Climate-driven changes in northeastern US butterfly communities

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Climate warming is expected to change the distribution and abundance of many species[1–3]. Range shifts have been detected in a number of European taxa for which long-term government-initiated or organized-survey data are available[4–8]. In North America, well-organized long-term data needed to document such shifts are much less common. Opportunistic observations made by citizen scientist groups may be an excellent alternative to systematic surveys[9]. From 1992 to 2010, 19,779 butterfly surveys were made by amateur naturalists in Massachusetts, a geographically small state located at the convergence of northern and southern bioclimatic zones in eastern North America. From these data, we estimated population trends for nearly all butterfly species (100 of 116 species present) using list-length analysis[10,11]. Population trajectories indicate increases of many species near their northern range limits and declines in nearly all species (17 of 21) near their southern range limits. Certain life-history traits, especially overwintering stage, were strongly associated with declines. Our results suggest that a major, climate-induced shift of North American butterflies, characterized by northward expansions of warm-adapted and retreat of cold-adapted species, is underway.

Climate warming has demonstrably altered the distribution and phenology of numerous plant and animal species[1–3]. Although a large and growing number of case studies have shown population-level effects of climate change, most of these examples come from unusually well-studied systems, such as government-organized or government-funded monitoring programmes in Europe[4–8]. There is an urgent need to know whether these trends extend into other geographical areas.

Natural history observations by amateurs have the potential to document the distribution and abundance of species in places where systematically collected monitoring data do not exist. Many amateur organizations are now holding decades-long data sets of the occurrence and abundance of species[9,12,13]. However, sampling effort is often poorly controlled in citizen-collected data and until recently these data have not been widely used because they have been considered unreliable. As efforts have unfolded to properly organize and archive amateur observations, their use by the scientific community is becoming mainstream[9]. Effort control and reliability remain an issue, but, because of their potential wide coverage, the development of robust statistical methods to analyse citizen science data is an active area of research.

We used list-length analysis[10,11], a new analytical approach for citizen-collected observations, to analyse population trends of butterflies observed in Massachusetts by the Massachusetts Butterfly Club (MBC) between 1992 and 2010 (Supplementary Fig. S4 and Table S1). List-length analysis uses the number of species reported

in a particular outing as a proxy for observation effort. Though list-length analysis was originally intended to control for effort, it controls for all factors that affect detectability on a particular day (see Supplementary Information for complete methods). Effort and weather are the most important day-to-day factors affecting detection probability, but phenology is also strongly reflected in list length, and list length implicitly controls for this effect as well (see the Supplementary Information for further discussion). After controlling for list length, the residual detectability can be used as an index of abundance and changes in detectability used to estimate changes in abundance though time[10,11].

Population trends of butterflies in Massachusetts indicate strong climate-driven changes in abundance. Trends in abundance were estimable for 100 of the 116 butterfly species reported (Supplementary Table S2), 21 of which were northern species, defined as those with ranges centred north of Boston (41.78° N, 70.50° W). Northern species were significantly overrepresented in declining species (permutation test $p = 0.0003$). Of the 21 northern species, 17 were declining, one was increasing and three did not show significant trends through time (Fig. 1 and Supplementary Table S3). Regional trends in abundance corroborate the presence of climate-driven trends. We divided Massachusetts into five subregions based on environmental conditions (Fig. 2). All regions of the state have warmed significantly in the past 100 years (Supplementary Fig. S10). Northern species, however, were less likely to be declining in cooler, higher-altitude regions, but were strongly declining in warmer, lower-altitude regions (Fig. 2). Higher regions probably still contain cooler microclimates, which could allow cold-adapted species to increase their altitude and remain in an appropriate climate envelope[14–16].

Furthermore, we identified species that had recently expanded their ranges by comparing our species list with the *Massachusetts Butterfly Atlas* (MBA; ref. 17), compiled between 1986 and 1990. Of the 100 estimated population trajectories, 14 were from species that were very rare or not reported in the atlas (four or fewer reports). Of these, 12 have southerly ranges, one has a northerly range and one is near its range core. The species with a northerly range was the only one in decline, whereas the 12 with southerly ranges were all increasing. Many of these growing populations are new to the state and represent invasions from the south (Fig. 1). Declining northern species are being replaced by warm temperate and subtropical species such as the giant swallowtail (*Papilio cresphontes*) and zabulon skipper (*Poanes zabulon*)[18]. Permutation tests indicate that this pattern of increase by historically (1980s) rare southern species is highly significant ($p = 0.0003$).

