

## TECHNICAL RESPONSE

## ECOLOGICAL GENOMICS

# Response to Comment on “Genomic signals of selection predict climate-driven population declines in a migratory bird”

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Fitzpatrick *et al.* discuss issues that they had with analyses and interpretation in our recent manuscript on genomic correlates of climate in yellow warblers. We provide evidence that our findings would not change with different analysis and maintain that our study represents a promising direction for integrating the potential for climate adaptation as one of many tools in conservation management.

In our recent study, we examined climate-associated genomic variation in a migratory songbird, the yellow warbler (*T.*). We identified genetic variation associated with climate variables and estimated the distance between current and future genomes needed to maintain the currently observed relationships, a metric we termed “genomic vulnerability.” Fitzpatrick *et al.* (2) present concerns regarding some of our methodology, and we respond to these concerns below. Specifically, we detail why Fitzpatrick *et al.* do not provide compelling evidence that our findings or conclusions would change had we analyzed the data in a different manner.

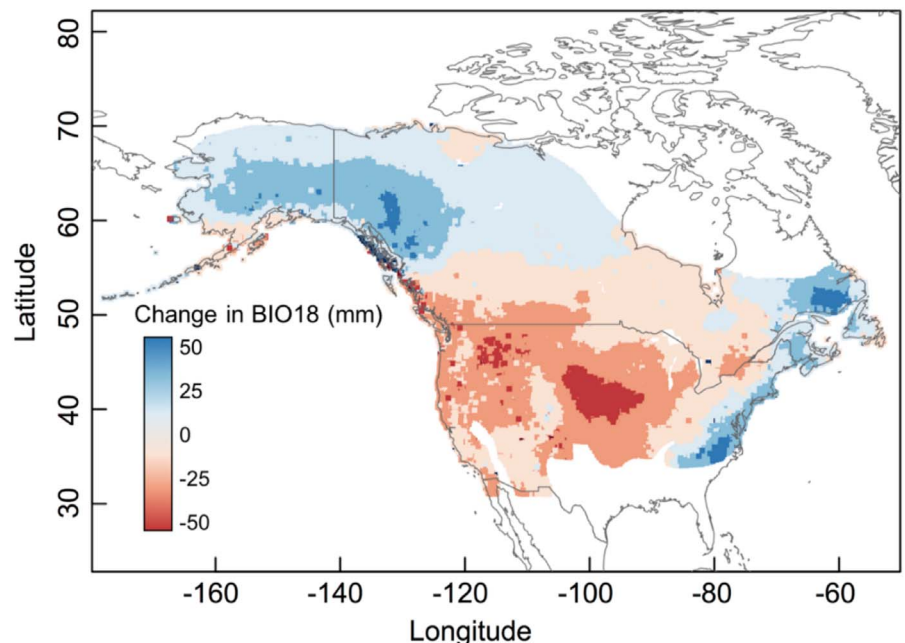
We used Breeding Bird Survey (BBS) data (3) to show a correlation between genomic vulnerability and recent population trends. This comparison relies on two datasets spanning different time periods, and we were therefore necessarily cautious with wording: We stated “If future climate change is correlated with recent shifts (for example, if regional drying over the last century in some regions will continue and become more severe)...” Fitzpatrick *et al.* pointed to this as erroneous, suggesting that the majority of the range will experience increased precipitation. Although this was a hypothetical example, precipitation predictions vary widely among climate models. In our ensemble model, more than

70% of the breeding range should experience summer drying between now and 2050, consistent with our claim (Fig. 1).

Detecting the emergence of a robust climate change signal at local levels in the historical period presents many challenges (e.g., data quality, natural variability, small signal-to-noise ratio); consequently, climate scientists often depend on

model studies to detect such signals (4). Our logic for discussing future climate trends and recent declines together is that we have no reason to believe that the present is a turning point in any climate change trajectory. This idea is echoed in climate science publications. Duffy and Tebaldi (5), for example, state that “the changes ahead appear of increasingly larger magnitude, consistent with a warming climate...similar to what already appears in observations and historic model simulations.” Likewise, a special report by the Intergovernmental Panel on Climate Change (IPCC) (6) states that “there is medium confidence that droughts will intensify in the 21st century in some seasons and areas, due to reduced precipitation and/or increased evapotranspiration” and points to central North America as one region in which this is expected to occur. These studies support our assumption regarding the directionality of the climate change trajectory, but it is important to note that a formal analysis of this idea is nontrivial.

Fitzpatrick *et al.* attempt to test this assumption and report that historical and future climate changes are not correlated, but we have several concerns with their analysis. First, the signal-to-noise ratio in historical climate data is high, which makes robust estimates of rates of change over the past half century challenging. Second, they leave out our top (most predictive of genetic variation) variable, precipitation of the warmest quarter (BIO18), without explanation. Third, their analysis of historical and future climate change fails to account for the resolution of available



**Fig. 1. Change in precipitation of the warmest quarter (BIO18) from normal BIOCLIM estimates (1961–1990) to estimates for 2050 across the yellow warbler range.** Future estimates are for IPCC representative concentration pathway RCP2.6 based on an ensemble average of 19 different climate models. On the basis of this model average, regions shown in red will experience less precipitation in future years, whereas regions shown in blue will experience more.

