

Warming summer temperatures are rapidly restructuring North American bumble bee communities

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Abstract

A rapidly warming climate is driving changes in biodiversity worldwide, and its impact on insect communities is critical given their outsized role in ecosystem function and services. We use a long-term dataset of North American bumble bee species occurrences to determine whether the community temperature index (CTI), a measure of the balance of warm- and cool-adapted species in a community, has increased given warming temperatures. CTI has increased by an average of 0.99°C in strong association with warming maximum summer temperatures over the last 30 years with the areas exhibiting the largest increases including mid- to high latitudes as well as low and high elevations—areas relatively shielded from other intensive global changes. CTI shifts have been driven by the decline of cold-adapted species and increases in warm-adapted species within bumble bee communities. Our results show the pervasive impacts and ecological implications warming temperatures pose to insects.

KEYWORDS

bumble bee, climate change, community composition, community temperature index, ecoinformatics

INTRODUCTION

Climate change is driving profound changes in animal occurrence and community composition worldwide. Long-term increases in average temperature as well as increases in acute, extreme weather events (e.g., heat waves) have been linked to both positive (Crossley et al., 2021; Kammerer et al., 2021) and negative outcomes for biodiversity (Oliver et al., 2016; Outhwaite et al., 2022; Sirois-Delisle & Kerr, 2018). Regardless of the direction of such outcomes, a rapidly changing climate has the potential to alter biological processes fundamentally, including the biodiversity that maintains ecosystem services and supports global agricultural production (Johnson et al., 2023; Settele et al., 2016).

Insect responses to climate change are of specific concern given the growing documentation of declines in a variety of taxa and regions (Halsch et al., 2021; Raven & Wagner, 2021). Although several anthropogenic drivers of

global change are at play (Goulson et al., 2015; Hemberger et al., 2021), a changing climate is particularly menacing because of the many direct and indirect impacts it can have on insects and its capacity to be a force multiplier, interacting with other factors to exacerbate changes in insect populations (Forrest et al., 2017; Hoover et al., 2012; Kenna et al., 2023). Like many global change drivers, rapidly increasing temperatures favour some species while potentially leading to local extirpations of others (Marshall et al., 2018). Although temperatures above the critical limits of most species (e.g., CT_{max} ; Oyen et al., 2018) are unlikely, the extent to which climate warming has contributed to local shifts in insect abundance and community structure remains mostly unknown. This knowledge gap greatly hampers our understanding of a host of ecological processes and services and our ability to build resilience to future climate stressors.

Even among the most studied insect taxa, there is debate about the extent, severity and direction of abundance

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and range effects associated with climate change. Bumble bees are a prime example: as a genus adapted to cooler climates, they are likely sensitive to the effects of warming temperatures. However, some studies reveal extensive declines (Soroye et al., 2020; but see Guzman et al., 2021) while others suggesting resilience and relative stability (Guzman et al., 2021; Maebe et al., 2021) or mixed patterns of decline and increases over time (Jackson et al., 2022). Most current approaches examining the long-term influence of climate on bumble bees use occupancy models to relate changes in species occurrence to trends in climate, such as increasing temperature and changing precipitation (Janousek et al., 2023). Although this method yields valuable insights, it can be challenging to align the framework with the incidental and imperfect occurrence data that abound in large-scale insect databases, making model outcomes sensitive to occupancy assumptions (Guzman et al., 2021). More notably, the occupancy approach framework does not explicitly capture the physiological mechanisms driving species responses to warming temperatures. As such, a more thorough understanding of where and when insects are most impacted by climate change requires exploring alternative analytical methods that better tie climatic changes to estimates of insect physiological temperature preferences and limits.

We characterize bumble bee community responses to recent climate warming at the continental scale by examining changes in the community temperature index (CTI), a physiologically informed metric of community responses to climate based on the composition of cool- and warm-adapted species (Devictor et al., 2008). At its core, CTI tracks the weighted average of species' historical thermal preferences (i.e., the species temperature index, STI) within communities over time. When modelled explicitly with changes in temperature, CTI also can help determine whether species are keeping pace with the velocity of temperature trends (i.e., an increase in warm-adapted species and a loss of cool-adapted species in rapidly warming areas; Fourcade et al., 2019) or whether communities are accruing "climate debts," as rising temperatures outpace species turnover (Devictor et al., 2012).

Using 50 years of records from the Bumble bees of North America database (Richardson et al., 2023), we tested whether rising temperatures have had a measurable effect on bumble bee communities across North America by quantifying the association between changes in CTI with spatially explicit trends in maximum summer temperature. Specifically, we addressed the following questions: (1) Has bumble bee CTI increased over time across North America? (2) Are changes in CTI associated with increases in summer temperatures? (3) Are CTI changes greater in areas particularly vulnerable to a changing climate (e.g., higher latitudes and elevations)? and (4) Is a loss of cool-adapted or an increase in warm-adapted species driving the observed changes in CTI? We

predicted a steady increase in bumble bee CTI in accordance with documented increases in average maximum summer temperatures over the past century. We also expected that changes would be more dramatic at higher latitudes and elevations where the rate of temperature increases has been greater (Pyke et al., 2012, 2016). Finally, we predicted that a host of common, warm-adapted species that have increased in occurrence over the past several decades would be the strongest contributors to changes in CTI across the continent.