In contrast to climate change, butterfly population trends did not seem to be systematically related to habitat or landscape change. We found no evidence ($p > 0.1$) that host-plant rarity,

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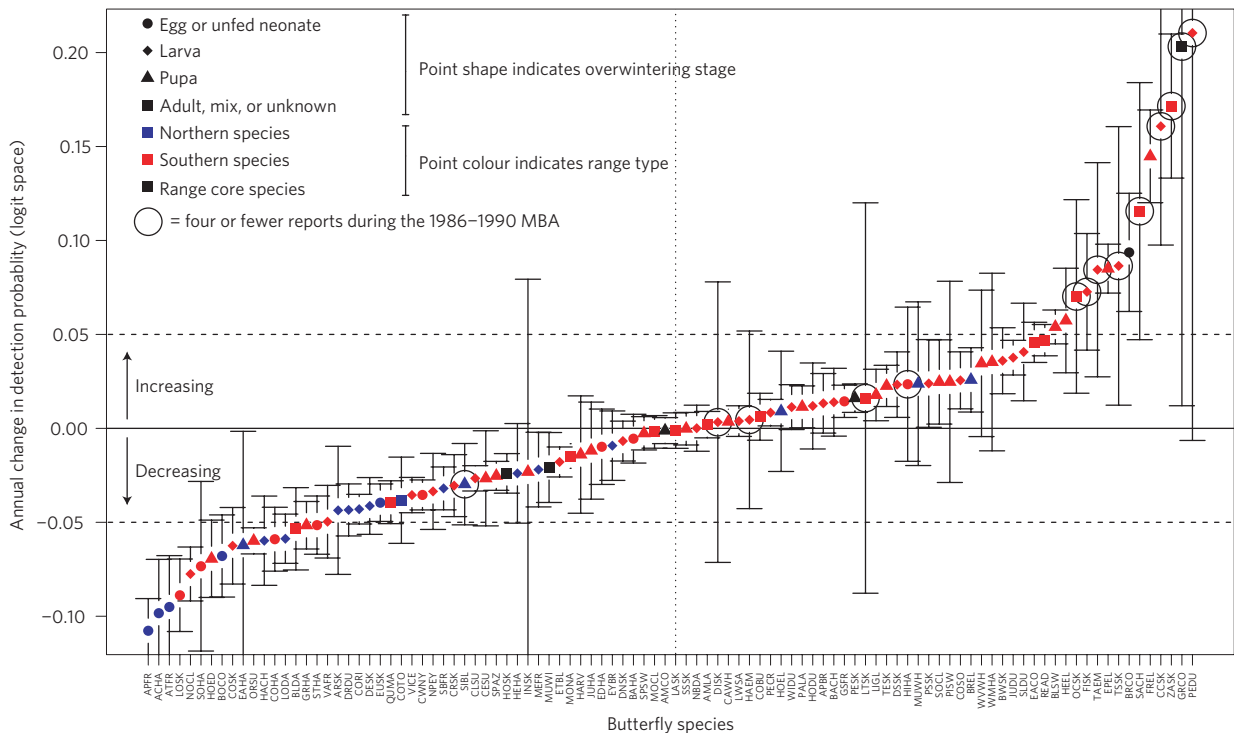
Figure 1 | Population trajectories with 90% confidence intervals for butterfly species in Massachusetts, with range type (northerly versus southerly, symbol colour) and overwintering stage (symbol shape) superimposed. Species that were rare or not present in the 1986–1990 MBA are circled. The solid horizontal line denotes the zero-population-growth estimate and the vertical dotted line separates declining species with negative growth estimates (to its left) from increasing species (to its right). Population changes for each species as a percentage of the 1992 population are shown in Supplementary Table S3; the species performing least well represent about an 85% decline over the 18-year time series.
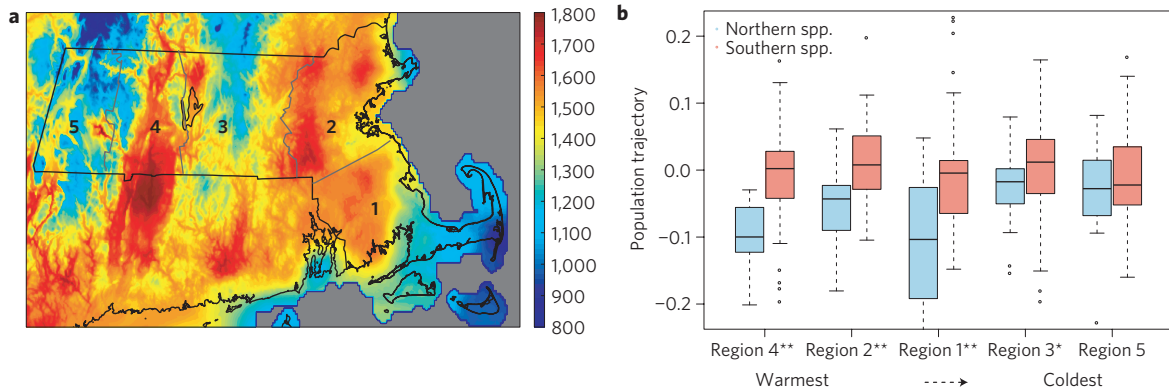

