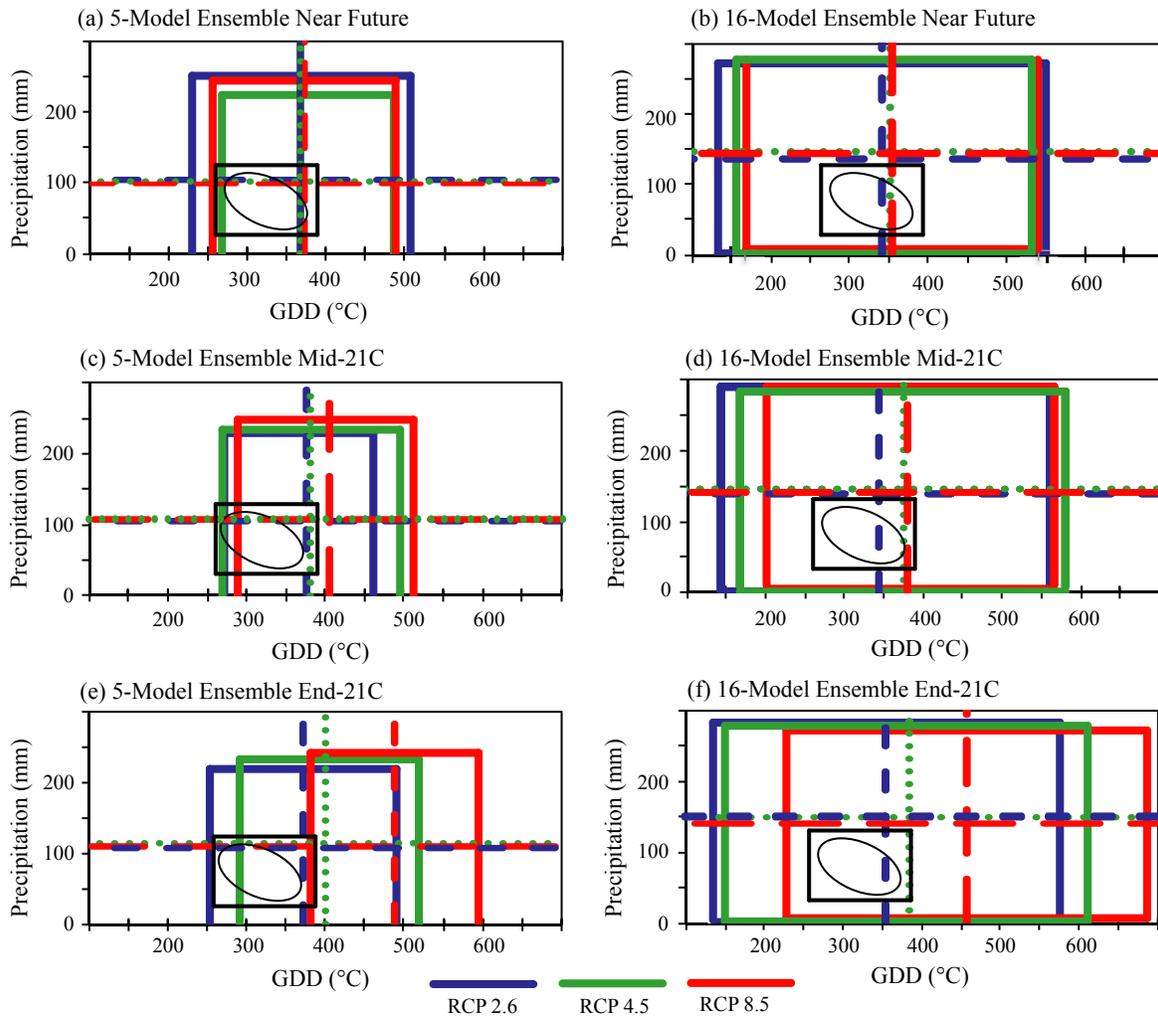


Fig. 5. Mean (cross-hairs)  $\pm$  2 SD (colored boxes) of projected GDD and precipitation in Texas's spring in the near future (2018–2038), mid-21st century (2040–2060), and end-21st century (2080–2100). Variability in projections are based on global warming simulations under RCP2.6 (blue box), RCP4.5 (green box), and RCP8.5 (red box) scenarios from selected 5-model ensemble (panel left) and complete 16-model ensemble (panel right). In each panel, the black box shows bounds the same conditions as the inset box in Fig. 3 (indicating range of 1980–2005 conditions). The oval from Fig. 3 is also reproduced and indicates the range of mean GDD ( $^{\circ}$ C) and total precipitation (mm) in Texas springs that had the highest predictive accuracy of monarch population size in their summer breeding grounds based on Saunders et al. (2016).