METHODS

North American bumble bee occurrence and community data

We used occurrence records for 59 species of North American bumble bees from the bumble bees of North America database (BBNA; Richardson et al., 2023). This database comprises 781,280 records from 1805 to 2020 from a variety of sources (e.g., natural history collections, research studies, citizen science programmes). To match the temporal range of available climate data, we used bumble bee records collected between 1960 and 2018. Because the database consists of an amalgam of sources, we took several steps to account for known biases (Bartomeus et al., 2019; Gotelli et al., 2021). The species and community temperature indices at large scales of our analysis are robust to imprecision in the underlying distributional data (Devictor et al., 2008); nonetheless, we filtered the original dataset to include only complete records (i.e., identified to species, containing complete coordinates) and unique collection events (distinct combinations of species, date, coordinates and observer; Figure 1a). This step helps to minimize the bias associated with unequal sampling efforts and differential data collection methods across all observers. Moreover, we conducted a range of sensitivity analyses (see below) to determine whether our results were robust given our assumptions and methodological decisions.

Is there evidence of an increase in bumble bee CTI over time?

Calculating the CTI first requires a determination of the species temperature index (STI; the historical average summertime temperature experienced over a species' approximate range; Figure 1b) for all species present within a community. For this calculation, we first extracted the subset of the bumble bee occurrence records between 1960 and 2000 as the baseline period to compare changes against. These records delineated the approximate historical range of each species. Because range estimates for North American bumble bees are largely based on records from this dataset

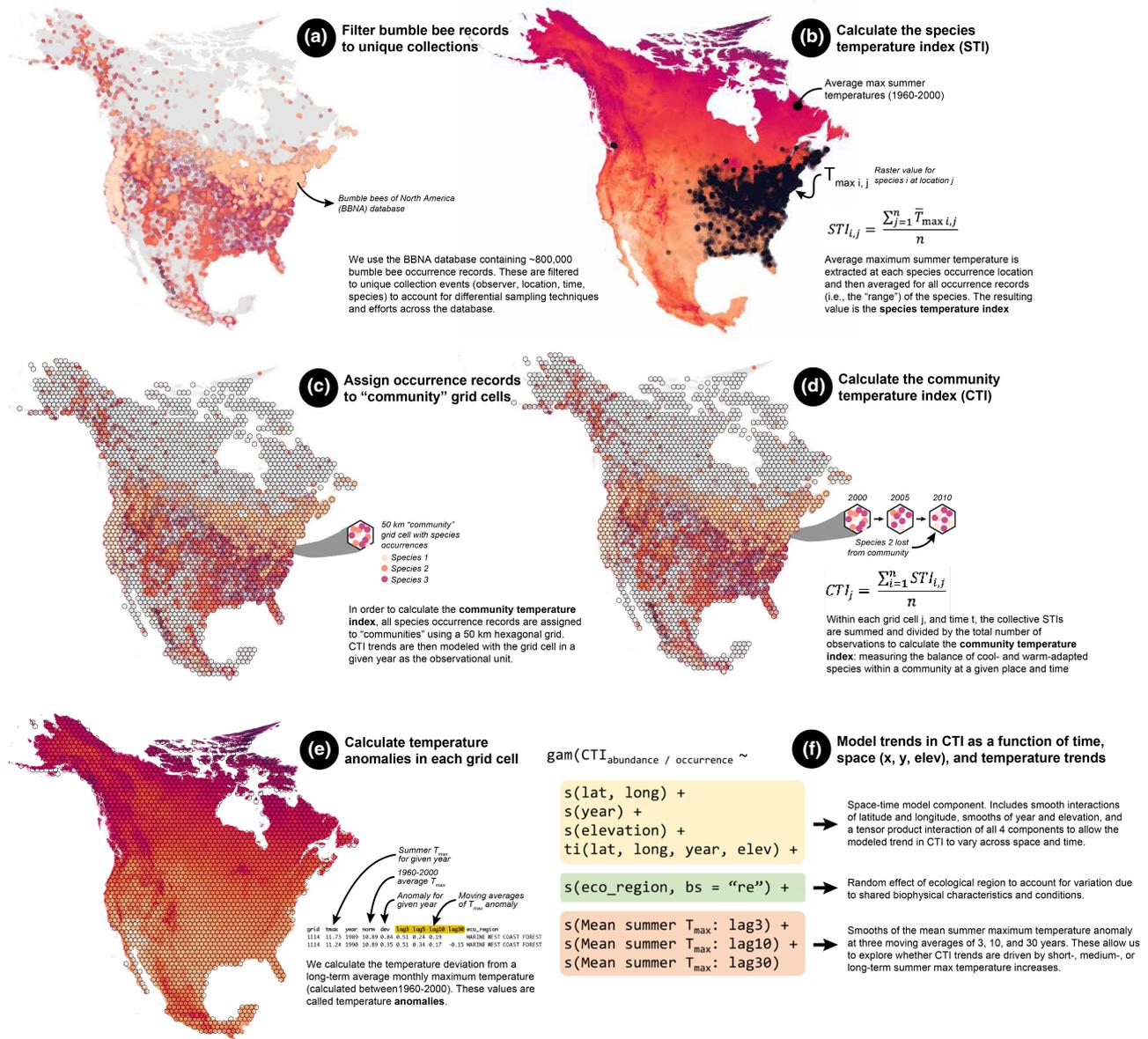


FIGURE 1 Conceptual figure of data cleaning (a), species temperature index calculation (b), community assignment (c), community temperature index calculation (d), temperature anomaly calculations (e) and modelling procedures used in our analyses (f).