Figure 2 | Regional analysis. Region 1: Cape Cod/Long Island terminal moraines and Narragansett/Bristol Lowland; region 2: Metro Boston; region 3: Worcester Plateau; region 4: Connecticut River Valley; region 5: Berkshire Mountains. **a,** Regional divisions superimposed over a state map of 30-year mean 15 °C degree days. The colour scale indicates annual accumulated degree days above 15 °C (data from ref. 29). **b,** Northerly distributed butterflies are declining much faster in warmer regions of Massachusetts (**regions 1,2,4: $p = 0.0055$, $p = 0.0053$, $p < 0.0001$, respectively). *Region 3, which is cooler and higher, had only marginally significant declining trends in northerly species ($p = 0.0530$) and region 5, which is mountainous and much cooler, had no trend ($p = 0.4346$). The open circles are outliers.

degree of host plant or habitat specialization, or the kinds of habitat preferred, had any relationship to the pattern of decline (see Supplementary Figs S6 and S7), suggesting that climate and not habitat alteration is driving broad patterns of community change. Landscape changes and habitat destruction have probably affected some species, but it is difficult to attribute the community-wide pattern of decline in cold-adapted species and invasion and growth of warm-adapted species to any mechanism other than climate warming. Furthermore, changes in abundance do not seem to be strongly associated with phylogeny. For example, although two of the three most rapidly declining species were from

the genus *Speyeria*, another *Speyeria* species (*Speyeria cybele*) is increasing in abundance.

