INVITED REVIEWS AND SYNTHESES
Natural history collections as windows on evolutionary processes

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Abstract

Natural history collections provide an immense record of biodiversity on Earth. These repositories have traditionally been used to address fundamental questions in biogeography, systematics and conservation. However, they also hold the potential for studying evolution directly. While some of the best direct observations of evolution have come from long-term field studies or from experimental studies in the laboratory, natural history collections are providing new insights into evolutionary change in natural populations. By comparing phenotypic and genotypic changes in populations through time, natural history collections provide a window into evolutionary processes. Recent studies utilizing this approach have revealed some dramatic instances of phenotypic change over short timescales in response to presumably strong selective pressures. In some instances, evolutionary change can be paired with environmental change, providing a context for potential selective forces. Moreover, in a few cases, the genetic basis of phenotypic change is well understood, allowing for insight into adaptive change at multiple levels. These kinds of studies open the door to a wide range of previously intractable questions by enabling the study of evolution through time, analogous to experimental studies in the laboratory, but amenable to a diversity of species over longer timescales in natural populations.

Keywords: environmental change, evolution, genomics, morphology, natural history collections, phenotypic change

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Natural history collections as records of evolutionary change

Most of evolutionary biology is retrospective: we look at the present and attempt to make inferences about the past. For example, the distribution of a trait among species today can be used to infer the origin and evolution of that trait in the past. Similarly, patterns of genetic variation in present-day populations can be used to infer how allele frequencies have changed over the recent past. While powerful, these approaches are indirect, based on inference, and thus depend on assumptions of the underlying models. Observing evolutionary change directly is more difficult and typically comes from either laboratory studies of evolution or from very long-term field studies. Laboratory studies of experimental evolution over multiple generations are extremely powerful but are necessarily limited to organisms with short generation times (Barrick & Lenski 2013). These studies have mainly been conducted with microbes such as viruses (e.g. Wichman *et al.* 2005), bacteria (e.g. Wiser *et al.* 2013) and yeast (e.g. Lang *et al.* 2013) or with small multicellular organisms such as *Drosophila* (Burke *et al.* 2010). As these studies rely on the relatively simple conditions of a laboratory environment, it is often unclear how to extrapolate from them

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to the more complex conditions of natural populations. Long-term field studies have produced some spectacular successes with direct observations of evolutionary change in complex organisms (e.g. Coulson *et al.* 2001; Grant & Grant 2002), but such studies often require decades of work in challenging field environments and are still relatively rare.

Natural history collections (NHCs) offer an alternative way to study evolution over reasonably long timescales (Fig. 1). NHCs constitute an impressive record of life on earth with billions of specimens housed in museums around the world. These collections have provided a rich source of material for studies of phylogenetics, biogeography, conservation and many other areas of ecology and evolutionary biology (Suarez & Tsutsui 2004). However, the value of museum collections for studying the process of evolution directly – as genetic and phenotypic changes in populations through time – is less appreciated.

Collections provide a historical record of specimens against which modern samples can be compared, with many collections dating back 100 years or more. For organisms with short generation times, this represents a timescale over which substantial changes in allele frequency can be expected if selection is strong. Comparison of historical and modern samples can be used to study changes in phenotype, genotype or both (Box 1). If changes in the environment are well documented, in some cases it is even possible to ascribe observed changes to specific selective forces.
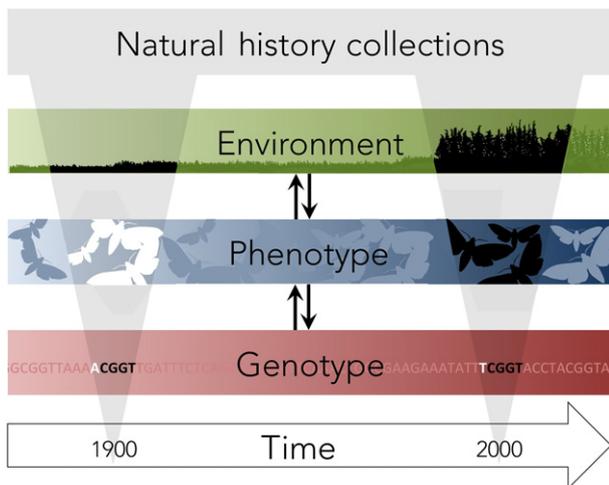

Fig. 1 Natural history collections provide specimens dating back, in some cases, over 100 years. These large repositories provide an opportunity to study evolution in response to changes in the environment. Whereas it has always been possible to study phenotypic change, new advances in genomic techniques are allowing researchers to also study the impacts of environmental change on genetic processes.

Here, we review developments in this new field, highlighting the potential for NHCs to be used as resources to study evolutionary change directly. First, we document the extent of available collections in major museums and the associated data that enable this kind of study. Next, we describe some of the major anthropogenic environmental changes that are likely to have acted as agents of selection over the timescales in question. We then discuss the use of genetic and genomic tools to study evolutionary change using collections, focusing on empirical studies as well as theoretical approaches that utilize time-series data. Finally, we discuss studies that have focused primarily on phenotypic changes, highlighting those with greatest potential to make links between genotypic and phenotypic changes over time.

Natural history collections are large and diverse

Natural history collections worldwide contain large numbers of plant and animal specimens (Fig. 2). Nearly 90% of all specimens consist of insects, marine invertebrates and fish, and these are usually preserved in 'lots' consisting of groups of specimens. The holdings of select taxa in several of the best-known collections are summarized in Fig. 3A. Specimens may include dry skins, skulls, skeletons, fluid-preserved whole organisms, frozen tissue samples, pressed plants, pinned insects, nests, eggs, seeds, scat and gut-contents, parasites, and cleared and stained organisms (Table 1). Different traits are preserved in this variety of specimens, permitting a wide range of studies. Since the 1970s, frozen tissues have often been preserved along with other kinds of specimens, facilitating molecular studies.