(e.g., Williams et al., 2014), we are confident that they capture the range of almost all included species. Next, we extracted historical summertime maximum temperatures (June–September) at all occurrence locations for a species from WorldClim2.1, a global climate database (Fick & Hijmans, 2017) at a 30 arc-second resolution. We used summer maximum monthly temperature because the bulk of bumble bee records are collected during this period corresponding to the peak flight for most North American species. Last, for each species, we then calculated the mean of the extracted values to determine the STI estimate.

The CTI framework requires occurrence records to be delineated into communities to calculate CTI values for given locations/times (Devictor et al., 2008; Figure 1c). To do this, we created a hexagonal grid

across North America at a broad spatial scale (50-km hexagonal grid resolution, centre to side: ~6600 km²) to represent "community" boundaries. We chose a 50-km resolution to ensure we would capture sufficient records within each grid cell to provide a robust estimate of the broad spatiotemporal trend of CTI (Jackson et al., 2022). Although these species assemblages are larger than the scale of a traditional ecological community for bees, the analysis is ultimately agnostic to this point, and it does not affect our specific questions. We refer to them as communities/CTI to maintain consistency with the existing literature.

We calculated CTI within each grid cell where at least 2 species records were present based on the full set of bumble bee occurrence records from 1989 to 2018 (Figure 1d). We were constrained to using CTI calculations from

1989 onward because 1989 was the first year for which we could calculate a 30-year moving average summer temperature anomaly (see below). We calculated CTI using two different methods, first using occurrence records for species i occurring within a given community (grid cell) j

$$\text{Occurrence CTI}_j = \frac{\sum_{i=1}^n \text{STI}_{i,j}}{n} \quad (1)$$

and then using abundance-weighted estimates of species within each community:

$$\text{Abundance-weighted CTI}_j = \frac{\sum_{i=1}^n a_{i,j} \times \text{STI}_{i,j}}{\sum_{i=1}^n a_{i,j}} \quad (2)$$

where $a_{i,j}$ is the abundance of species i at grid cell j and n is the total number of species within a grid cell (Princé & Zuckerberg, 2015). In our case, the true abundance is not known, but we use the total number of individuals of unique collection events of species i within the community of bees at grid cell j as a proxy of abundance. These two approaches, though similar, emphasize the two mechanisms of change in CTI. Using occurrence records (Equation 1) allowed us to test shifts in CTI due to changes in occurrence (i.e., immigration/extirpation), while calculating CTI using abundance weighting (Equation 2) allowed us to understand shifts in CTI as a function of changes in local relative abundance (i.e., species becoming more common/rare within a given community).

Are changes in CTI associated with increases in summer temperatures?

We used generalized additive models (GAMs) to quantify trends in CTI over space and time and determine whether changes in CTI were related to short-, medium- and long-term trends in temperature anomalies (Appendix S1; Figure 1f). Generalized additive models provide a highly flexible computational framework to account for variable trends in spatiotemporal processes (Pedersen et al., 2019) and are especially well-suited for the analysis of potentially complex time series and can readily identify periods of significant change (Simpson, 2018).

For occurrence and abundance-weighted measures of CTI, we fitted GAMs to model the effects of spatial location (latitude, longitude and elevation), long-term trend (year), and short-, medium- and long-term estimates of rising temperatures (3-, 10- and 30-year summertime maximum temperature anomalies). For the remainder of this manuscript, we refer to this GAM as the global model (Equation 3). See Appendix S1 for model fitting and diagnostic details.

$$\text{CTI}_{i,j} \sim s(\text{lat}_j, \text{long}_j) + s(\text{year}_i) + s(\text{elevation}) + \text{ti}(\text{lat}_j, \text{long}_j, \text{year}_i, \text{elevation}_j) + s(\text{eco region, bs} = "re") + s(\bar{T}_3) + s(\bar{T}_{10}) + s(\bar{T}_{30}) \quad (3)$$

Are CTI changes greater in areas particularly vulnerable to a changing climate (e.g., higher latitudes and elevations)?

To determine whether CTI changes were largest (i.e., greater slope in fitted GAM) in areas experiencing accelerated climatic changes, we examined the rate of change in the slope of our fitted model smooth function across latitudes and elevations (Figure S1; Appendix S1: Identifying areas of greatest change in CTI).

Which species are driving any observed changes in CTI?

To generalize the mechanism underlying the observed changes in CTI across North America and determine whether a loss of cool-adapted and/or an increase in warm-adapted species best explained the change in CTI, we modelled the trend in the relative abundance of cool- and warm-adapted species (Appendix S1: Cool-warm adapted contributions). We also quantified species-specific contributions to the CTI trends using a jack-knife approach, iteratively removing species from the global model and then re-fitting the model to quantify their spatially explicit impact on the predicted change in CTI (Appendix S1: Species-specific contributions, Figures S7–S60).

We conducted all data wrangling, GIS operations, modelling and visualization using R (R Core Team, 2017) using the aforementioned and following packages: tidyverse (Wickham et al., 2019), raster (Hijmans, 2023), sf (Pebesma, 2018), gratia (Simpson, 2023), mgcv (Wood, 2011), performance (Lüdecke et al., 2021), DHARMA (Hartig, 2022), janitor (Firke, 2021), paletteer (Hvitfeldt, 2021), exactextractr (Daniel Baston, 2022), foreach (Microsoft & Weston, 2022) and data.table (Dowle & Srinivasan, 2023) packages.