Past studies of climate-induced changes in species distribution have widely shown lower-latitude species expanding into higher latitudes[4–6,8]. Range retractions have been documented, but not nearly as well[7,19]. Nearly all of the past studies have relied on changes in the occupancy of survey grid cells. Unlike expansions into previously unoccupied territory, retreating species may occupy lower-latitude range margins long after warming has occurred. These areas, however, will be increasingly marginal, and sensitive populations that remain present will decline. Populations may
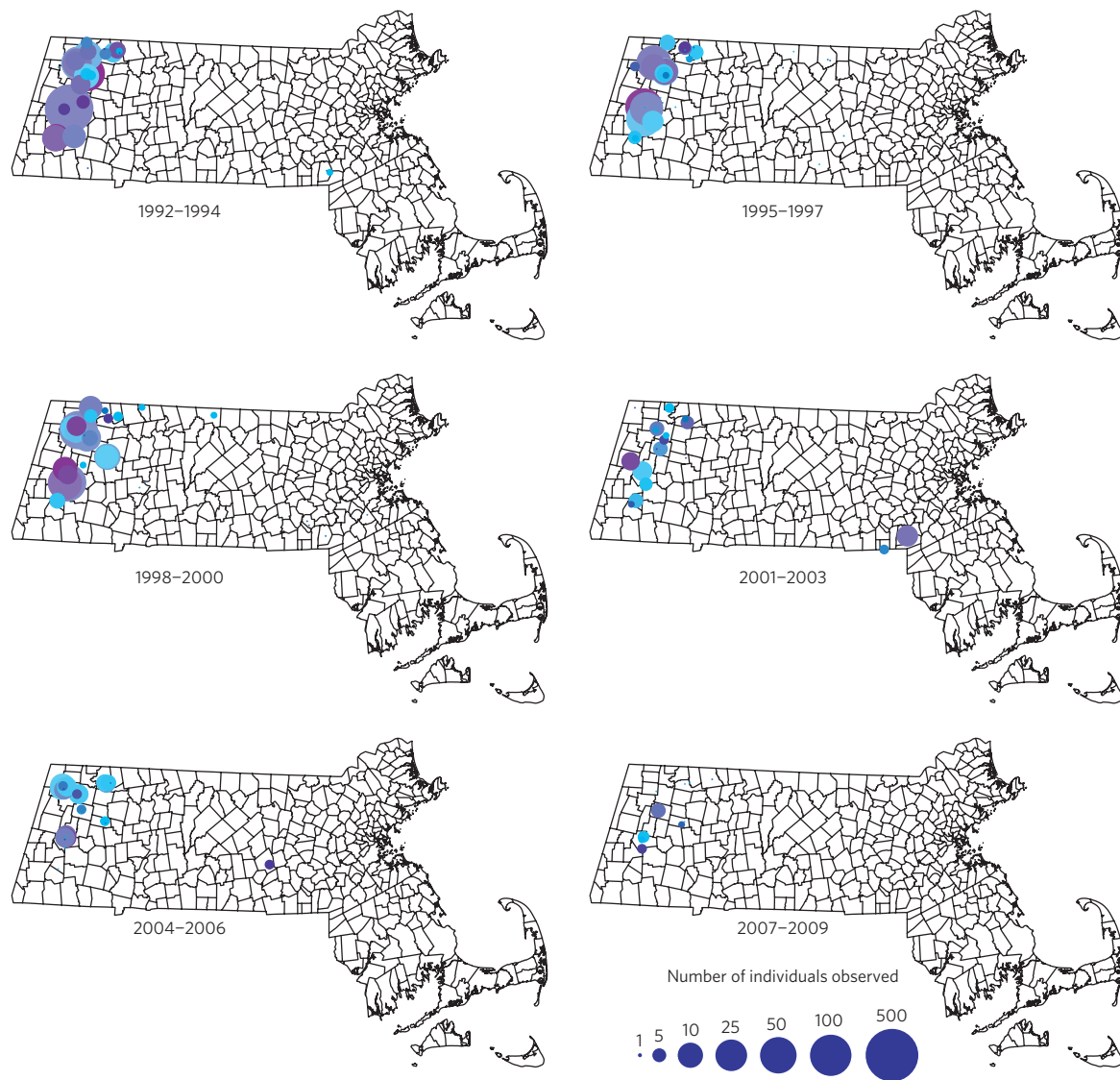
Figure 3 | Raw MBC reports for the atlantis fritillary (*Speyeria atlantis*), which is near its southern range limit in Massachusetts. Hue of each report is randomly offset so that overlapping reports are more visible. The size of the circles represents the number of individuals reported. Circle size is log scaled so that large reports do not overwhelm the map.

decline slowly or quickly and extinction may become certain in slowly declining species well before it actually occurs—a climate-induced extinction debt[19,20]. In other words, analyses of static distribution maps are likely to underestimate range retractions, whereas our approach using estimates of population trends provides much greater insight into why, and how fast, ranges are retracting or expanding.

As well as demonstrating widespread changes in butterfly communities, our results indicate that differences among species are partly predictable from life-history traits. Species that overwintered as eggs or unfed neonate larvae were highly overrepresented in declining species ($p = 0.0008$), with many of the fastest-declining species having this life-history trait (Fig. 1). Overwintering eggs and neonates are probably more susceptible to dehydration if summers, autumns and winters become warmer, dryer and with less snow cover, as they have very limited water and energy reserves and cannot actively augment them before diapause. To a lesser degree, butterflies that are obligately univoltine were also significantly over-represented in declining species ($p = 0.0117$, see Supplementary Fig. S5). One previous study tested for life-history correlates of range expansions[8]. They found that habitat availability and motility,

but not overwintering stage, explained rates of poleward expansion. Life-history traits may help to predict species' responses to climate change, but our data suggest that different life-history traits are likely to be associated with range expansions versus retractions. Life-history limitations have been experimentally shown to limit butterfly range changes in response to climate change[21,22]. Finally, mechanisms of climate change affecting overwintering mortality may be more complex than a simple warming or desiccation effect. Others have suggested that macroclimatic warming may cause microclimatic cooling through earlier bud burst and foliage growth, which cools larvae by shading and transpirative cooling, slowing larval growth in species that overwinter as larvae and mature in the spring[23].

