

Review



Cite this article: Kharouba HM, Lewthwaite JMM, Guralnick R, Kerr JT, Vellend M. 2018 Using insect natural history collections to study global change impacts: challenges and opportunities. *Phil. Trans. R. Soc. B* **374**: 20170405. <http://dx.doi.org/10.1098/rstb.2017.0405>

Accepted: 23 August 2018

One contribution of 16 to a theme issue 'Biological collections for understanding biodiversity in the Anthropocene'.

Subject Areas:

ecology

Keywords:

specimens, museum, range shifts, climate change, seasonal timing

Author for correspondence:

Heather M. Kharouba

e-mail: heather.kharouba@uottawa.ca

Using insect natural history collections to study global change impacts: challenges and opportunities

Heather M. Kharouba¹, Jayme M. M. Lewthwaite², Rob Guralnick³, Jeremy T. Kerr¹ and Mark Vellend⁴

¹Department of Biology, University of Ottawa, Ottawa, Ontario, Canada K1N 9B4

²Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

³Department of Natural History and the Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA

⁴Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada J1 K 2R1

HMK, 0000-0002-3250-9253

Over the past two decades, natural history collections (NHCs) have played an increasingly prominent role in global change research, but they have still greater potential, especially for the most diverse group of animals on Earth: insects. Here, we review the role of NHCs in advancing our understanding of the ecological and evolutionary responses of insects to recent global changes. Insect NHCs have helped document changes in insects' geographical distributions, phenology, phenotypic and genotypic traits over time periods up to a century. Recent work demonstrates the enormous potential of NHCs data for examining insect responses at multiple temporal, spatial and phylogenetic scales. Moving forward, insect NHCs offer unique opportunities to examine the morphological, chemical and genomic information in each specimen, thus advancing our understanding of the processes underlying species' ecological and evolutionary responses to rapid, widespread global changes.

This article is part of the theme issue 'Biological collections for understanding biodiversity in the anthropocene'.

1. Introduction

The unprecedented velocity of modern climate change, and its interaction with other global change drivers (e.g. land-use change, species introductions), has made it difficult to forecast the future structure and function of ecological communities. Recent evidence suggests widespread variation within and across taxonomic groups in species' responses to global change (e.g. [1,2]). Moreover, attempts to use biological characteristics like ecological or life-history traits to explain some of this variation have had varying degrees of success (e.g. [3,4]). Understanding the causes and consequences of this variation remains critical in order to anticipate the ecological and evolutionary impacts of global change.

For centuries, natural history collections (NHCs) have been critical for basic biological research (e.g. taxonomy, systematics [5]). Over the past two decades, these collections have played an increasingly vital role in detecting plant [6] and animal [5] species' ecological and evolutionary responses to global change. However, use of NHCs in insect global change studies are still rare and most efforts are often restricted to a few species, small geographical areas and short timeframes [7,8]. By providing information on the place and time of collection, specimens can be used to generate spatio-temporal data on the geographical distribution, phenology and other phenotypic traits of organisms. Billions of specimens have been collected all around the world over the past century [5], such that collections can provide the long-term and broad spatial

extents needed to determine the influence of multi-scale environmental change on diverse taxa.

Insects are the most diverse taxon on Earth, but they are vastly under-represented in global change research, especially relative to their diversity [9]. The most charismatic insect groups, like butterflies, are abundant in NHCs, providing a remarkable and underused resource, and a wealth of opportunities for global change research [9]. Insects play integral roles in ecological communities and ecosystems as herbivores, predators, pollinators and prey. As ectotherms, insects are highly sensitive to temperature and are often used as indicators of environmental change for other organisms [10,11]. Changing climates can directly affect insect species in several ways: including physiologically, developmentally, behaviourally or indirectly through interspecific interactions (e.g. moderated through changes to a host plant) [12]. Previous reviews have focused on the valuable role of plant collections (herbaria) in global change research (e.g. [13,14]), but few, if any, have synthesized the overall contribution of insect collections.

The aim of this review is to provide an overview of the challenges and opportunities associated with using insect collections to detect and understand the influences of the main drivers of global change—particularly climate and land-use changes—over the past century. We focus our review on the best-studied ecological and evolutionary responses: geographical distributions and phenology (i.e. the timing of recurring life-history events), as well as other key phenotypic and genotypic characteristics such as body size and melanism. We focus on responses within individual species rather than on emergent properties of biological communities.

(a) Nature of the data

Through curated collections of individual specimens, NHCs provide direct evidence of: (i) a species occurring at a particular location at a particular point in time; (ii) the identification of that species' life stage (e.g. adult); and (iii) its morphological traits (e.g. wing size [15]). Depending on the collection effort for a given species, specimens housed in NHCs are likely to have been collected from many sites across its geographical range and from different time periods; however, there is often high variation in sampling intensity for both dimensions. Because these collections necessarily consist of presence-only data, and specimen collection often reflects opportunistic sampling rather than long-term monitoring of particular sites, NHCs generally provide limited means to draw inferences about a particular species in a given location or even presence at a particular site, except for very well-collected species and locations. Inconsistent or incomplete sampling is a general problem in detecting species' responses to global change that plagues many long-term datasets [16]. In a meta-analysis with other sources of distribution data (including species atlases and citizen scientist observations), museum data were found to be the most cosmopolitan [17]. While we recognize that NHCs are often used in combination with other data sources (e.g. using field-based occurrence data to assess a species' current geographical range), here we focus on global change research only made possible by insect NHCs (e.g. estimating historical range shifts).