RESULTS

Bumble bee community temperature index has increased across a majority of North America

From 1989 to 2018, bumble bee CTI increased substantially across most of North America. Overall, CTI increased on average $0.99 \pm 1.98^\circ\text{C}$ (mean \pm SD) over 30 years. The magnitude of change in CTI was spatially variable, ranging from a decrease of 6.30°C to an increase of 7°C (Figure 2a). CTI increases primarily occurred from 2010 onward (Figure 3a) after being relatively stable from 1989 to 2000. Such changes strongly mimic the

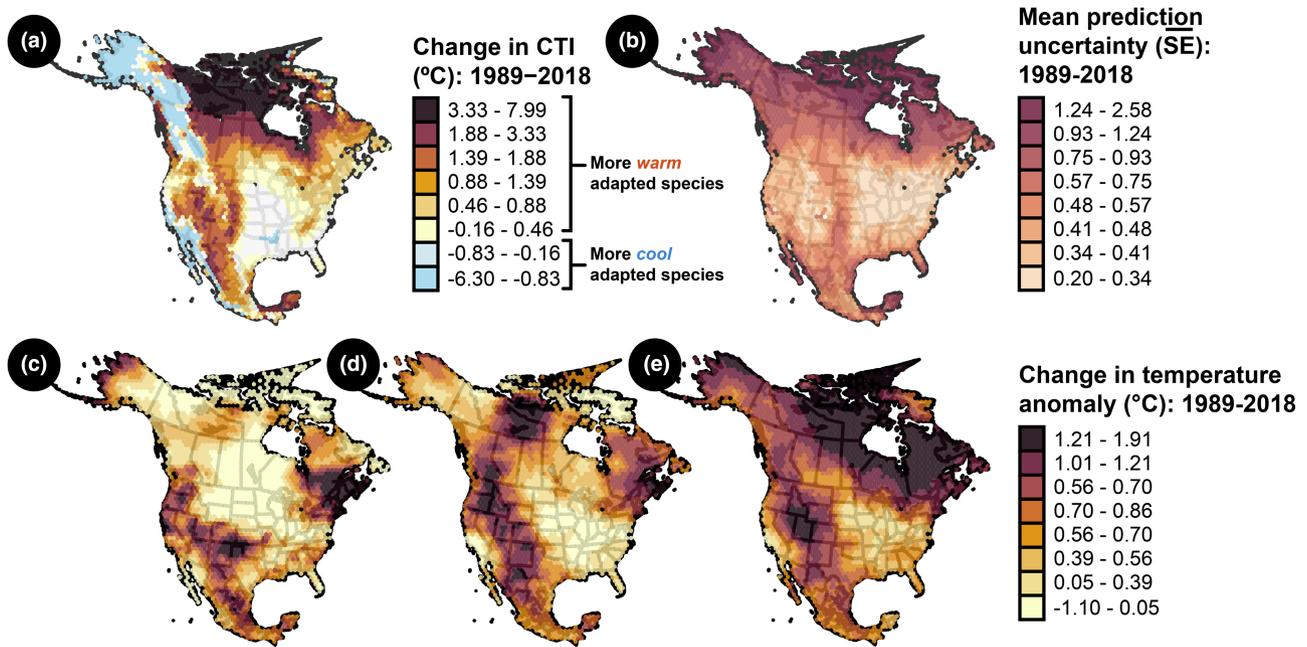


FIGURE 2 (a) Extrapolated spatial projection of the estimated change in community temperature index from 1990 to 2018 across North America. Differences in the community temperature index were calculated for each grid cell by subtracting the model predicted $CTI_{t=1989}$ from predicted $CTI_{t=2018}$. (b) Spatial projection of the mean uncertainty estimates across years from 1989 to 2018. (c) Spatial projection of the change in the 3-year, 10-year (d) and 30-year (e) average temperature anomaly. Differences were calculated by subtracting the 1989 anomaly from the 2018 anomaly for each grid cell. Hexagonal grid cells are 100 km from side to side ($\sim 8600 \text{ km}^2$).

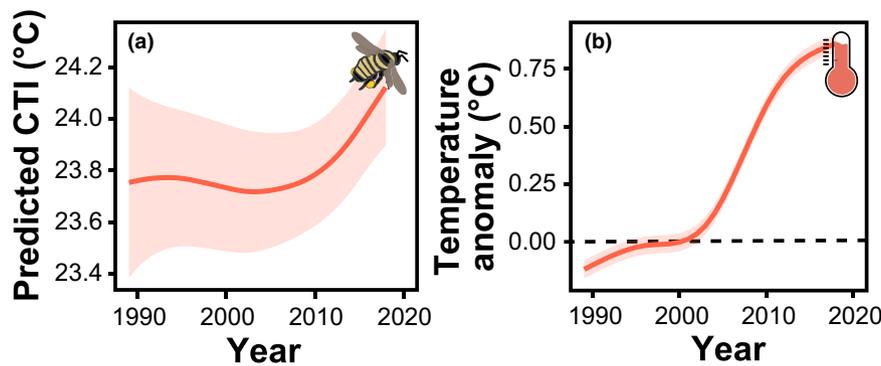


FIGURE 3 A significant increase in bumble bee community temperature is strongly associated with long-term warming and has accelerated in the last 15 years. (a) Model estimated temporal trend in community temperature index across North America plotted as the partial effect of “year” from the global GAM. (b) Model estimated temporal trend in 30-year average summer maximum temperature anomaly across North America plotted as the partial effect of “year.” Both panels include the 95% confidence interval.

