

## TECHNICAL COMMENT

## ECOLOGICAL GENOMICS

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

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Bay *et al.* (Reports, 5 January 2018, p. 83) combine genomics, spatial modeling, and future climate scenarios to examine yellow warbler population trends in response to climate change, and they suggest that their methods can inform conservation. We discuss problems in their statistical analyses and explain why the concept of “genomic vulnerability” needs further validation before application to real-world conservation problems.

Organisms respond to environmental change through multiple mechanisms (1), including adaptation, but incorporating evolution into climate change impact assessments remains an elusive goal. Fitzpatrick and Keller (2) proposed estimation of a “genetic offset” as a predictive measure of how much locally adapted alleles will be perturbed from their current frequencies within a population for a given magnitude of environmental change, and suggested that this might serve as a metric of climate change vulnerability for long-lived, sessile organisms. Evidence that genetic offsets reflect changes in fitness associated with environmental change would help to validate this concept, but whether genomic variation across space can be used to estimate the amount of evolutionary change required to maintain adaptation through time remains untested.

Bay *et al.* (3) did not attempt to validate the genetic offset concept (which they refer to as “genomic vulnerability”); rather, they associated future projections of genomic vulnerability with historical population trends for the yellow warbler. They reported a weak but significant negative relationship between historical population trends and future genomic vulnerability, and concluded that failure to adapt to climate change may already be having a negative impact on yellow warbler populations. However, Bay *et al.* did not estimate genomic vulnerability as a function of known historical climate trends, which would have allowed examination of whether genomic

vulnerability reflects population changes in response to climate change. Nor did they test whether “future climate change is correlated with recent [climate] shifts,” which they pose as a key assumption underlying their expectation that recent climate change has “already negatively affected populations with high [future] genomic vulnerability.”

We compared historical and future climate trends and found little evidence to support their assumption that historical and future climate shifts are related (Fig. 1). In addition, they mention “regional drying” as potentially driving population declines, but their measure of precipitation [BIO13; precipitation of the wettest month (4)] is expected to increase in the future at nearly all locations where yellow warblers have been observed (Fig. 1; BIO13 future anomalies > 100%). It is conceivable that yellow warblers could respond negatively to increases in precipitation, or similarly to historical and future climate changes even if these are unrelated. However, predicting future climate-driven population dynamics based on historical associations ideally should first involve evaluation of relationships between population trends and historical climate. Although this claim is implied by the title of the paper, Bay *et al.* did not test whether “genomic signals of selection predict climate-driven population declines.”

We also question the effect of neutrality on their estimates of genomic vulnerability, which Bay *et al.* based on all single-nucleotide polymorphisms (SNPs) with  $r^2 > 0$  in gradient forest (5) models—a total of approximately 8000 SNPs. No attempt was made to correct for population structure or to select a subset of candidate SNPs based on a priori knowledge. We are concerned that a genome-wide test of association with environment could identify selectively neutral signals that are unrelated to local adaptation, because autocorrelation in allele frequencies can lead to

false-positive neutral loci. Therefore, their genomic vulnerability estimates likely include signals of neutral genetic variation, such as isolation by distance, declines in population size, or historical movement, especially if genetic variance in allele frequencies due to neutral population structure aligns with environmental gradients (6, 7). This appears to be the case for yellow warblers, especially along longitude and covarying aspects of the environment (precipitation). Including neutral variation will influence relationships between environmental gradients and allele frequencies that underlie the predictions of genomic vulnerability, such that they no longer characterize a putative change in adaptive associations with the environment.

We further question the robustness of the fitted relationship between population trend and genomic vulnerability [figure 2C in (3)] upon which Bay *et al.* base their primary conclusions. Yellow warblers have been detected at approximately 3700 Breeding Bird Survey routes (8), although not all routes have enough data to estimate trends. However, when fitting the relationship between population trend and genomic vulnerability, Bay *et al.* generated 100,000 random locations and used these to extract (i) estimates of population trends based on spatially interpolated Breeding Bird Survey data and (ii) predictions of genomic vulnerability based on data from 21 populations. This pseudo-sampling treats extrapolations as observations, artificially inflates their sample size, and could exacerbate spatial non-independence in the data while increasing the likelihood of finding a significant relationship. An appropriate approach would be to compare predicted genomic vulnerability based on historical climate data to population trends at survey locations where population data were collected. Establishing this historical relationship first would then support (or not) making future projections and associated inferences regarding population declines and climate adaptation.