(Fig. 5). The complete (16-model) ensemble produced a range of projected uncertainty so expansive that it is impossible to predict whether the climate will generally be too cold or too hot at the end of the century for spring development (Fig. 5f). In contrast, the ensemble of the five best-performing models projected distinct differences at the end of the century between the three

emission scenarios (Fig. 5e), but not in earlier time periods (Fig. 5a, c). Only in the trimmed set of models did we demonstrate a clear divergence of predicted outcomes, whereas in the complete ensemble, no obvious trends were predicted, only increased variability (Fig. 5f).

Our findings are similar to that of Cavanagh et al. (2017), who demonstrated that a trimmed

and complete ensemble of future projections of Antarctic sea ice extent showed similar means, but vastly different ranges of uncertainty. The authors concluded that any ecological application of their predictions may only be meaningful when considering a trimmed set of models. However, trimming GCMs may elicit concerns about “cherry picking” results or attempting to proactively minimize uncertainty. In confronting these concerns, future approaches could follow a path in between those two extremes. One straightforward approach would be to simply present results from multiple approaches to ensemble building (e.g., complete vs. trimmed) as we do here. Until relatively recently, few ensemble models have been implemented in ecological studies due, in part, to computational constraints (Lutz et al. 2016). With ever-increasing computational capacity, multiple approaches of building ensembles are more attainable, and the presentation of multiple modeling scenarios promotes a more transparent, reproducible approach to scientific investigation.

Currently, we are able to accurately predict summer monarch population sizes only for springs that would be considered “typical” in our modern climate (Saunders et al. 2016, illustrated by the oval insets in Figs. 3, 5), which indicates nonstationarity in model projections. Despite the challenges of projecting specific monarch population sizes, mechanistic studies of monarchs allow us to consider the potential consequences based solely on our knowledge of their measured physiological responses to a range of temperature conditions. For instance, we showed that under the RCP 8.5 “business-as-usual” emission scenario, spring growing conditions could get substantially warmer and, in some years, could provide enough energy to allow two broods to develop during a moderately expanded spring season. This is because a monarch egg requires 323 of accumulated GDD to develop into an adult (and so 646 GDD to produce two broods); projections from the trimmed ensemble suggest some spring breeding windows could provide up to 600 GDD (Fig. 5e). To date, the hottest spring temperatures have not been associated with larger summer population sizes, on average (Saunders et al. 2016, 2018), but there has also been no historical analog to a year in which two generations could be produced during a single spring breeding season.

Although the possibility of two generations in spring is purely speculative, if it were to occur, it could substantially increase spring recruitment and, subsequently, could lead to larger peak summer population sizes. Previous work has shown that summer monarch population sizes are primarily driven by spring conditions (Saunders et al. 2016, 2018) and that there is a correlation between spring population size and summer population growth (Ries et al. 2015a, Inamine et al. 2016). Alternatively, increased spring temperatures could have negative impacts on larval development. Larval mortality rates can increase when daytime temperatures reach highs of 38°C (Nail et al. 2015), which will become more common at the end of the century, even during spring, according to our trimmed ensemble (Fig. 6). Of course, this neglects the potential for monarchs to shift their spring distribution or migratory timing to match ideal temperatures. However, this would also require an associated shift in their hostplant distribution and phenology, so future considerations of monarch adaptation to climate should consider future projections of their interacting species as well (Wisz et al. 2013). This highlights the complexities of considering future conditions, but also provides a framework to explore those in subsequent research.