pattern summer maximum temperature anomalies, particularly for the 30-year average (Figure 3b). The predictions were most certain across the coterminous United States where bumble bee records are numerous and less certain in the most northern grid cells in the high Tundra and Queen Elizabeth Islands as well as in the tropical wet forests of Mexico (Figure 2b). The spatial trends of the increase in CTI were nearly identical between occurrence and abundance-weighted CTI; however, changes in occurrence CTI were smaller ($0.78 \pm 1.75^\circ\text{C}$). On average, the community grid cells contained 4.2 species per year (range 2–22). The global model, which quantified the change in CTI as a function of space, time and

changes in short-, medium- and long-term temperature increases, explained a substantial portion of the deviance in both the abundance-weighted (Table S1; 86.0%, $\text{adj-}R^2=0.849$) and occurrence models (Table S1; 86.3%, $\text{adj-}R^2=0.851$).

The results of our analysis were consistent irrespective of the grid scale used in aggregating communities (Figure S2; Table S2). The exception was in areas of British Columbia and Alaska where a highly concentrated spatial pattern of bumble bee records likely led to a predicted decrease in CTI in grid cells when aggregated at the 50 and 25 km grid scale. Aggregating at the largest scale (100 km centre-to-side hexagonal grid) revealed the

most wide-spread increases in CTI, with nearly all grid cells exhibiting an increase in CTI from 1989 to 2018.

Our models performed well when cross-validated using withheld data from the BBNA database (Figure S3). Coefficient of determination (R^2) values ranged from 0.79 to 0.81; root mean squared error (RMSE) ranged from 1.22 to 1.31; and mean absolute error (MAE) ranged from 0.91 to 0.96. In addition, our model performance was consistent across the three tested grid scales. Predictions were most accurate for CTI values ranging from 23 to 28°C which corresponded to the regions where the bulk of the occurrence records were collected. Prediction accuracy was most variable among cool regions in the north and sub-arctic (CTI < 23°C).

Shifts in CTI are strongly related to long-term increases in summer temperature

Summertime maximum temperatures have increased over 1989–2018 (Figure 2c–e), with increases most apparent at 10-year ($0.630 \pm 0.405^\circ\text{C}$) and 30-year average anomalies ($0.969 \pm 0.342^\circ\text{C}$; Figure 1d,e; Figure S4). Increases in bumble bee CTI had a strong statistical association with increases in the 30-year summertime maximum temperature anomaly (Figure 4a; $F=4.561$, $p=0.002$). Increases in the 30-year temperature anomaly between 0 and 0.5°C had no impact on CTI. However, increases of over 0.5°C were associated with a rapid increase of up to 1°C in bumble bee CTI (partial effect due solely to 30-year temperature anomaly). Beyond a 1°C change in the 30-year temperature anomaly, changes in bumble bee CTI rapidly increase, with gains of 1 to 6.8°C . There was no statistically supported relationship between the 10-year average anomaly and bumble bee CTI (Figure 4b; $F=0.064$, $p=0.802$). The relationship of CTI with the short-term, 3-year moving average shifts in summer temperature anomalies, while statistically supported, was weak and variable over the range of the anomalies (Figure 4c; $F=2.584$, $p=0.032$).

CTI is increasing fastest at low and high elevations, high latitudes and more recent years

We examined patterns in the rate of change in CTI across the continent to determine where and when the most extreme changes in CTI were occurring and whether these areas overlapped with areas known to be heavily impacted by a warming climate (Janousek et al., 2023). The rate of change in CTI was greatest at low (<800 m) and high elevations (>2000 m; Figure 5a) and increased with increasing latitude (Figure 5b). CTI increases predicted at high elevations also had greater uncertainty than those at low elevations, due in part to a higher concentration of occurrence records at lower elevations. The rate of change in CTI has increased from 1989 to 2018 and most rapidly after 2010 (Figure 5c). These results varied slightly when analysed with predictions from only grid cells containing occurrence records, with changes in CTI being greatest at high elevations (Figure S5a; >2000 m) and mid-high latitudes (Figure S5b; 35–60°). The temporal patterns of the rate of change were largely similar but were positive only from 2003 and beyond (Figure S5c), confirming the accelerating rate of CTI change from 2010 onward that is exhibited when using predictions from all grid cells (Figure 5c).