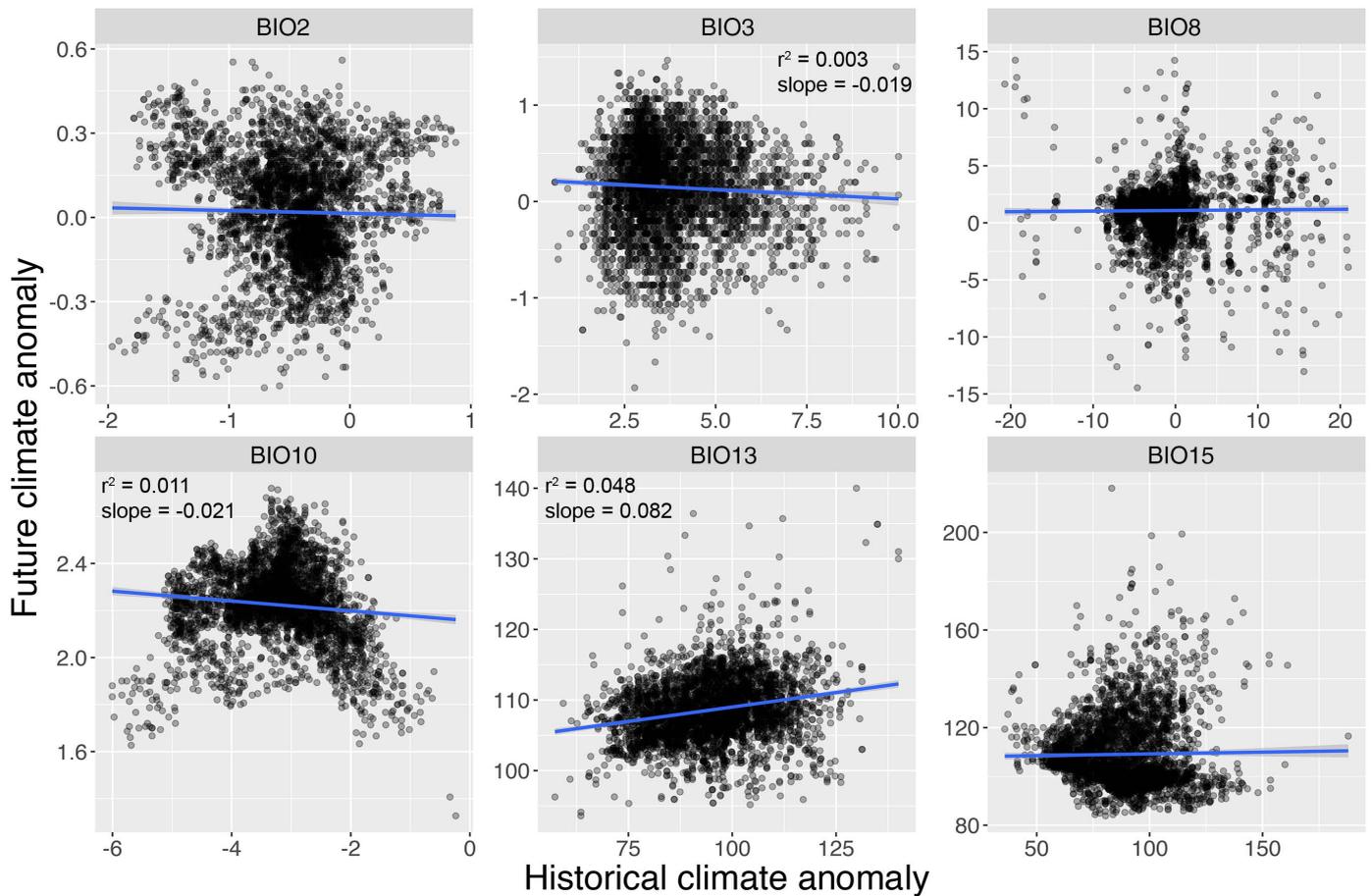
Bay *et al.* provide an exciting example of how we want to use genomics to understand local adaptation and inform conservation. However, even if the authors had addressed our concerns regarding their analyses, it remains an open question under what conditions and assumptions genetic offsets might provide reliable estimates of vulnerability to climate change. Like all space-for-time analyses and gene-environment associations, genetic offsets are inherently correlative. The key assumption is that after correcting for neutral population structure, correlations between allele frequencies and environmental gradients reflect current patterns of local selection and relative fitness. Population genetic theory predicts that allele frequencies will evolve on the landscape to a migration-selection balance (9–12). Therefore, an assumption that the observed allele frequencies at a particular environment reflect fitness may not always hold. A failure to test and meet this assumption makes it difficult to justify the use of genomic signals as predictors of climate-driven population declines. Further testing and validation are needed to verify the

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**Fig. 1. Comparison of historical versus future climate anomalies at 3731 Breeding Bird Survey routes where yellow warblers have been detected.**

The plots show that according to the variables used by Bay *et al.* (3) to estimate genomic vulnerability, the way in which climate changed during the period when the yellow warbler population data were collected (1966 to 2013) has little relationship to the expected future changes in climate (2050, as defined by representative concentration pathway RCP2.6 of the Intergovernmental Panel on Climate Change). Historical anomalies were estimated using the CRU 4.01 climate dataset (14) by calculating changes

in average climate between the first (1966–1975) and last (2004–2013) decades of the Breeding Bird Survey population trend data (8). Future anomalies were estimated using the same current and future climate data (4) used by Bay *et al.* Temperature anomalies were calculated by subtracting older values from newer values, whereas precipitation anomalies are percentages calculated by dividing newer values by older values. BIO2, mean diurnal range; BIO3, isothermality; BIO8, mean temperature of wettest quarter; BIO10, mean temperature of warmest quarter; BIO13, precipitation of wettest month; BIO15, precipitation seasonality.

extent to which genetic offsets reflect changes in fitness expected in new environments. Robust validation of this concept—ideally through the combined application of population genetic simulations and empirical experiments—is essential before genetic offsets can be considered “an important tool for making more-informed conservation decisions” (3) or “a powerful tool for estimating genomic vulnerability to climate change” (13).

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