Following Meyer *et al.* [18], we distinguish three terms related to taxonomic, geographical and temporal information

associated with NHCs: coverage, uncertainty and bias. *Coverage* is closely related to the quantity of records whereas *uncertainty* is associated with the quality of data on each specimen. *Bias* arises when observations represent non-random samples *with respect to particular quantities of interest*. For example, geographical coverage of collection records may be biased towards areas close to towns with universities [19], but this does not necessarily constitute bias with respect to the environmental conditions across a given species range (e.g. if university towns are randomly distributed with respect to the climate within the species' range).

In the next section, we review the literature on the four key applications of NHCs—geographical changes, phenological, other phenotypic (e.g. morphological) responses and genetic responses—aimed at understanding insect responses to global change. For each application, we discuss key challenges and opportunities for future research.

2. Application 1: geographical changes

Over the past century, there have been two major causes of changes in species' geographical distributions: (i) climate and/or land-use change-driven redistributions within continents (e.g. [1,20]); and (ii) intentional or non-intentional introductions to new continents or new areas within continents and their subsequent spread. Detection and attribution of causes of species' geographical range shifts require the measurements of species' ranges from multiple time periods [21,22]. NHCs have been especially valuable in documenting 'historical' ranges, thus providing crucial baselines for detecting ongoing and widespread range shifts in many groups, including butterflies [23], spiders [24], dragonflies [25] and grasshoppers [26].

Understanding past species' responses to global change or introduction to novel environments informs predictions of the impacts of future environmental changes and, for some species, prospects for conservation. For example, NHCs were used to reveal larger range losses and slower distribution shifts in threatened versus non-threatened butterflies in Finland [27]. They were also used to show that the period of greatest range contractions and local extirpations in many bumblebee species in Illinois over the past century coincided with large-scale agricultural intensification during the middle of the century [28]. In both Europe and North America, NHCs were instrumental in demonstrating the failure of many bee and butterfly geographical ranges to track shifting climates ('climatic debts' [29–31]), and particularly acute range losses in the warmest (southern) areas [30,31]. NHCs allowed estimates of climatic debts over much longer time scales than recent plant-focused studies [32,33]. When directly compared, flying insects show smaller climatic debts than more mobile groups like birds [29], probably because they have shorter life cycles and are ectothermic.

To quantify climatic debts, NHCs provide the critical historical observations for parametrizing climate-based niche models (figure 1), which are projected (from past to present) and compared to current distributions [34]. A prerequisite for robust forecasting is the ability of models to predict changes that have already occurred [35] and these climate-based niche models have shown some success in predicting northern range shifts of Canadian butterflies over the past few decades [23,34].