CTI changes driven by loss of cool-adapted and increase in warm-adapted species

In the model predicting the temporal trend coefficient for species relative abundance, there was a significant interaction between species thermal niche, latitude and propagated error ($\chi^2=14.53$, $p<0.001$, Table S3). The relative abundance of cool-adapted species ($n\sim 32$ species; Table S4) has declined across North America, with the rate of decrease (i.e., binomial model coefficient estimates) slowest at high latitudes (Figure 6a). In contrast, the relative abundance of warm-adapted species ($n\sim 27$ species; Table S4) has increased across all areas south of $\sim 50^\circ$ latitude. North of this 50° parallel, warm-adapted

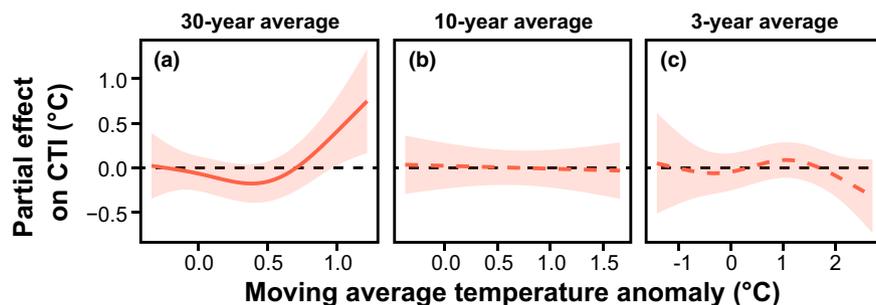


FIGURE 4 Generalized additive model partial plots (i.e., marginal effects) show the model predicted effect of (a) 30-, (b) 10- and (c) 3-year moving average temperature anomalies on the community temperature index. Positive values on the y-axes indicate an increase in community temperature index, while positive values on the x-axes indicate an increase in the average temperature relative to the long-term average. Solid line indicates strong evidence of a relationship.

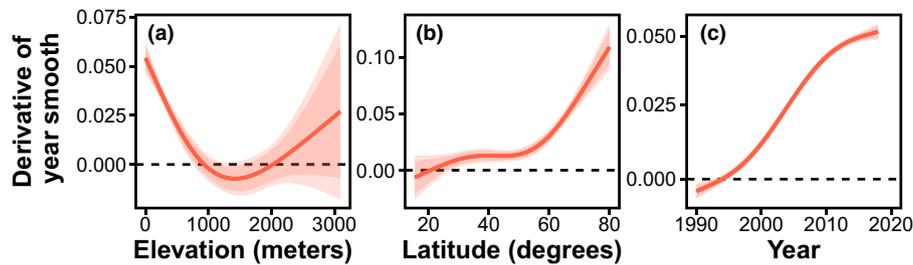


FIGURE 5 Estimates of the rate of change in community temperature index over time across (a) elevation, (b) latitude and (c) year. Yearly predictions of community temperature index are calculated from the global model for each grid cell using a generalized additive model with a single smooth of year to determine the temporal trend in community temperature index within the grid cell. For each fitted smooth (except for the year, c), we then calculated the mean derivative across its range (1989–2018) for each grid cell. We then plotted these derivative estimates against elevation and latitude to explore, across the extent of North America, where the rate of community temperature index change is greatest. We visualized the relationships (red lines) using a simple GAM. Model fits include the 95% confidence interval.

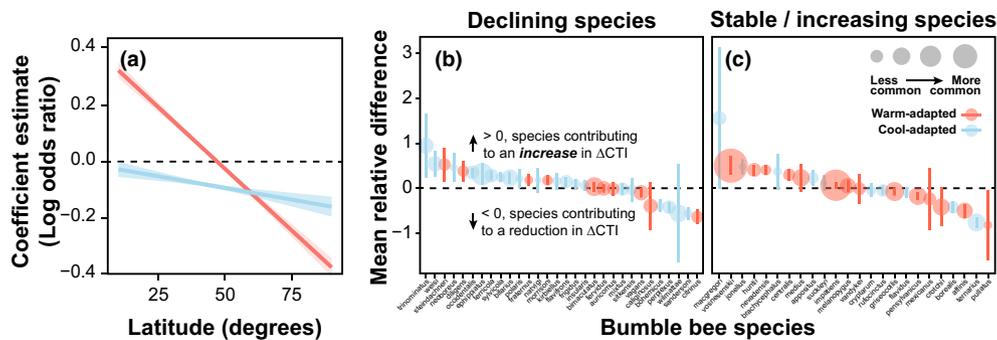


FIGURE 6 Marginal effect plot of the predicted coefficients for the temporal trend in warm- and cool-adapted species relative abundance across latitude in North America (a; $\pm 95\%$ CI). Values above zero indicate an increase in relative abundance from 1989 to 2018, while values below zero indicate a decrease. Mean relative difference ($^{\circ}\text{C}$) between the jackknife and global model change in the community temperature index (ΔCTI) separated into species whose relative abundance had declined (b) or has been stable/increased (c) from 1989 to 2020. Species are colour-coded by whether they are warm- or cool-adapted, and the point size is scaled by the relative commonness of the species (mean number of occurrence records per grid cell) with larger points indicative of species that are more common across their range ($\pm 95\%$ CI).

species are also decreasing in relative abundance. This general trend, a consistent loss of cold-adapted species and increase in warm-adapted species across most latitudes, was broadly consistent across ecological regions (Figure S6). The jackknife analysis revealed that the observed increases in CTI were driven by a host of declining cool-adapted species (Figure 6b) and increasing warm-adapted species (Figure 6c). While several common species were included within the species with the largest observed effect on the increase in CTI, there was a relatively uniform contribution across many species, indicating that a rapidly changing climate is having an extensive, genus-level impact (Figures S6–S60).