In addition to the specimens themselves, collections often contain detailed supplementary data such as field notes, observations, georeferences, audio/video recordings and photographs (Table 2). Georeferences and photographs enable precise revisitation of historically surveyed sites to provide contemporary points of reference. Field notes can be used to calculate sampling effort and measure population densities. Field notes and photographs may also provide insight into the changes in overall community structure over time. For example, along with collections of bird and mammal specimens from extensive surveys in the western United States, Grinnell (1943) left detailed field notes and photographs of collecting localities. These ancillary data allowed for precise site revisitation and replication of survey methods in contemporary resurveys, in addition to providing supplementary occurrence and nonoccurrence data, all of which were essential to the documentation of extensive shifts in avian species richness over the last century in the Sierra Nevada mountains (Tingley *et al.* 2012; Tingley & Beissinger 2013).

Box 1. Case study: changes in stickleback armor over 50 years
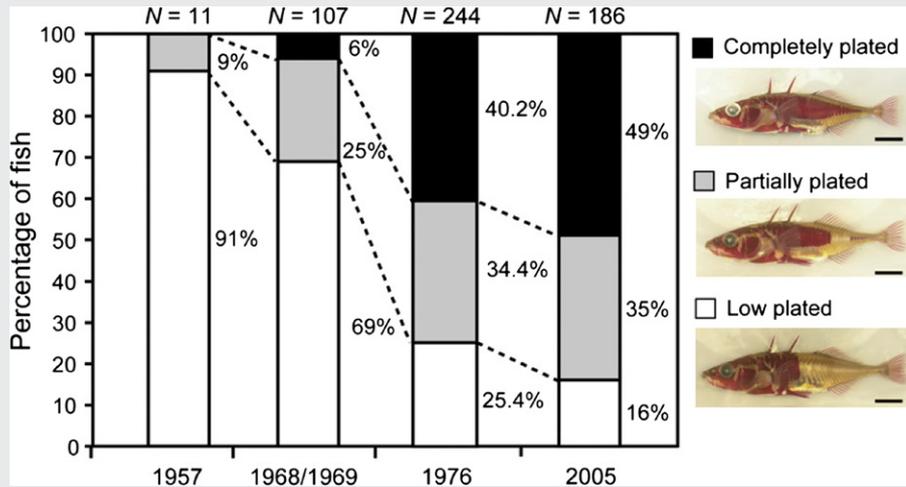
Kitano *et al.* (2008) examined threespine stickleback fish, *Gasterosteus aculeatus*, specimens from Lake Washington, WA, to show that over a 48-year period (equivalent to 48 stickleback generations) the frequency of the completely plated morph had significantly increased. The graph shows the proportion of completely plated (black) to partially plated (grey) and low plated (white) fish at four time points (1957, 1958–9, 1976, 2005); sample sizes are listed on the top of each bar. In combination with behavioural tests and lake transparency data collected over time, these data led the authors to hypothesize that an increase in lake clarity due to the prevention of eutrophication had allowed trout to increase their predation on sticklebacks, acting as a selective force for increased plating. Genotyping revealed that the *EDA* gene largely controls this morphotype. This example, which combines morphological data from museum specimens, environmental data collected over time, and genetic analyses, illustrates the power of placing a time series of museum specimens in an ecological context to demonstrate adaptive evolutionary change. Figure reproduced from Kitano *et al.* (2008).
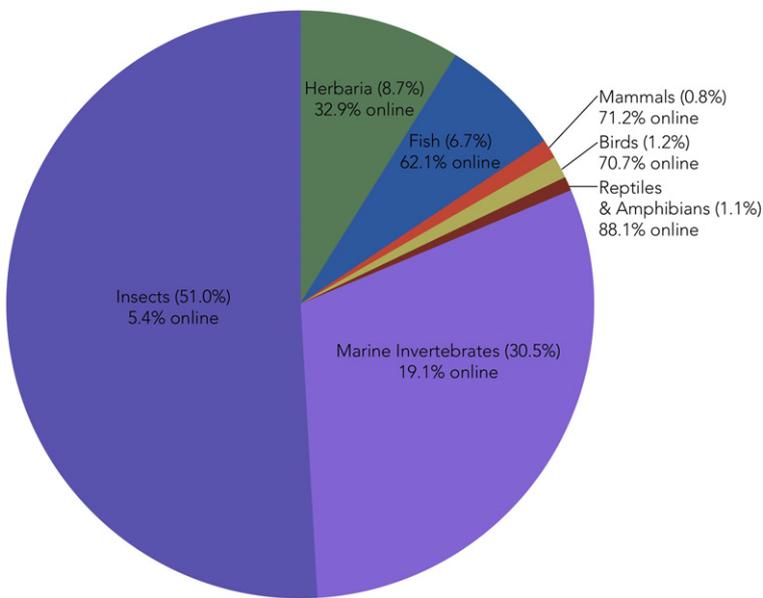