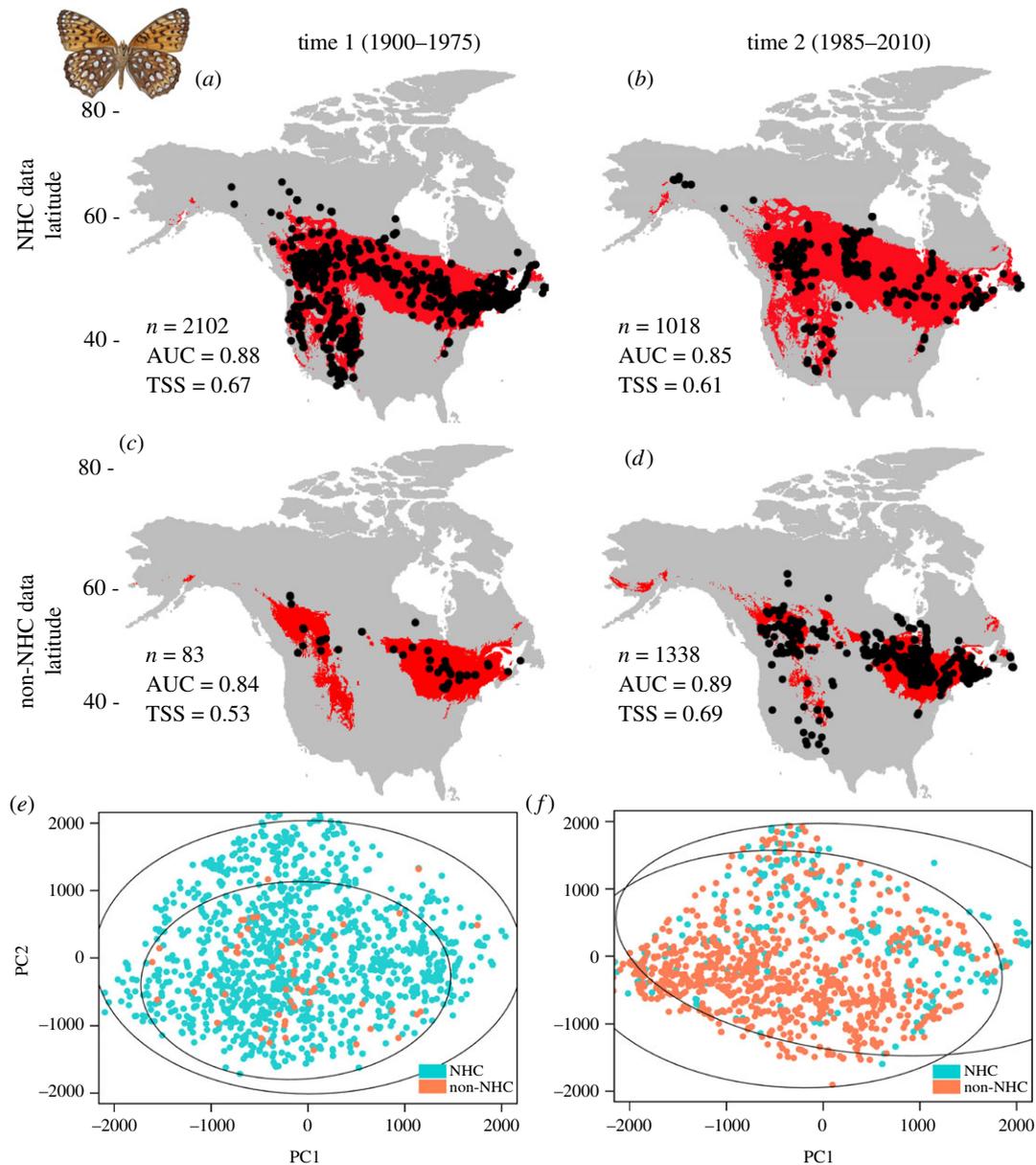


Figure 1. A demonstration of the role of NHCs in modelling species distributions using the Atlantis fritillary butterfly (*Speyeria atlantis*) as a case study. (a–d) Environmental niche models (ENMs) constructed using two sources of data: (a,b) NHCs and (c,d) non-NHCs. Models were calibrated on 1900–1975 distribution points (a,c) using an ensemble approach. The cross-validated, consensus ENM was then projected using contemporary (1985–2010) climatic conditions to model potential distributions (b,d). Observed distribution data for each respective time period is overlaid (black dots). See [34] for a complete description of the modelling methods. Goodness of fit for each ENM was measured using area under the curve (AUC) and the true skill statistic (TSS). Also shown is a principal component (PC) analysis of the climate space occupied by *S. atlantis* from (e) 1900 to 1975 and (f) 1985 to 2010, where green points are NHCs and orange are non-NHCs (95% confidence intervals (CIs) are indicated by the ellipses). Occurrence data from NHCs are from the Smithsonian Institute’s National Museum and Global Biodiversity Information Facility (GBIF), and the occurrence data from non-NHCs included: eButterfly, the Toronto Entomological Association and records from GBIF not labelled as a museum collection. (Online version in colour.)

NHCs have been used less often to study species invasions than to study native species’ range shifts. They can provide invaluable historical occurrence data [17] that help distinguish historically unprecedented introduction and range expansion events from periodic recolonizations of a given geographical area [36]. A common use for NHCs is in the quantification of a species’ native range [19], from which niche models can be constructed and then used to predict potentially suitable areas in the introduced range—an approach that has been applied to a couple of Asian beetle species in North America [37]. NHCs have also been used to determine the timing of initial establishment of exotic ants on islands [38] and the harlequin ladybird beetle

(*Harmonia axyridis*) in South Africa [39], as well as the rates of range expansion of exotic ant species [40]. Assembling observations across entire biological communities from NHCs have been used to measure the impacts of invasive ant species on community structure [38].

NHCs can be used to understand conditions enabling successful invasions [40,41]. For example, Ward *et al.* [40] used NHCs to determine that new occurrence records of the Argentine ant in New Zealand were too far from known populations to be explained by natural dispersal and concluded that human-mediated dispersal was the primary driver of invasive spread. For a globally widespread invasive ant species (*Linepithema humile*), Roura-Pascual [41]