For this study, we did not project future summer conditions in the Midwest because currently there is a lack of evidence indicating that summer climate conditions have a strong impact on monarch population growth (Saunders et al. 2016, 2018), although the hottest summers at the hottest sites in the Midwest showed a slight decline in local populations (Zipkin et al. 2012). However, the models that were used only include data through 2015 and 2015–2019 had many of the hottest years on record for global temperatures (Dunn et al. 2020). Indeed, recent work that included data through 2018 (Zylstra et al. 2021) indicated an increasing, but still secondary, impact of summer temperatures on monarch populations, suggesting that the influence of summer conditions may continue to grow in the future. An active, growing network of public scientists continues to monitor monarchs annually (Ries and Oberhauser 2015), which will facilitate model development and improvement (Dietze et al. 2018). As climate continues to

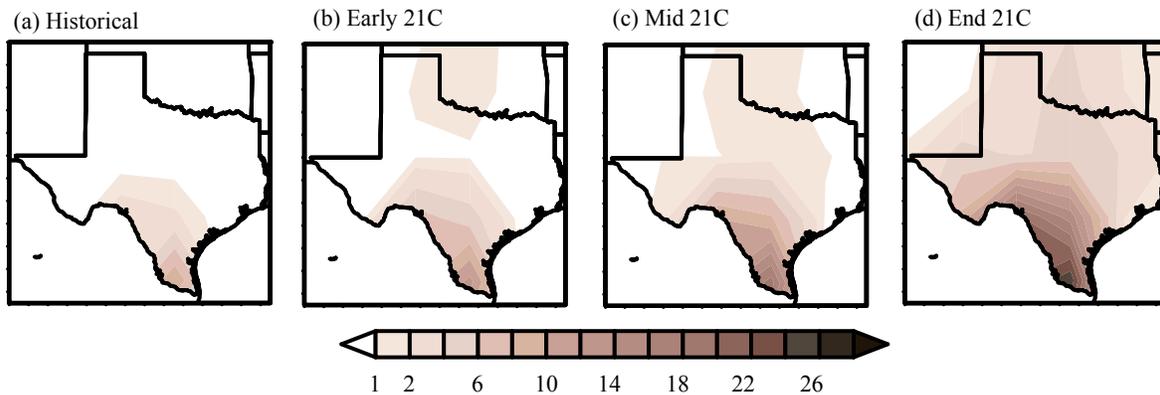


Fig. 6. Number of days with daily maximum temperatures greater than 38°C in spring (22 March–2 May) from CCCMA historical (1980–2005), and RCP8.5 global warming scenarios in early (2019–2038), middle (2040–2060), and end (2080–2100) of the 21st century.

change, we can iteratively expand the range of spring and summer climate conditions for which we can achieve reasonable model performance, better characterize nonlinear dynamics and thus more confidently make projections and account for nonstationarity. Further, other factors can be equally or even more important than climate; ideally, these additional conditions should also be factored into future scenarios and estimates of uncertainty (Sohl 2014). For monarch dynamics specifically, these would include factors such as milkweed availability and pesticide use (Thogmartin et al. 2017) but the most important factors are likely to change over time (Saunders et al. 2018, Zylstra et al. 2021). Despite these caveats, forecasts from our trimmed GCM ensemble are valuable in identifying the most realistic range of physiological outcomes for monarchs in spring, given our current knowledge. Based on projections from our trimmed ensemble, we suggest that monarchs may be able to produce up to two generations during their normal spring migration period by the end of the century under the most pessimistic emissions scenario (Fig. 5), but they may also be subject to adverse temperatures (Fig. 6) which could substantially limit their population growth in some years or push them further north during spring.

The recent trend toward including an increasingly large number of GCMs in ensemble predictions is reasonable when there is little mechanistic basis for projecting particular

environmental conditions (Braunisch et al. 2013), but it may also limit our ability to interpret the results (Cavanagh et al. 2017). When ecological models can be informed by mechanism and there is empirical evidence to support those mechanisms, as is true for the monarch butterfly, then trimming the number of GCMs in the ensemble used to make projections can help exclude excessive uncertainty by focusing on key environmental forecasts that have the most support. Ecological forecasts are essential to inform the public and decision-makers, but it is also imperative that we are able to interpret those projections, or they lack utility. Many modeling decisions impact our ability to account for multiple sources of uncertainty and influence the meaning of those projections (Zylstra and Zipkin 2021). As highlighted by many other authors (e.g., Araújo and New 2007, Braunisch et al. 2013, Sohl 2014, Cavanagh et al. 2017, Yates et al. 2018), these trade-offs between uncertainty and interpretability call for clear communication about modeling choices and how those decisions impact the interpretation of downstream results. Here, we provide an evidence-based approach for building GCM ensembles, while accounting for nonstationarity. We also demonstrate how these forecasts can inform our thinking about future environmental conditions despite considerable sources of uncertainty using a well-studied, long-distance migrant that sparks considerable public interest. Continually shaping

such approaches for other species and systems will help advance ecological and evolutionary research in the face of rapid global change.

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