Fig. 2 Overview of holdings from a sample of thirteen well-known NHCs that together house approximately 392 million individual specimens. Holdings are colored by taxonomic group. The exact proportion of specimens accounted for by each group is listed in parentheses; the percentage of each group that is digitally databased and online-accessible ("online") is also listed. For fish, insects and other invertebrates, collections are typically made as lots, where individual lots may contain tens to thousands of specimens, thus, estimates for the number of specimens in these collections are approximate. The 13 NHCs summarized here are listed in the caption for Fig. 3
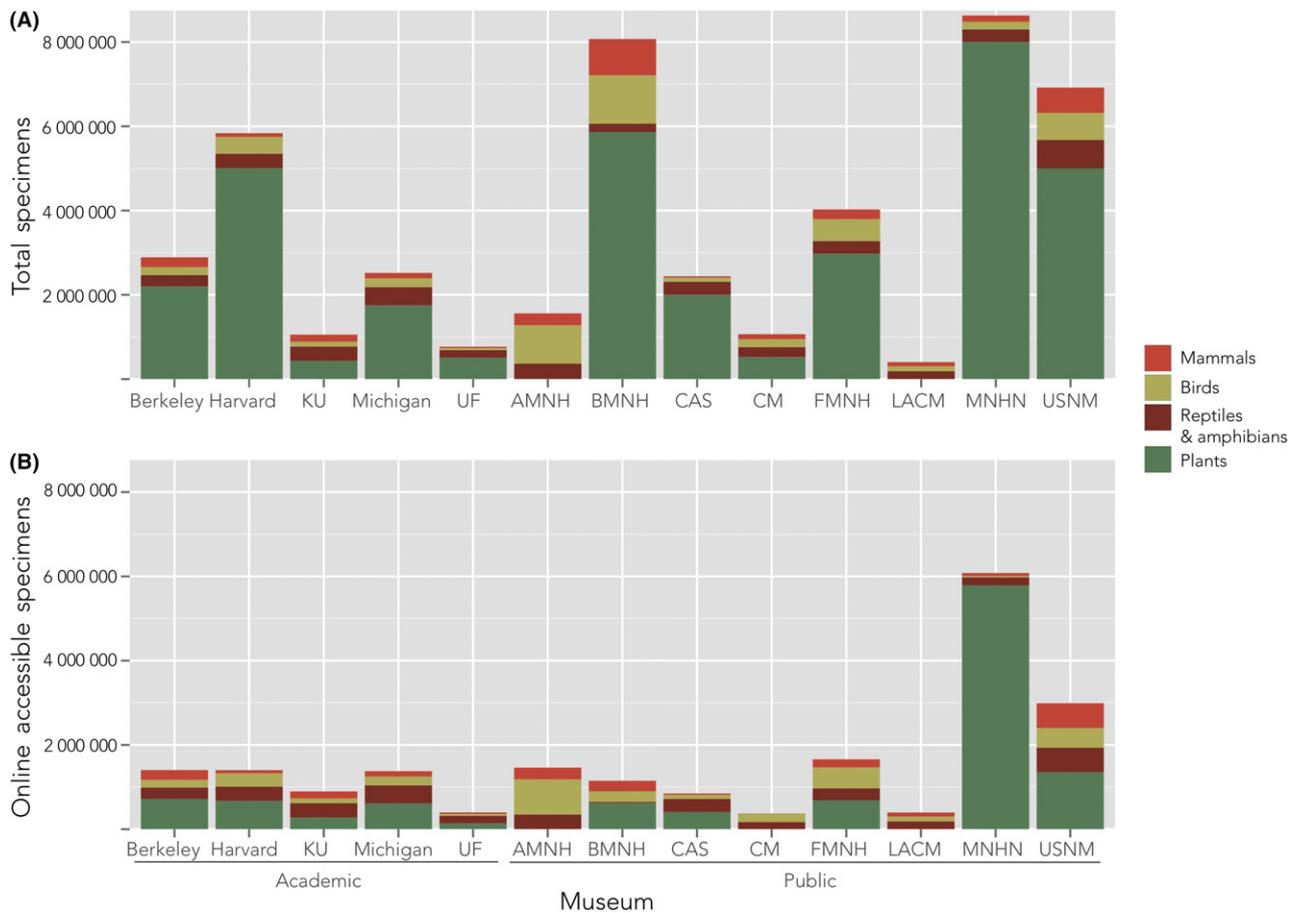
Fig. 3 Overview of available specimens in terrestrial vertebrate and herbaria collections in thirteen of the world's most diverse and well-known academic and public collections. (A) Total number of specimens in several major taxonomic groups. (B) Number of specimens that are digitally databased and available online. Numbers were acquired from museum websites, online databases, and/or from curators and are estimates, as collections and digitization efforts are constantly growing. Estimates for many herbaria include plants and fungi; we have not distinguished between these taxa here. This figure includes only non-lot-based taxonomic groups, which are easier to precisely quantify in a standardized manner. Abbreviations: Berkeley: Berkeley Natural History Museums, Berkeley; Harvard: Harvard University Herbaria and Museum of Comparative Zoology, Cambridge; KU: University of Kansas Biodiversity Institute, Lawrence; Michigan: University of Michigan Herbarium and Museum of Zoology, Ann Arbor; UF: Florida Museum of Natural History, Gainesville; AMNH: American Museum of Natural History, New York; BMNH: Natural History Museum, London; CAS: California Academy of Sciences, San Francisco; CM: Carnegie Museum, Pittsburgh; FMNH: Field Museum of Natural History, Chicago; LACM: Natural History Museum of Los Angeles County, Los Angeles; MNHN Muséum National d'Histoire Naturelle, Paris; USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Importantly, NHCs can serve as repositories of evolutionary change because they often contain large samples from the same localities at different points in time. For example, Schroeder *et al.* (2009) examined specimens of the black-tailed godwit, *Limosa limosa*, from museums in the Netherlands and Denmark to reveal a decrease in the extent of male feather ornamentation over time, attributing this change to increased costliness of ornaments in human-dominated environments. Primack *et al.* (2004) showed that flowering date had advanced by an average of 8 days in dozens of herbarium species over a hundred year period in Boston. Moritz *et al.* (2008) characterized changes in the distri-

butions of mammals collected over 80 years in California, finding that half of the small mammal species in the Yosemite region have shifted their elevational ranges upslope. These kinds of studies highlight the importance of long-term data series from the same localities.

Data from many NHCs are increasingly available online (Fig. 3B). Museum databases range from single- to multi-institutional and from taxon-specific (e.g. VertNet: Constable *et al.* 2010) to taxonomically broad (e.g. GBIF: Flemons *et al.* 2007). In the best cases, online specimen records are detailed and can include morphological measurements, body condition indices, age and

Table 1 Types of data available in museum collections.