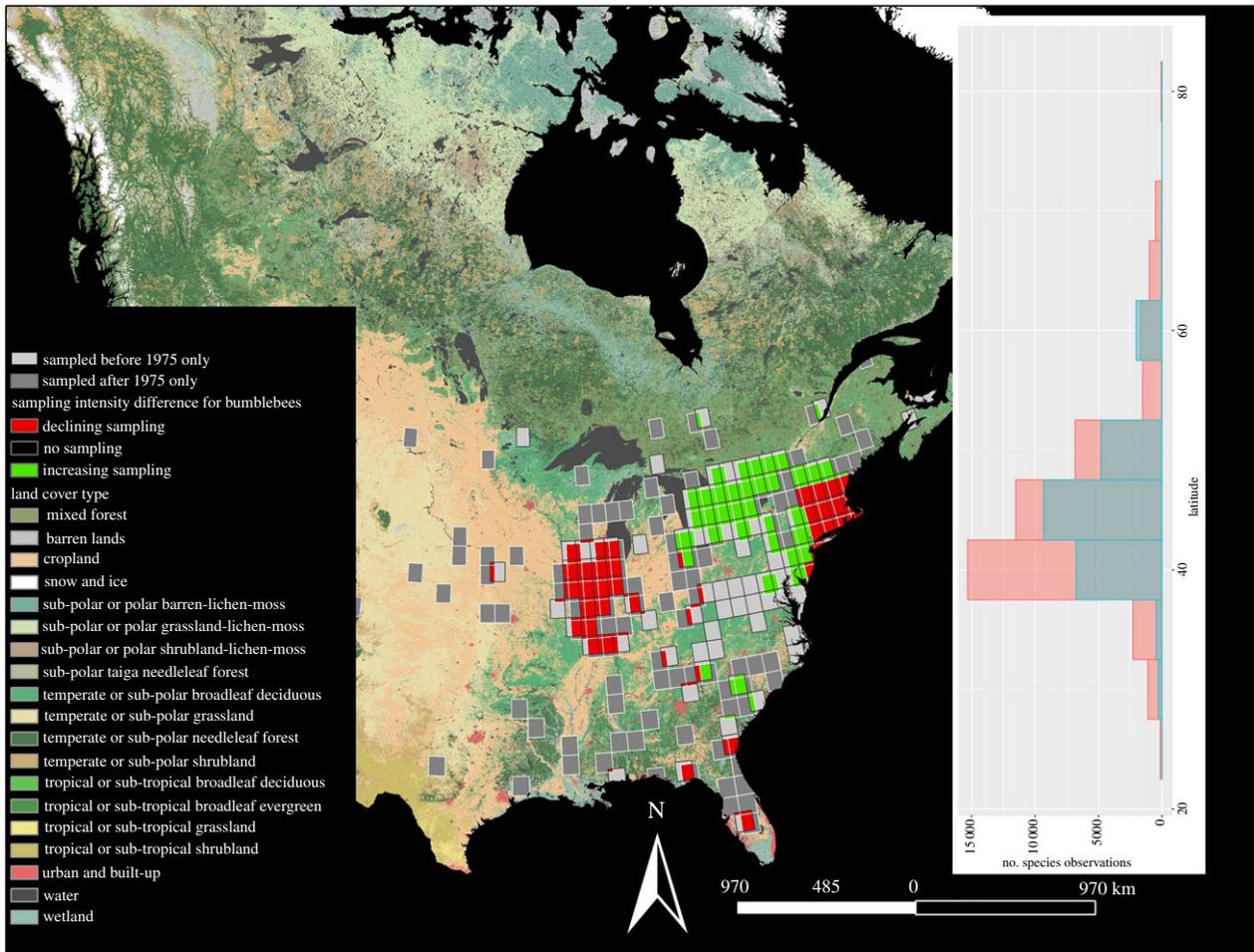


Figure 2. Differences in sampling intensity for bumblebees in eastern North America between 1900–1975 and 1976–2010. Blocked out areas of dark green show increasing sampling intensity, while red colours indicate declining sampling intensity between these time periods. Areas of light grey were sampled in the first time period but not in the second, and areas in dark grey were sampled in the second time period and not earlier for this group of species. The background is MODIS land cover data for North America (250 m resolution) for 2005. The inset histogram shows variation in sampling intensity with respect to latitude between the time periods, with red showing sampling in the earlier time period and light showing sampling by latitude in the later time period. See [31] for a complete list of data sources and methods. (Online version in colour.)

used NHCs to show that climatic suitability and extent of human-modified habitats best predicted invasive spread. Despite the well-known link between human presence and the distribution of invasive species, relatively few studies have specifically tested human influence as a driver.

(a) Challenges

Detecting and explaining geographical range shifts among insects or other taxa using NHCs is challenging for several reasons. First, specimen collections typically do not provide information about species' absences [42]. Second, geographical coverage of records is typically biased towards accessible, populated or economically prosperous regions. Inaccessibility has limited Arctic insect collection [43] relative to other areas, and exploration of insect diversity in persisting wilderness areas remains severely limited [42]. Although many NHC databases are global in their focus (such as the Global Biodiversity Information Facility), they are notably data-deficient in some of the world's biodiversity hotspots [44] and data concentration is skewed towards northern temperate latitudes [45]. For some applications (e.g. niche modelling), geographical gaps in sampling matter only to the extent that gaps are biased towards particular combinations of environmental conditions [19] (figure 1), as was found to

be the case for most of the dung beetle species' modelled in the Madrid region of Spain [46]. Geographical uncertainty, typically more problematic in historical records, also further reduces our ability to detect range shifts.