Our results have implications for conservation policy in changing environments. In the twentieth century, habitat loss was widely cited as the leading cause of species endangerment and extinction[24,25]. Here, climate seems to be the strongest driver of population trends. Formally listing species as threatened or endangered in political units (that is, states) that are on the very edge of their climate envelope could direct funding to habitat management that has little to do with the probable long-term survival of the species.

For example, in Massachusetts, the frosted elfin (*Callophrys irus*), a southern species at its northern range margin, receives formal protection by the state. Our analysis reveals this species to be one of the fastest-growing populations in the state, with an estimated 1,000% increase since 1992 (Figs 1 and Supplementary Fig. S9 and Table S3). This trend may be owing to habitat management in response to its conservation status, but it may also be that the climate in Massachusetts has become more favourable. At the same time, two of the state's historically common and conspicuous summer butterflies, the atlantis and aphrodite fritillaries (*Speyeria atlantis* and *Speyeria aphrodite*) have declined by nearly 90% since 1992, remain unprotected and continue to decline (Figs 1 and 3). Conservation agencies should not use our results to infer that all southern species are safe nor that all northern species are doomed to extinction. However, understanding mechanisms of population decline could improve management practices and limit potentially costly efforts that will have little influence on species conservation.

Our results highlight the power of data collected by amateur naturalist organizations such as the MBC (refs 12,13). They are part of a growing number of important findings derived from observations made by citizens, including range changes, changes in phenology and the spread of invasive species and diseases[9]. Citizen science data and the further development of analytical techniques for these data can fill key gaps in our knowledge of species' responses to climate change. With appropriate analytical methods, these data will be increasingly important for detecting climate-induced changes in plant and animal communities worldwide.

Methods

Data were collected from 1992 to 2010 by the MBC and included a total of 19,779 observation trips, each one producing a list of species observed (Supplementary Table S1). Data were sufficient to estimate population trends for 100 of the 116 species observed in the state. We excluded some species owing to taxonomic realignments or changes in how the MBC reported certain taxa. Two species, the Milbert's tortoiseshell (*Aglais milberti*) and little yellow (*Pyrisitia lisa*), were excluded because their populations exhibited major outbreaks in the middle of the time series, not reflective of overall population trends. Most excluded species were simply observed too rarely to reliably estimate population trends (Supplementary Table S2).

Species lists were analysed using list-length analysis[10,11]. This method fits a three-parameter logistic regression and makes the simple assumption that the more species that are reported in a particular outing, the greater the observation effort. Adding the list-length parameter to the regression accounts for observer effort[10,11]. The other two parameters were the intercept (overall detectability) and change in detectability through time, the slope of which is a robust estimate of population trajectory. The model was fit in a Bayesian framework using the free software package WinBUGS. The model was run in two independent chains, updated 20,000 times, used a burn-in of 10,000, a thin of five and vague priors for all parameters. All diagnostics, including Rhat values, pD (effective number of parameters) and chain mixing indicate good convergence for all species we report. Life-history traits for all species in the MBC database were gathered and cross-checked from numerous published accounts[26–28]. Species were considered northerly if more than 50% of their published range was north of the city of Boston (41.78° N, 70.50° W) and were considered southerly if more than 50% of their published range was south of that line (Supplementary Fig. S1). Furthermore, we drew on records from the 1986–1990 MBA, a five-year intensive survey programme, to identify species that had recently invaded the state[17]. To assess the impact of life-history traits, we ranked species based on their estimated population trajectory, then used simple permutation tests (1,000,000 permutations) to see if particular traits were clumped in a higher-than-random chance in increasing or decreasing population trajectories.

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Author contributions

E.E.C. and G.A.B. conceived the analysis. G.A.B. coded and implemented the analysis and created all figures. G.A.B. and E.E.C. wrote the manuscript. S.S. collected, organized and maintained the MBC observations database, provided help in understanding how the data were collected and archived, and provided feedback on earlier drafts.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to G.A.B.

Competing financial interests

The authors declare no competing financial interests.