Biological (storage method)	Common Taxa	Preserved traits
Fluid-preserved whole organisms (formalin, ethanol)	Fish, herpetofauna, invertebrates	Morphology, genetics
Fluid-preserved organism parts (e.g. gastrointestinal or reproductive tracts, stomach contents) (formalin, ethanol)	Mammals	Morphology, genetics, ecology
Frozen tissues (freezer, liquid nitrogen, ethanol, RNAlater)	Vertebrates	Genetics, isotopes
Pinned (dry)	Insects	Morphology, genetics
Pressings (dry)	Herbarium collections	Morphology, genetics
Seeds, spores (dry, frozen)	Herbarium collections	Morphology, genetics, isotopes, physiology, ecology, phenology
Skins (dry)	Birds, mammals	Morphology (e.g. colour), isotopes, genetics, physiology, environmental contamination
Skeleton (dry)	Vertebrates	Morphology, genetics, isotopes
Nests (dry)	Birds	Behaviour, ecology
Eggs, egg sacs (dry, formalin, ethanol)	Birds, insects, herpetofauna,	Morphology, ecology, environmental contamination

**Table 2** Types of metadata available in museum collections.

Metadata	Preserved information
Audio/video Files	Vocalizations (e.g. specimen-linked bird/herp calls)
	Behaviour
	Ecology (e.g. habitat associations, species interactions)
Field notes, Observations	Trapping effort (population size/demographics), collecting method, distribution/biogeography, locality (time series site matching), habitat associations, species interactions, behaviour
Georeferences/ Maps	Distribution/biogeography, time-series site-matching
Photographs	Time-series site-matching
	Habitat change
	Colour in life (especially herpetofauna)
Relationships	Genetic relationships, species interactions (e.g. parasite/host interactions, predator/prey interactions, mating behaviour), habitat associations

reproductive status, and georeferenced localities. Pressed plants often yield particularly complete digitized records, as many of their characteristics are easily captured online in an image or scan. Some current effort exists to create 3D scans of specimens that are available through databases such as iDigBio (Integrated Digitized Biocollections: https://www.idigbio.org/). Some collections also provide links to digitized field notes, audiovisual recordings, photographs and, increasingly, genetic data via GenBank. Ecoinformatics, the field that integrates and increases the accessibility of multiple lines of ecological and environmental data, will further advance the usefulness of online NHCs. Still, even the largest museums are not completely digitized. Terrestrial vertebrate collections, which are usually nonlot based and smaller than invertebrate and fish collections, are well-represented in online databases (Fig. 3B), while huge efforts are currently underway to digitize the massive resources available in fish and invertebrate collections (e.g. CalBug, http://calbug.berkeley.edu), for which significant advances are being made (Fig. 2). Here, we have focused on botanical and zoological collections of extant species, although we appreciate the wealth of data available in palaeontological collections (Box 2).

Sampling considerations

There are certain caveats to bear in mind when using NHCs to study evolutionary change (Shaffer *et al.* 1998; Wandeler *et al.* 2007; Boakes *et al.* 2010; Wehi *et al.* 2012). First, museum collecting is sometimes opportunistic and nonrandom and this may introduce sampling biases. In general, specimens are not proportionately distributed across taxonomy, geography, season or age. For example, common or local species are more likely to be repeatedly and regularly sampled. In some cases, populations have been intensively sampled during a short period of time, but poorly sampled since that period; these populations could be targeted for current and future sampling to increase the pool of available time series. Tropical areas are very diverse but are usually not proportionately represented in collections. For temperate areas, specimens are more likely to be collected during the summer

Box 2. Woodrat body size and historical temperature
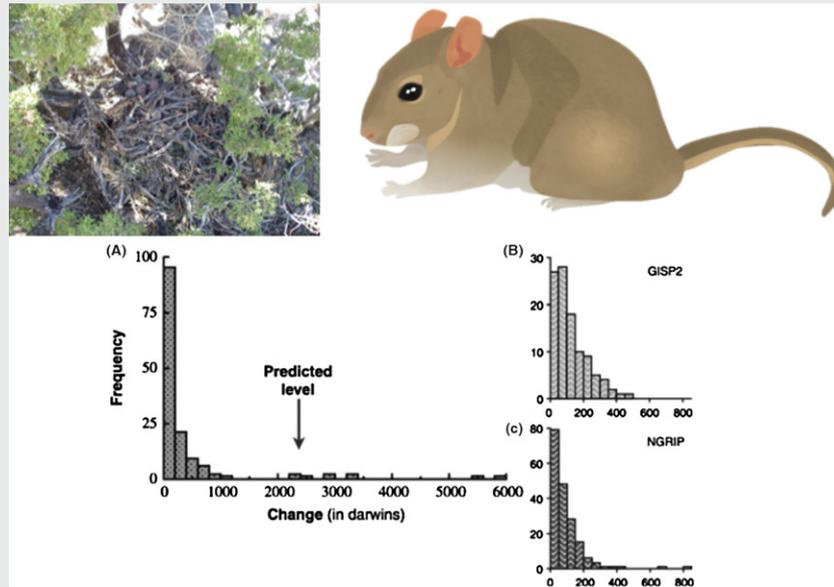
Palaeontological collections can also be used to study evolutionary change over time. The use of fossil and subfossil specimens allows for an assessment of phenotypic and genotypic change over long time periods and in response to dramatic and prolonged environmental transformations. Both morphological and genetic studies are possible with fossil and subfossil specimens.

The first study using ancient DNA (aDNA) sequenced a 229-bp fragment of mtDNA from a museum specimen of the extinct quagga (Higuchi *et al.* 1984). This sparked a flurry of studies utilizing aDNA from fossil and subfossil specimens. More recent studies have documented population genetic changes using heterochronous aDNA from temporal series of fossil and modern specimens (Hadly *et al.* 2004; Ramakrishnan *et al.* 2005; Chan *et al.* 2006; Ramakrishnan & Hadly 2009). Both exome capture (Bi *et al.* 2013) and targeted bait capture techniques (Mamanova *et al.* 2010; Carpenter *et al.* 2013; Peñalba *et al.* 2014) can generate large numbers of loci or SNPs from many individuals allowing for population-level studies in fossil organisms. The efficacy of targeted enrichment protocols for aDNA has been recently demonstrated with some samples yielding as many as 150 k SNPs (Carpenter *et al.* 2013). These technologies provide the foundation for the nascent field of *paleopopulation genetics* (Wall & Slatkin 2012), adding to our knowledge of how species responded to environmental changes in recent geologic times (reviewed in Hofreiter & Stewart (2009) and de Bruyn *et al.* (2011)).