Collection gaps near species' range margins, where populations may already be sparse [47] and ephemeral [48], create acute challenges for determining whether a 'new' observation in a given area represents range expansion or simply a failure to detect historical presence. In the context of climate warming in the northern hemisphere, a lack of northern records either early or late in the data record could lead, respectively, to commission errors (predicting range expansion when it did not occur) or omission errors (predicting no range expansion when it did occur).

Sparse temporal coverage (both within and across years) and biases also present challenges. Insect species, even when common and/or highly mobile, can be missed in well-collected areas if they have short-lived adult life stages and specimens are collected over brief time periods [42]. There is a little quantification of temporal bias in insect collections but some evidence for bumblebees in North America suggests geographical variation in sampling intensity changes over the past 120 years (figure 2). Comparatively, there have been increases in collections over time for Canadian butterflies [49]. These patterns contrast with some

herbaria where the frequency of collections has declined in recent decades as field biologists shifted from taxonomic to ecological studies [50,51].

More broadly, there is a scarcity of insect range-shift studies in Asia, Africa and South America (although this is beginning to change; e.g. [52]). We might also expect—as is the case for plants [50]—less frequent sampling of non-native species, even in countries with strong collecting traditions. Recent digitization initiatives such as the Darwin Initiative and the Advancing Digitization of Biodiversity Collections programme in the USA, have begun assisting in these efforts [35].

(b) Opportunities

Recent advances in occupancy modelling aim to increase the robustness of estimates of range changes given uncertainties in NHC data for insects and other taxa [22]. Addressing sampling gaps is vital in global change applications of NHC data and new techniques in Bayesian and maximum-likelihood models [53] offer great improvements over algorithms that do not account for sampling biases. For detecting range shifts, one key advance is the probability of false absence tests (*P_{fa}*), which incorporate the number of surveys across a set of unoccupied sites to calculate the likelihood of a historic absence [22]. This approach provides a confidence estimate for observations of absence, helping to distinguish actual range shifts from apparent range shifts owing to data limitations (i.e. false absences in the historical data). Another advance is the use of a maximum probability approach where a species' environmental optimum is determined based on the maximum probability of occupancy across an environmental gradient [54]. Any recently documented range shift (and the environmental conditions within the colonization zone) is compared to the historical optimal range to judge whether it is more likely to be a true shift in distribution or a temporary fluctuation in a range limit [53]: newly occupied sites that are closer to a species' optimal conditions are considered more probable shifts rather than fluctuations. A major caveat of both of the above occupancy models is that they require repeated surveys at the same locations, which are rare in most NHCs. With further improvements in occupancy models, we are optimistic that they can provide useful predictions of future range shifts.

Relative to their use in documenting range shifts of native species, NHCs have been vastly underused in recording the spread of introduced insects. Moreover, insects have received far less attention compared with other taxa, such as plants, vertebrates and aquatic organisms [6,55], yet their geographical distributions are predicted to expand in the future to a greater degree than other groups like plants and birds [56]. For studies of introduced species, methods are being developed and applied in other taxa to account for biases such as the under-sampling of non-native species, including curves that compare the cumulative area occupied by native versus introduced species [50]. In poorly sampled areas, the ranges of native species may increase through time simply as a function of improved spatial sampling and coverage; quantifying such apparent range expansion provides a baseline 'null' rate against which to compare introduced species [50]. While this approach has been applied to herbarium specimens of several invasive plant species [50], it has not yet been applied to insects.

Insect NHCs can also provide information about changes in the geographical distribution of other taxonomic groups. Insect specimens could be examined for the presence of parasitoids, parasites, pathogens or even pollen [57]. For example, the composition of pollen loads on the specimens of bumblebees in northwestern Europe was used to show distribution changes in flowering plant taxa over the past century, including the spread of an invasive plant species [58].

3. Application 2: phenological responses

Despite the potential of NHCs to provide phenological data over long timeframes [35], they have only recently been used as a tool to measure phenological shifts owing to climate change, a commonly documented response. Moreover, very few studies have focused on insects. Insect NHCs most often consist of specimens of adults. Therefore, NHCs can be used to estimate the timing (phenology) of adult activity. NHCs have been shown to provide estimates of phenology comparable to those generated using field observations, despite possible biases inherent in both types of data [17,51]. For example, the average collection date of bee collections was found to be a valid proxy for peak adult activity in bees estimated from field observations [59]. Comparisons to the 10th percentile for mean first appearance date were also found to be accurate [51].

Thus far, NHCs have been used to show that over the past century in North America, the UK and Europe, Lepidoptera (mostly butterflies) and bees have shifted the timing of adult activity earlier in the year and increased the number of generations per year [49,59–64] over the past century. NHCs have also helped to shed light on variation in temperature sensitivity of phenology (days °C⁻¹) within [49,51] and across taxonomic groups like bees [59,63] or butterflies [64,65] and their host plants, or between different types of pollinators [62]. Estimates of phenological sensitivity to temperature using NHCs appear to be comparable to estimates derived from other methodological approaches ([62]; but see [59]). Understanding interspecific variation in temperature sensitivity is a key challenge for future research as species with different temperature sensitivities are likely to show different responses to global changes.