DISCUSSION

We documented significant, rapid spatially extensive shifts in the thermal composition of North American bumble bee communities in response to long-term increases in summer temperatures. Over the last 29 years across the continent, bumble bee communities increasingly consist of fewer cool-adapted and more warm-adapted species with resultant increases in the

community temperature index, a measure of the balance of warm- and cool-adapted species. Changes are most pronounced at mid- to high latitudes and high elevations in the American Rockies, Intermountain West and central Mexico. We also document an alarming trend suggesting that above 50°N , both cool- and warm-adapted species are declining in relative abundance, indicating that warming temperatures are outpacing the capacity of bumble bee species to respond or adapt (Kerr et al., 2015). The community temperature index increased according to both occurrence and abundance-weighted indices, suggesting that shifts in local abundance (i.e., reduced abundance of cool-adapted species) and broader changes in species occurrence that are consistent with range shifts underlie the observed changes in community composition. Though relatively small areas exhibited a decrease in the CTI, such changes were largely due to sampling artefacts in relatively remote regions (e.g., Alaska). Increasing the spatial resolution of the “community” revealed increases in the CTI across the entirety of North America (Figure S2). Our model results are consistent with occupancy patterns that reveal both winners and losers among bumble bee species in response to anthropogenic climate change (Jackson et al., 2022).

Overall, our work provides strong evidence of the pervasive impacts a warming planet has for insect biodiversity, particularly for historically cool-adapted species. It also identifies regions of concern where anthropogenic climate warming is rapidly restructuring the communities of an ecologically important group of insects.

An increase in species turnover within biological communities is a logical consequence of a rapidly warming climate (Tingley & Beissinger, 2013). Similar shifts in community composition have been observed in birds in response to both warming summer (Devictor et al., 2008, 2012) and winter (Princé & Zuckerman, 2015) temperatures. Because insects are ectotherms, temperature-induced shifts in range and abundance may be even more pronounced. Indeed, large changes in CTI have been reported for bumble bees (Fourcade et al., 2019) and butterflies (Devictor et al., 2012); however, these trends in CTI are descriptive and not explicitly tied to spatial and temporal patterns of warming temperatures. Our results explicitly link these two phenomena—revealing a strong relationship between increases in CTI and long-term increases in maximum summer temperatures across North America. Our results identified a clear threshold: areas experiencing a 30-year temperature anomaly of greater than or equal to 0.5°C exhibited a rapid increase in bumble bee CTI (Figure 2; dark orange and red areas, Figure 4a). Critically, our ability to explain increases in CTI was dependent on the scale of the moving average temperature anomaly. As such, we recommend using caution when investigating community responses over more restrictive (i.e., shorter) periods of time. Also worth noting is that the historical baseline period we choose for calculating species STI values is due to the availability of rasterized climate data. Choosing an earlier baseline period could reveal different patterns in community change; however, we believe this is unlikely given the stability of historical summer temperatures relative to the dramatic increases observed in recent decades.

The most severe responses to climate have tended to be at high latitudes. For example, regions north of 45° have experienced rapid increases in temperature leading to pronounced phenological shifts across taxa (Parmesan, 2007). Our results support this trend, revealing the largest rates of bumble bee CTI change at higher latitudes and high elevation. The bumble bee species in these locations tend to have narrower geographic ranges and be cold-adapted, traits identical to other insect taxa that have exhibited declines due to climate (Engelhardt et al., 2022; Halsch et al., 2021; Neff et al., 2022). Alarming, our results found that even warm-adapted species are struggling to respond to the pace of warming temperatures at higher latitudes: both cool- and warm-adapted bumble bee species north of 50° N have exhibited significant declines in relative abundance. This result supports previous work describing the limited capacity of bumble bees to track their northern range limits in accordance with warming temperatures

(Kerr et al., 2015). Though additional confirmation is needed, our results suggest that northern bumble bee communities may be in crisis, with significant species turnover and declines in abundance that may threaten the persistence of populations in the coming decades.

Rapidly increasing CTI at high elevations suggests that cold-adapted species are being displaced by warm-adapted, low-elevation species. This phenomenon has been observed in the US Rocky Mountains where bumble bee communities are increasingly dominated by low-elevation species using high-elevation habitats as a thermal refugia (Pyke et al., 2011, 2012; Miller-Struttman et al., 2022). An upslope range expansion appears to be a common response of bumble bee communities to warming temperatures rather than expansions of northern ranges which require longer dispersal distances (Kerr et al., 2015; Sirois-Delisle & Kerr, 2018). Despite the rapid changes observed at higher latitudes, biological communities in southern latitudes and lower elevations are not protected from a changing climate (Dillon et al., 2010), and we documented shifts in CTI in central Mexico and at low elevations. Important to note is that if the species lost from communities have similar STI values to those species remaining, shifts in CTI may effectively be masked, highlighting a limitation of our approach.

We identified increases in CTI from changes in occurrence and changes in relative abundance between cool-adapted versus warm-adapted species. Shifts in local relative abundance align with existing research (Cameron et al., 2011; Hemberger et al., 2021); however, substantial range expansion of warm-adapted bumble bees has not been described (Kerr et al., 2015) and may be unlikely given bumble bee dispersal capacities (Fijen, 2021). That said, select species of bumble bees may be capable of long-distance dispersal (Fijen, 2021), and significant range shifts by other insect taxa have been observed (Warren et al., 2001; Hickling, 2005). Regardless, our analysis revealed there are multiple warm-adapted species whose relative abundance is increasing significantly and that exhibited a large contribution to the increasing CTI across North America. Similarly, a host of declining, cool-adapted species exhibited large contributions. Contributions to the CTI trend were spread out remarkably evenly among different species and not driven exclusively by common species (e.g., *B. impatiens*, *B. vosnesenskii*). This result indicates that certain species are sensitive to and more capable of effectively tracking or adapting to ideal climatic conditions (Maebe et al., 2021). Several bumble bee species have exhibited both range increases (e.g., *B. impatiens*, Looney et al., 2019; Palmier et al., 2019) and increases in local abundance. However, other species (e.g., *B. occidentalis*) are not able to track warming and are likely to suffer substantial reductions in range as a result (Janousek et al., 2023). Such contrasts highlight the species-specific nature of bumble bee responses to a