Morphology-based studies have been able to draw explicit links between body size proxies and environmental (climate) change for extant species (Smith *et al.* 1995; Hadly 1997; Blois *et al.* 2008; McGuire 2010). In a landmark study, Smith *et al.* (1995) examined the change in body size of woodrats (*Neotoma* spp.) over thirty thousand years. Woodrats, illustrated in the figure above (top right) next to a typical *Neotoma* midden (top left), show a tight negative correlation between body size and ambient temperature, a primary adaptation to climate change in *Neotoma* species. Broad-sense heritability estimates for body size are high [$H^2 > 0.8$ (Smith & Betancourt 2006)], indicating that this trait is under substantial genetic control. Smith & Betancourt (2006) showed that body size change in woodrats from many geographic sites rapidly tracks climate change. The distribution of body size changes during the Holocene, measured in darwins, across 55 sites in the Western U.S. is shown in graph (A). The predicted rate of phenotypic change expected under current estimates of climate change for the next 100 years is shown with an arrow and falls within the range of rates of change observed during the Holocene. Graphs (B) and (C) depict histograms of changes in oxygen isotopes estimated from the GISP2 ice core and the NGRIP ice core respectively; higher oxygen isotope levels correspond to warmer temperatures. The distributions of inferred temperature changes (B and C) are similar to the distribution of body size changes (A). This series of studies on woodrats used fossilized faecal pellets and historical and modern museum specimens to create a highly integrative picture of environmentally driven evolutionary change over time. Figure reproduced from Smith & Betancourt (2006).

than the winter. Adult specimens are generally more likely to be targeted than juveniles. If certain morphotypes of a species are more visible or easily captured, they may be disproportionately represented in collections. These biases must be kept in mind when using specimens for demographic, distributional, and evolutionary studies (Wehi *et al.* 2012) and should help guide future collection efforts.

Some uses of museum specimens require 'destructive sampling' in which a portion of a specimen is destroyed to obtain data. This applies to such things as frozen tissues or portions of specimens used for DNA studies or isotope analyses. As specimens represent finite resources, most museums have strict policies governing destructive sampling and these may limit the availability of some samples.

Environmental drivers of change

Understanding the evolutionary process requires an understanding of links between genotype, phenotype and environmental selective pressures (Fig. 1). Although it can be difficult to attribute organismal change to a specific selective agent, recent studies suggest that five major anthropogenic causes of environmental change have been particularly important in the past century. *Habitat destruction,* including loss and fragmentation, is one of the most critical and immediate causes of biodiversity loss (Ewers & Didham 2006). *Overexploitation*, or exhaustive resource use via human hunting or harvesting, has driven numerous recent extinctions (e.g. the great auk, *Pinguinus impennis*; Steller's sea cow, *Hydrodamalis gigas*; and the passenger pigeon, *Ectopistes migratorius*). *Pollution* has long been recognized as a major force of environmental change (Candelone *et al.* 1995) with extensive impacts on population structure (Blaustein *et al.* 2003) and evolution (e.g. Bradshaw & McNeilly 1981). *Invasive species* have similarly precipitated widespread ecological disruptions by outcompeting native species (Powell *et al.* 2013). These four agents can work together and in combination with the global phenomenon of *anthropogenic climate change*. Climate change has significantly altered Earth's ecosystems (Parmesan 2006) and undoubtedly set in motion a cascade of ecological and evolutionary events that await discovery. These drivers of environmental change are affecting biodiversity, altering everything from population genetic composition to community dynamics. By examining long-term collections from museum repositories, we can elucidate the phenotypic and genotypic changes experienced by populations as they adapt to specific environmental changes.

Genetics and genomics

Over the last forty years, NHCs have shifted from almost exclusively housing traditional specimens (*e.g.* prepared skins) to an increasing focus on the preservation of tissues and genetic samples. This has opened the door to studies of molecular variation, including studies of changes in genotype frequencies through time. Most work to date has focused on documenting and understanding demographic changes; however, there is now great potential to make links between genotype and phenotype.

Allan Wilson and colleagues were the first to use museum specimens to make temporal comparisons of genetic variation (Thomas *et al.* 1990). They isolated mitochondrial DNA from 43 specimens of the Panamint kangaroo rat, *Dipodomys panamintinus*, from three populations collected between 1911 and 1937 and compared these to contemporary specimens collected in the same localities. The comparisons allowed them to ask whether populations were more connected spatially or temporally; they discovered that populations exhibited temporal continuity. This study was followed by many others that utilized museum specimens to examine genetic variation in historical and present-day samples (e.g. Lozier & Cameron 2009; Pinsky *et al.* 2010; Spurgin *et al.* 2014; reviewed in Wandeler *et al.* 2007), including fossil and subfossil specimens (Box 2). Many of these studies have documented declines in population size, although some have provided insight into more complex demographic processes (Weber *et al.* 2000; Groombridge *et al.* 2009; Lozier & Cameron 2009; Pinsky *et al.* 2010; Spurgin *et al.* 2014). For example, Pearse *et al.* (2011) suggested that migratory routes have been interrupted in steelhead trout, *Oncorhynchus mykiss*, from comparisons of modern-caught and historical specimens.

Most studies utilizing historical museum specimens have been limited to small fragments from a few loci. DNA from dried specimens is typically degraded and therefore difficult to PCR amplify and sequence unless the target region is short (typically 100–200 bp). However, newer methods such as Illumina sequencing are based on libraries with relatively short fragments and thus can be used on the degraded DNA in museum specimens (Rowe *et al.* 2011; Bi *et al.* 2013; Hykin *et al.* 2015; Suchan *et al.* 2015). For example, Bi *et al.* (2013) used exon capture and Illumina sequencing to study the patterns of genetic variation across the genome in historical and modern population samples of alpine chipmunks, *Tamias alpinus*. *T. alpinus* has retracted its range in response to climate change (Moritz *et al.* 2008), and Bi *et al.* (2013) showed that modern samples exhibit more genetic subdivision compared to historical samples. This genome-scale work supported results from

previous studies on *T. alpinus* based on fewer markers (Fig. 4) (Rubidge *et al.* 2012).