(a) Challenges

While some studies using NHCs have demonstrated insect phenological shifts over time, other studies did not detect temporal trends [49,59–64]. The detection of directional phenological trends over time has been shown to depend on the ecological or life-history strategy of the species (e.g. generation length [49,62]), the type of data (e.g. atlas versus incidental sampling [62]) and the timeframe of study [65] (figure 3). This is unsurprising given that long-term phenological trends are easily obscured by interannual variation [66]. This is exacerbated when there is low and/or uneven temporal coverage (within and across years) for species in NHCs, or in the presence of large interannual variation in temperature across locations [65]. Together, these issues can lead to increased uncertainty around estimates of phenological shifts (figure 3). Indeed, studies using NHCs are less likely to detect phenological trends than studies of the same species using direct and systematic observations (e.g. [51] versus [67]). Kharouba *et al.* [49] suggest that at least, at

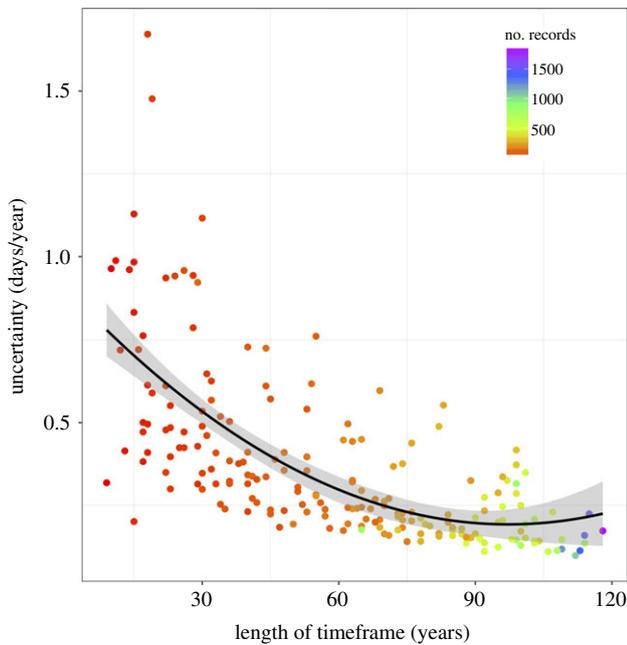


Figure 3. The relationship between uncertainty around estimates of butterfly species' phenological shifts (days/year) over the past century across Canada and the length of time frame (years) for each species ($n = 196$). Uncertainty was measured as the length of the 95% CI for each estimate of phenological shift (days/year). The distribution of number of records across species is shown. The line of best fit with the 95% CI ($y = 0.9 - 0.02x + 0.0008x^2$) is also shown. Data were taken from [49]. (Online version in colour.)

broad scales, the difference is unlikely to be owing to temporal sampling biases of butterflies (e.g. systematically surveying earlier in warmer years). However, the likelihood of these biases remains to be formally tested.

NHCs have shown more potential for quantifying interspecific variation in the sensitivity of adult flight timing to temperature. However, adult flight time may not be representative of other life stages: recent evidence shows that there is variation across ontogenetic stages in temperature sensitivity [68,69] and the metric of the temperature of greatest relative importance [70]. Therefore, organisms with complex life cycles, where different environments are experienced during different life stages, are likely to have differing responses of each life stage [68].

Finally, given the complexity inherent to phenological records assembled over long timeframes (e.g. temporal autocorrelation, non-stationarity), there are statistical challenges when applying NHCs to detect and understand phenological responses of insects and other taxa to climate change [71,72]. However, these issues are rarely accounted for in studies using NHCs, potentially affecting the robustness of their conclusions. Recent advances in statistical techniques and approaches aim to deal with these complexities more rigorously. For example, MacGillivray [73] established the existence of nonlinear trends in peak flowering using herbarium records by applying generalized additive models for location, scale and shape. Bayesian approaches can more comprehensively account for uncertainty [71] and the recent developments of more accessible packages (e.g. Stan (www.mc-stan.org)) in open-source statistical computing platforms (e.g. R (www.r-project.org)) will hopefully increase the application of these methods to phenology studies using NHCs.

(b) Opportunities

An as-yet underexplored opportunity using NHCs is to use the sex associated with specimens to test for differential responses of male and female insects to climate change. Distinguishing responses between sexes could help understand the impacts of climate change on the success of mating processes, effectiveness of pollination and refine estimates of species-level phenological sensitivity to temperature [59]. For example, studies using NHCs have found that female butterflies are flying progressively earlier in recent decades than males [64] and female bees are more responsive to temperature than males [59].