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historical data. The authors base historical climate measures on the CRU 4.01 dataset, which has a resolution of  $0.5^\circ \times 0.5^\circ$  (7). In North America, this equates to roughly  $50 \text{ km} \times 50 \text{ km}$ , a spatial resolution far too coarse for the analyses they present. One of Fitzpatrick *et al.*'s main concerns was with the resolution at which we analyzed the correlation between population trend and genomic vulnerability (although a reanalysis based on BBS route locations yielded nearly identical results: generalized additive model  $R^2 = 0.10$ ,  $P = 0.006$ ), but their reanalysis suffers a similar issue. Because of the coarse resolution of the historical climate data, multiple BBS routes (up to nine) are located within a single climate pixel, resulting in pseudo-replication (Fig. 2).

Further, the authors do not appear to account for spatial autocorrelation. The lack of high-resolution historical climate data was the very reason we chose to analyze the data as two separate time periods. Further, the linear correlation used by Fitzpatrick *et al.* may not be warranted, given that climate change is likely to follow an exponential trajectory, with future changes being much larger than past changes. Differences in means between the 1960s and 2010s therefore might not accurately reflect the rate of climate change, especially in recent decades. A robust test of whether past climate trends are indicative of future ones would be welcome and could provide valuable insights relevant to climate adaptation.

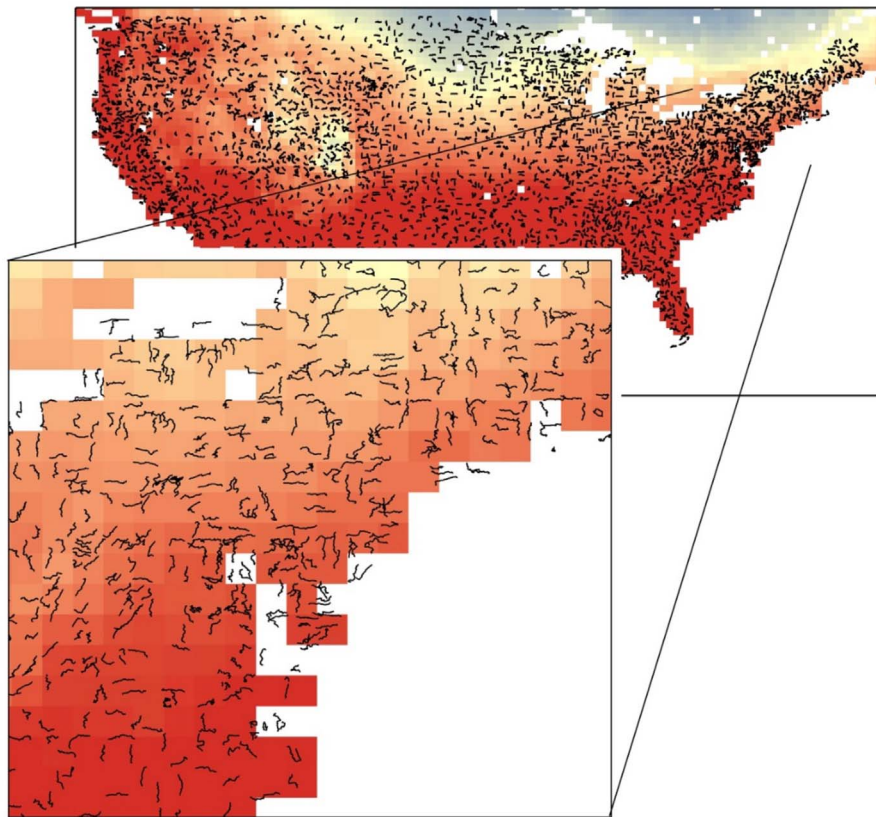
Another issue that Fitzpatrick *et al.* bring up is the potential confounding effects of neutral loci. The question of false positives and their impact on downstream inference has been an issue throughout the history of population genetics and genomics (8, 9). Unlike Fitzpatrick and Keller's earlier paper (10), we did not have a priori single-nucleotide polymorphisms associated with adaptation. This is because birds, like many species threatened by climate change, are not amenable to large-scale controlled experiments. Although false positives almost certainly exist in our (and most other) genome scans, the assumption is that signal overwhelms noise. Improvements in genome scan methods for detecting adaptation have been made in recent years, but perfecting such methods remains one of the more prominent challenges to population genomic studies in natural systems (8, 11).

The ability to examine climate-associated genetic variation has led to many exciting findings and promising methods for integrating genomics into conservation. We agree that caution should be taken when applying these approaches to conservation, and that tests validating such findings are a necessary next step. However, we feel that our findings are robust to the issues raised by Fitzpatrick *et al.*, and we maintain that an understanding of adaptive capacity is one of many important tools that managers need to conserve species. It is important to remember that climate change is happening now, with one in every six species at risk of climate change-driven extinction (12). The sooner that we as scientists can work together to improve methods for incorporating adaptive capacity into management plans, the more likely we will be to stem global biodiversity loss in the face of climate change.

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**Fig. 2. Example of pseudo-replication from Fitzpatrick *et al.*** The underlying map shows mean annual temperature from 2001 to 2010 from the CRU 4.01 climate database, which has a resolution of approximately  $50 \text{ km} \times 50 \text{ km}$  at this latitude. Overlaid on this map are the BBS routes used by Fitzpatrick *et al.* to determine correlations between past and future climate. Of the 3257 routes along which breeding yellow warblers were found in the past decade, only 2234 of these are located in unique pixels as a result of pseudo-replication created using these coarse-scale historical layers. We counted as many as nine BBS routes being given the exact same climate value when using these two sources of information, and counted an average of 1.67 routes per pixel of data, nearly doubling the apparent unique values used in figure 1 of Fitzpatrick *et al.*

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