rapidly changing climate (Jackson et al., 2022; Whitehorn et al., 2022). Additional research is needed detailing species responses to warming conditions—focusing on identifying the physiological and evolutionary mechanisms that drive species' plasticity or susceptibility to changing environmental conditions.

An increase in the occurrence and abundance of warm-adapted species suggests a physiological or climate preference mechanism is at play. Several studies document significant, direct effects of warming on insect pollinators (CaraDonna et al., 2018; Kenna et al., 2021; Hemberger et al., 2023); however, indirect effects mediated through biotic interactions may be just as important (Ockendon et al., 2014, but see Iler et al., 2021). In the context of our study, this implies that shifts in bumble bee community composition are occurring partly in response to climate-induced changes in the floral resource landscape. Warming climates can decrease the abundance and temporal availability of resources due to earlier snowmelts, which in turn may lead to a decrease in bumble bee abundance (Ogilvie et al., 2017). Warming may also create phenological mismatches that reduce available forage for bees (Pyke et al., 2016, but see Bartomeus et al., 2011). Similarly, an increase in hot, dry summer conditions can significantly reduce floral resources and the bumble bees that depend on them (Iserbyt & Rasmont, 2013; Timberlake et al., 2019; Williams et al., 2012), and similar patterns have been observed for butterflies (Crossley et al., 2021). Unfavourable conditions, often a result of extreme weather events such as heat waves that are expected to increase significantly in the coming century (Lopez et al., 2018; Meehl & Tebaldi, 2004; Thompson et al., 2022), can create resource bottlenecks that lead to population declines and local extirpation (Maron et al., 2015). Because our study could not differentiate between direct and indirect pathways, parsing their relative impacts on bumble bees and other taxa is a critical research need. In the meantime, supporting bumble bees in the face of both direct and indirect effects may be accomplished by maintaining climate refugia, such as heterogeneity in vegetation structure, that can provide respite from temperature extremes to both bees (Pincebourde & Woods, 2020), plants and other taxa (e.g., birds, Kim et al., 2022) in addition to increasing spatial and temporal resource continuity to minimize negative indirect effects (Maron et al., 2015).

Given the spatiotemporal extent of our study, it is likely that warming summer temperatures and the temperature profiles of bumble bee assemblages co-vary with other, known factors that influence bumble bee community composition and occurrence. For example, losses in certain species across their range may be linked to disease (Colla et al., 2006; Szabo et al., 2012). At large scales, a loss of suitable habitat via land-use intensification and change is also of concern (Hemberger et al., 2021), but

when examined together with shifts in land-use, climatic variables (and their associated indirect effects) tend to have as much or more power to explain long-term species trends than land-use or resource availability in bumble bees (Kerr et al., 2015), other wild bee species (Duchenne et al., 2020) and other insects (Dalton et al., 2023). That said, our and most previous analyses cannot exclude the potential confounding effect of habitat changes. For example, regions with a strong statistical association between temperature increases and CTI may also be experiencing rapid habitat changes that simultaneously impact bumble bee abundance and community composition. Our analyses cannot statistically detect such an overlap; however, it is unlikely, and we show that the areas of greatest increase in the community temperature index are in areas removed from the most significant effects of land-use change (e.g., high latitudes and elevations; Halsch et al., 2021). Regardless, managing habitat offers a critical tool that can be used to mitigate the impacts of a changing climate (Kim et al., 2022; Oliver et al., 2015, 2016; Outhwaite et al., 2022).

CONCLUSIONS

Climate change is causing significant, cross-scale impacts on insect behaviour, populations and communities (Halsch et al., 2021; Høye et al., 2021; Lehmann et al., 2020; Raven & Wagner, 2021). In this paper, we document a substantial shift in the functional composition of bumble bee communities that is tied to a long-term increase of summer temperatures in North America. Several species appear to be tracking climate warming; however, cold-adapted species appear to lack the adaptive capacity to cope with rapidly climbing temperatures and are being lost from bumble bee communities across the continent. Although the relative impact of direct and indirect climate effects on these community-level shifts remains unknown, our work contributes strong evidence that climate change is having a significant, negative impact on many important pollinating insect species with unknown consequences for ecosystems, both natural and agricultural. It is critical that we focus on designing resilience measures, such as climate refugia and climate-focused habitat conservation, to combat the ongoing direct and indirect impacts a rapidly warming planet threatens. Such efforts must be paired with substantial decreases in emissions (Oliver et al., 2015)—a non-negotiable step to safeguard the planet's biodiversity for generations to come.

AUTHOR CONTRIBUTIONS

JH and NM conceived of the project. JH conducted all data acquisition, cleaning and analysis and wrote the first draft of the manuscript. JH and NM contributed to revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and R code for analyses, figures and manuscript are available on FigShare (doi.org/10.6084/m9.figshare.24043338).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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