NHCs may also provide a critical but so far underused resource for examining the possibility of shifts in the timing of species interactions over longer time scales and with more species than local field studies. A recent exemplary study by Robbirt *et al.* [59] used NHCs for plants and insects (covering greater than 100 years), along with field observations, and showed that a pollinator and its host showed differential phenological responses to climate change, which is likely to lead to temporal mismatches under future climate scenarios. The rapidly expanding digitization of NHCs could greatly expand the potential for addressing phenological mismatch questions.

4. Application 3: responses in phenotypic traits

Insect NHCs provide not only spatial and temporal occurrence information, but whole preserved organisms, and therefore the possibility of examining phenotypic responses to global change. Particularly notable are studies of body size responses to global changes [70,74–77]. These studies are among the first to explore global change-driven body size changes in insects, a group whose body size changes were previously not well studied [78]. For instance, stream-dwelling beetles in the southern USA [64] and the butterfly *Melitaea cinxia* in Sweden [79] have increased in body size in recent decades owing to land-use [79] and climate changes [64]. Conversely, predatory bugs (*Orius*; Heteroptera: Anthrenidae) in Israel [76] and a population of wild honeybees (*Apis mellifera*) in the USA [80] have shown no change [76] or a decline in body size over the past few decades [76]. Based on results from studies on beetles in Israel [76] and British Columbia, Canada [77], some of the interspecific variations in temporal changes in body size can be accounted for by the mean body size of the species, with larger bodied beetles decreasing in size over time the most [77]. As Bartomeus *et al.* [81] showed with nearly 50 000 bee specimens, a larger body size, as well as a limited phenological breadth (i.e. number of days of adult activity per year), can also correlate with a decreased abundance over time in the face of climate change. Using NHCs allowed these last few studies to move beyond the documentation of localized effects on body size and to define broad-scale patterns in body size changes in response to climate change.

NHCs have also been used to study phenotypic traits—other than body size—underlying evolutionary responses of insects to global changes. For example, Carroll *et al.* [82] showed that the mouthparts of the Australian soapberry bug (*Leptocoris tagalicus*), measured on NHC specimens, have increased significantly in size to take advantage of larger fruits from an invasive Neotropical balloon vine

(*Cardiospermum grandiflorum*). Traits that affect thermoregulatory capacity, such as wing melanism and body size, are expected to respond to climate warming. However, MacLean *et al.* [83] found results counter to expectations: wing melanism and body size in the sulfur butterfly (*Colias meadii*) was found to increase with warming temperatures over time, thus challenging models of evolutionary response to global changes.

(a) Challenges

Similar to the other applications, uneven sampling efforts can limit the power to detect trait changes in studies based on insect NHCs. Data for most insect taxa are too sparse to measure shifts in particular species' traits through time or across environmental gradients. This is particularly problematic for more integrative studies that aim to consider multiple responses simultaneously and are thus data-hungry. Where such records have not been collected in the past, there is no solution to this challenge. However, the digitization of collections, with specimen imaging and rapid expansions of databases containing curated specimen information in standardized formats, promises to expose particularly useful historical collections for study and for potential targeted resurveys (e.g. [84]).

(b) Opportunities

Integrative studies that fully use NHCs, now enabled via digitization, are still emerging. One of the most exciting research avenues will require more than just digital products: physical specimens offer untapped potential for isotopic studies [85]. Ratios of stable carbon and nitrogen isotopes in specimen tissues provide a record of diet and habitat change through time and allowed English *et al.* [85] to infer a decline in the contribution of insects to insectivorous bird diets over a 125-year period. More common applications of cutting edge imaging techniques such as micro-computed tomography scanning, promise to provide dense internal and external morphological data [86] coupled with three-dimensional morphometric approaches. For example, taxonomically important characters, such as genitalia in male Lepidoptera, can be distinguished using pinned specimens [86]. Application of these approaches using insect NHCs is in its infancy.

5. Application 4: responses in genotypic traits

Specimens from NHCs are increasingly being used for the genetic and genomic information they harbour to help shed light on the evolutionary component of species responses to global change. With the advent of next-generation sequencing and optimization of DNA extraction techniques, it has become much easier to successfully extract and sequence DNA from museum specimens [87], including insects. Sequencing studies across a species' range often look for signals of adaptation to spatial environmental variation [88] and the same conceptual approach could be applied temporally. By providing historical samples before episodes of environmental change, NHCs can provide a means of inferring demographic changes (e.g. population declines or expansions) over time [89]. For example, Mikheyev *et al.* [80] conducted whole genome sequencing on individuals from NHCs and current populations. Their results suggest that

genetic diversity may have buffered populations of wild honeybees (*Ap. mellifera*) through bottlenecks caused by introduced *Varroa* mite parasites. Similarly, historical NHCs for four British bumblebee species that were introduced in New Zealand were compared to modern populations to study the genetic impact of 100-year old population bottlenecks and novel environments [90]. NHCs of the garden tiger moth (*Arctia caja*) in the UK were used to reveal a loss of genetic diversity, as well as significant changes in wing size and shape, following a widespread population crash in the 1980s [91].