The ability to sequence much or all of the genome from historical samples opens the door to new avenues of research. For example, just as genome scans for selection have been applied to make spatial comparisons between different present-day populations, temporal comparisons can be made for a single population across multiple points in time. F_{ST} outlier and other approaches can be used to identify specific genes with allele frequencies that have shifted, identifying candidate genes for responses to environmental change. Following this logic, Mikheyev *et al.* (2015) recently sequenced the genomes of population samples of 32 colonies of honeybees collected near Ithaca, New York. Using museum specimens from the Cornell University Insect Collection, they compared populations from 1977, sampled before the introduction of an ectoparasitic mite (*Varroa destructor*), to those col-

lected in 2010. They documented phenotypic changes in these bees and also conducted scans for selection, identifying genes that may underlie resistance to this mite. Notably, some of the identified genes overlap with previously identified quantitative trait loci (QTL) for resistance to *Varroa* mites.

This kind of temporal genome scan using museum specimens is conceptually similar to 'evolve-and-resequence' studies in which experimental laboratory populations of organisms are selected for a particular trait (e.g. Turner *et al.* 2011) or allowed to evolve in a new environment (e.g. Orozco-ter Wengel *et al.* 2012) and then sequenced at different time points to identify changes in allele frequency (reviewed in Schlötterer *et al.* 2015). Sophisticated analytic methods have recently been developed to explicitly analyse data from evolve-and-resequence studies (e.g. Illingworth *et al.* 2012; Terhorst *et al.* 2015).
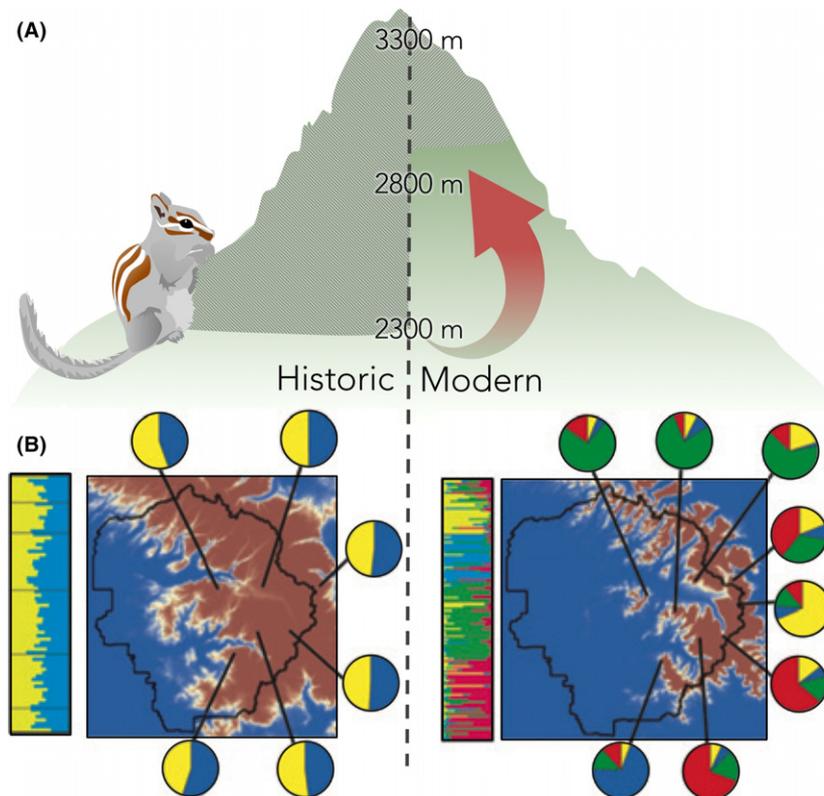

Fig. 4 Ecological and genetic investigations on alpine chipmunks, Tamias alpinus, show the value of museum specimens for documenting ecological shifts and analyzing genetic change over time. (A) Cross-hatching indicates elevational range occupied by *Tamias alpinus* from the historical (left) to the modern (right) era. This species has retreated upslope as temperatures have warmed over the last century, isolating populations once open to gene flow. (B) Maps show Yosemite National Park (black outline) colored with the occupation probabilities (based on elevation) for *T. alpinus* (red: high probability, blue: low probability) in historical (left) and modern (right) eras. STRUCTURE barplots to the left of each map indicate population membership by individual; these data are split by site and represented in pie charts on the map. The greater diversity in pie charts in the modern samples compared to the historical samples is indicative of greater population subdivision. The availability of historical and modern specimens from the same localities was critical in revealing an increase in genetic subdivision of the alpine chipmunk populations over the past century (Rubidge *et al.* 2012). Figure based on data and figures from Rubidge *et al.* (2012) and Moritz *et al.* (2008).

Population genetic approaches utilizing time-series data

Inferring selection or demographic parameters from multiple time points has advantages over inference from single time points. For example, sampling from multiple time points can provide resolution on the strength of selection based on the rate of allele frequency shifts over time. This permits quantitative estimates of selection coefficients as well as more accurate estimates of demographic parameters (Bank *et al.* 2014).

A number of theoretical models have been developed for the analysis of time-series data; the first of these focused on estimating changes in effective population size over time (e.g. Krimbas & Tsakas 1971; Nei & Tajima 1981; Waples 1989; Williamson & Slatkin 1999; Anderson *et al.* 2000). More recently, methods have been developed to detect selection, estimate selection coefficients, estimate the age of alleles or estimate migration rates (e.g. Bollback *et al.* 2008; Malaspinas *et al.* 2012; Mathieson & McVean 2013; Feder *et al.* 2014). For example, Malaspinas *et al.* (2012) developed a likelihood method to jointly estimate the strength of selection and the age of an allele, while Mathieson & McVean (2013) developed a method for jointly estimating selection coefficients and migration rates in structured populations. Jensen and colleagues have developed a Wright–Fisher approximate Bayesian computational (ABC) method to infer selection coefficients and have used this to study the evolution of drug resistance in influenza in cultured cells (Foll *et al.* 2014). Foll *et al.* (2015) extended this approach to estimate the selection and dominance coefficient of the *medionigra* allele in the scarlet tiger moth, sampled over a 60-year period.