Molecular genetic and genomic approaches are also yielding insights into insect invasions. NHCs offer unique opportunities to examine the genetic variation of populations during the multiple stages of invasions over long time scales [57]. Recently, Cridland *et al.* [92] used museum specimens of the introduced honeybee (*Ap. mellifera*) to analyse the impact of demography and selection on introduced populations during the past century. They discovered hundreds of candidate genes underlying recent adaptations, including potential resistance to parasitic mites in their invaded range. Herbaria can also provide information about historic insect distributions. Using DNA from larvae of a leaf-mining moth (*Cameraria ohridella*) pressed within leaves of herbarium samples collected as early as 1879, Lees *et al.* [93] revised the date of introduction of this herbivorous species to Europe by more than a century and uncovered previously unknown mitochondrial haplotypes and locally undocumented alleles. The authors also documented genetic homogenization across the species' range following the invasion, which led to questions about how allele frequencies have changed, and whether these are associated with any genes that enable invasion success [93].

(a) Challenges

Using NHCs to explore evolutionary responses to global changes face some unique challenges that affect inferences made about insects and other taxa. First, given the low sample size and inconsistent spatio-temporal sampling typically associated with insect NHCs, specimens are sometimes pooled to obtain a useful sample size but this can reduce overall heterozygosity [90]. Second, there remain few reference genomes for insects (relative to their diversity), which can complicate genome assembly and the assessment of gene function. Third, in addition to the sampling biases mentioned in earlier sections, certain morphotypes of a species may be more likely to be captured owing to visibility (e.g. more colourful) or ease of detection (e.g. larger), resulting in biased samples of genetic variants in a given population [89,94]. Lastly, old specimens may accumulate more DNA damage, which can produce biases in genome mapping [80]. However, some potential biases, for example in allele frequencies, can be tested against theoretical expectations from population genetics to help guide quality control [80].

(b) Opportunities

To date, there have been few studies applying genetic and genomic approaches to insect NHCs, but there is great potential [89]. For example, in other taxa, researchers have combined NHCs with modern data to (i) improve our understanding of the genetic consequences of range dynamics (e.g.

in chipmunks [95]); and (ii) predict future vulnerability of populations to climate change based on relationships between allele frequencies and climate variation (e.g. in a migratory bird [96]). Genetic data could also help identify potential source populations that are pre-adapted to the environmental conditions in target sites for assisted colonization [97]. With the rapidly declining costs of molecular analyses and the availability of new approaches that are well-suited for the type of DNA that is common in historical specimens (i.e. small amount, fragmented), we anticipate a wave of new studies based on DNA extracted from NHCs to address a wide range of issues involving rapid evolution, demographic changes or the consequences of invasive spread.

6. Final remarks

NHCs have made important and unique contributions to our understanding of how insects are responding to global change. In many of the studies we reviewed, NHCs provided the only means of achieving the necessary temporal depth to examine long-term change in distributions, phenology, morphological traits or genetic variation. While historical sampling is one of the most unique benefits of NHCs, it is also one of the biggest challenges: historical data are often accompanied by uneven coverage and sampling biases in space and time. Nevertheless, recent work demonstrates the enormous potential of NHCs for examining insect responses at multiple temporal, spatial and phylogenetic scales.

We have outlined several research avenues to enhance the role and impact of NHCs in understanding and predicting the ecological and evolutionary consequences of climate change for insects. Here we can highlight the overarching

issue of more carefully defining baselines that predate rapid recent warming (e.g. before the early 1980s in some regions [21]). Defining appropriate baselines can put shorter-term trends (i.e. 5–30 years) into context against longer-term trends (i.e. past century) and natural fluctuations [16,70]. In well-collected areas (e.g. North America, Europe) and for well-collected species, NHCs can provide sufficient data to define historical baselines.

Finally, the value of NHCs can be greatly amplified when integrated with other types of biological data (e.g. physiological, genetic and monitoring data) and when multiple responses are considered simultaneously. The weaknesses of NHC data (e.g. spotty temporal coverage) and its strengths (e.g. long timeframe) are often the perfect complement of the strengths (e.g. yearly data) and weaknesses (e.g. short timeframe) of contemporary monitoring studies. Integrated studies with NHCs and the continued long-term monitoring of relevant traits (e.g. body size, phenology), as well as sustained specimen collection and deposition in NHCs [35,70], will help forecast the future of the most diverse group of animals on Earth.

Data accessibility. This article has no additional data.

Authors' contributions. H.M.K. and M.V. drafted the outline of the manuscript; all authors wrote and edited the paper; H.M.K., J.M.M.L. and J.T.K. produced figures.

Competing interests. We declare we have no competing interests.

Funding. J.M.M.L. was supported by a Natural Sciences and Engineering Research Council of Canada Postgraduate Scholarship. H.M.K. was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant.

Acknowledgements. We thank the editors for their invitation to contribute to this issue.

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