These new theoretical models hold great promise for the analysis of time-series data from collections. Despite these advances, some limitations remain. It is still difficult to distinguish between the signatures of direct and indirect selection, as well as to correctly infer the joint effects of demographic changes and selection. While maximum likelihood-based methods are considered to be more accurate with small selection coefficients, they are computationally intensive. Newly developed ABC approaches, in contrast, are relatively computationally efficient, and thus hold promise for surveys of large genomic data sets (reviewed in Bank *et al.* 2014).

From phenotype to genotype

Below we highlight some of the best-documented examples of phenotypic change in botanical and zoological museum collections. This discussion is not intended to be comprehensive, but to illustrate the ways in which NHCs can be used to study evolution directly. In some cases, the documented changes have a clear genetic basis and likely represent an adaptive response to changes in the biotic or abiotic environment. In others, phenotypic change may be due in part to plasticity, occurring without corresponding changes in underlying genotypes. We attempt to highlight examples where connections between genotype and phenotype have either already been made or could be made because the traits are amenable to genetic analysis. This discussion is by no means taxonomically exhaustive; for example, we have not included some major groups, such as fungi and fish, although they are well-represented in many collections, and excellent studies exist (Box 1).

Plants

Because plants provide a three-dimensional habitat for many other organisms and are the source of energy in terrestrial ecosystems, their evolutionary responses to environmental change can have cascading effects on the food web and community structure. Plant phenotypes are sensitive to both temperature and atmospheric CO_2 concentrations, two aspects of recent anthropogenic environmental disturbances.

Environmental changes can affect both the microscopic and macroscopic morphologies of leaves. For instance, carbon dioxide concentrations have been linked to stomatal density in plants (Woodward 1987; Beerling & Woodward 1996). The relationship between stomatal density and CO_2 concentration has also been examined by comparing modern and historical specimens from herbaria (Beerling & Woodward 1996). Woodward (1987) measured stomatal densities of seven tree species and one shrub species collected over a 200-year time span beginning in the mid-18th century. Although the species differed in total stomatal density, a general trend emerged: a reduction in stomatal density by approximately 40% over the time period represented. Although it is not clear whether the changes seen by Woodward (1987) were genetically based or reflect phenotypic plasticity, a number of papers have investigated the genetic basis of stomatal density, revealing high heritability and individual QTL of large effect (Gailing *et al.* 2008; Muir *et al.* 2014). Moreover, a sign test for QTL underlying stomatal density provided strong evidence that genetic changes seen between species were driven by positive selection (Muir *et al.* 2014). Finally, individual genes contributing to stomatal density have now been identified, principally in *Arabidopsis* (e.g. Shimada *et al.* 2011; Engineer *et al.* 2014; Meng & Yao 2015). This suggests an intriguing arena for future work: candidate genes for stomatal density could be surveyed (or genomewide resequencing approaches

could be used) in historical and modern samples to look for evidence of changes in allele frequency over time. Given the importance of stomatal density in regulating CO_2 uptake, this would provide a direct link between climate change and the genetic basis of organismal response.

Plant phenotypes can also respond to environmental change at the macroscopic level. Guerin & Lowe (2013) analysed 255 specimens of narrow-leaf hopbush, *Dodonaea viscosa angustissima*, from collections spanning 127 years. Measuring leaf width, they found a decrease of 2 mm in this species. Furthermore, they were able to show that this phenotype is negatively correlated with maximum temperature. Leger (2013) studied herbarium collections of several species of plants spanning nearly 120 years to examine links between climate change and leaf morphology. Among these species, she found a general decrease in plant size with varying responses in leaf size and flower number to temperature changes over time. As with stomatal density, the extent to which these long-term changes in phenotype reflect plasticity or genetics is unclear. Nonetheless, the wealth of candidate genes underlying leaf morphology (Tsuge *et al.* 1996; Juenger *et al.* 2005; Hay & Tsiantis 2006) provides an opportunity to study changes in allele frequency at these genes using herbarium collections.

Changes in plant phenology are another important response to climate change (Wolkovich *et al.* 2012; Richardson *et al.* 2013). A recent study used a common garden experiment to rear cornflowers, *Centaurea cyanus*, from seeds that had been collected from the same locality 18 years apart (Thomann *et al.* 2015). They found that flowering time had shifted and floral display increased in both size and duration. Q_{ST}–F_{ST} comparisons suggest that selection has been acting, likely in response to climate warming and a decrease in pollinators (Thomann *et al.* 2015). Another recent study by Robbirt *et al.* (2011) examined flowering times of 192 early spider orchids, *Ophrys sphegodes*, with specimens spanning two long-term collection times, 1848–1958 and 1975–2006. They found that flowering times in both periods advanced by 6 days per 1 °C increase in mean spring temperature. The genetic basis of flowering time has been intensively studied (e.g. Chiang *et al.* 2009; Ehrenreich *et al.* 2009; Brachi *et al.* 2010; Srikanth & Schmid 2011; Irwin *et al.* 2012), providing many candidate genes that could be studied in NHC specimens. Moreover, the opportunity in some cases to perform crosses between plants grown from preserved and modern seeds opens the door to directly studying the genetic basis of changes that have occurred (Franks *et al.* 2007). In principle, this approach could be applied to any species that can be preserved in a dormant state (Orsini *et al.* 2013), a principle that has recently been applied to examine evolution of thermal tolerance in *Daphnia* (Geerts *et al.* 2015).

Invertebrates

An iconic example of evolution in response to anthropogenic environmental change comes from studies of melanism in the peppered moth, *Biston betularia*, in Britain. Following the Industrial Revolution, observers noted an increase in frequency of the previously rare melanic morph of *B. betularia*. Tutt (1896) was the first to suggest the role of pollution in driving the increase in melanism. Kettlewell (1955, 1956) later confirmed this hypothesis with field experiments showing increased predation on nonmelanic morphs. He strengthened his argument about the link between pollution, predation, and melanism using museum records, private collections, and other published work to obtain data on the presence and frequency of the melanic morph in several areas throughout Britain. He concluded that a correlation exists between melanism and heavy levels of industrialization, and called for further work on the genetic mechanisms underlying the spread of melanic genes (Kettlewell 1958). Kettlewell's work laid the foundation for an extensive body of work on industrial melanism (summarized in Majerus & Brakefield 1998) including one study that used museum specimens and material from private collections to investigate the genetics underlying melanism (van't *et al.* 2011). Using both laboratory-reared moths and specimens collected from 1925 to 2009, the authors concluded that industrial melanism in Britain is the result of a single mutation that spread rapidly in response to the strong selective force of pollution (van't *et al.* 2011).

Another striking example of the use of NHCs comes from the soapberry bug, *Jadera haematoloma*, which feeds by inserting its needle-shaped beak into fruits. The soapberry bug feeds on several native host plants, but is capable of expanding its diet to include introduced species. In the southern United States, Carroll & Boyd (1992) used museum specimens to document changes in beak length over 20–50 years (40–150 generations) following the introduction of three new host plants to the area. They showed an increase in beak length of museum and field-caught specimens over time consistent with expectations based on fruit size. To test whether these changes were genetic or plastic, reciprocal rearing experiments were conducted that showed support for host-dependent genetic differentiation (Carroll *et al.* 1997). More recently, QTL mapping has suggested that beak length in *J. haematoloma* may be controlled by a relatively small number of loci of moderate effect (Yu & Andrés 2014).

Because invertebrates have short generation times and are generally abundant in NHCs, many other invertebrate studies have been able to utilize collections to examine evolutionary changes over time; phenotypic changes have been attributed to climate change (Anderson *et al.* 2008; Babin-Fenske *et al.* 2008; Ożgo & Schilthuizen 2012; Timms *et al.* 2013), habitat fragmentation (Norberg & Leimar 2002; Anderson *et al.* 2008) and invasive species (Carroll & Boyd 1992), among other drivers. As more insect genomes are sequenced and annotated, insects will become a particularly suitable group in which the exploration of candidate genes could be combined with the unique temporal and high-resolution spatial dimensions provided by NHCs.

Reptiles and amphibians

Although environmental change affects all taxa, amphibians and reptiles may be among the most susceptible of the vertebrates. Both are ectothermic and have relatively poor dispersal ability, which sensitizes them to temperature fluctuations while limiting their capacity to respond through range shifts (Sinervo *et al.* 2010). Amphibians have long been considered 'canaries in the coal mine' for environmental change due to their permeable skin and a life history involving both aquatic and terrestrial stages (reviewed in Kerby *et al.* 2010). Reptiles with temperature-dependent sex determination may not be able to compensate behaviourally for climate change and may therefore experience skewed sex ratios and even demographic collapse (Refsnider *et al.* 2013). Furthermore, both amphibians and reptiles are experiencing elevated rates of extirpation and extinction often attributable to anthropogenic effects (Barnosky *et al.* 2011; Böhm *et al.* 2013).

Although much work on the response of reptiles and amphibians to environmental change has focused on phenology and associated reproductive behaviours such as nest depth (Urban *et al.* 2014), studies of morphological variation have demonstrated its close links to the ecology and fitness of herpetofauna (e.g. Losos 1990; Caruso *et al.* 2014; Vidal-García *et al.* 2014). For example, Caruso *et al.* (2014) measured museum specimens from 15 species of *Plethodon* salamander collected between 1950 and 1996 and compared them to specimens collected between 2009 and 2011 to show that several species have undergone a considerable decrease in adult body size, possibly due to increasingly warm and dry habitats. In another study, hindlimb length of *Sceloporus undulatus* has increased over seventy years across sites in the United States; this change was positively correlated with time since occupation by invasive fire ants, which can be better avoided by individuals with longer hindlimbs (Langkilde 2009). Work in well-stu-

died groups such as *Anolis* lizards has used common garden and laboratory experiments to tease out the roles of plasticity and genetics in determining limb length, body size, and other morphological traits (e.g. Losos *et al.* 2000, 2001; Thorpe *et al.* 2005; Eales *et al.* 2010). From anoles, we know that limb length is a largely plastic trait (Losos *et al.* 2000), and although body size has high broad-sense heritability (Berger *et al.* 1998), the genetic architecture remains uncharacterized. As more genomic resources become available for amphibians and reptiles, it may become possible to elucidate the genetic components of some of these ecologically important traits.

Perhaps the best-known example of the use of NHCs to examine change over time in herpetological specimens comes from studies of chytrid fungus, *Batrachochytrium dendrobatidis* (Bd) infection, in amphibians. Although the earliest studies of Bd involved identifying and characterizing the nature of the infection and subsequent extirpation of amphibian populations (Berger *et al.* 1998; Lips *et al.* 2006), more recent studies have used museum specimens and genetic techniques (PCR and qPCR) to detect and characterize historical chytrid infections from around the world (Lips *et al.* 2008; Crawford *et al.* 2010; Swei *et al.* 2011; Bataille *et al.* 2013; Shaw *et al.* 2013). For example, one study tested for Bd in museum specimens of 38 Central American amphibian species collected before their decline and during the year of their decline, and revealed many cases of coincident Bd emergence and population collapse (Cheng *et al.* 2011). Bd infection likely exerts a strong selective force on any population that it does not completely eliminate. Although the nature of the immune response to Bd infection is complicated and varies among individuals and species (Rosenblum *et al.* 2012; Ellison *et al.* 2014a,b), some work has found a potential role for MHC variability in resistance (Savage & Zamudio 2011; Bataille *et al.* 2015). Future work could use museum specimens to assess immunogenetic diversity in populations before and after Bd infection to test hypotheses about specific genes that may contribute to susceptibility or resistance.

Partially because of the limited number of herpetological genomes available, genomic studies of evolutionary change in these animals have been constrained. Nonetheless, due to their strong susceptibility to environmental change, work on amphibians and reptiles has the potential to be particularly useful, and in some cases, NHCs may provide the only remaining records of populations that have recently gone extinct.

Birds

The visibility and phenotypic variability of birds has long made them a subject of particular interest among

researchers and the public alike. This interest has driven a number of excellent resources for ornithological study, including long-term banding records, extensive citizen science data sets, and large, well-curated ornithological collections. In combination with the extensive genomic resources recently made available through the 50 genomes project (Jarvis *et al.* 2014; Zhang *et al.* 2014), there is potential to make direct phenotype–genotype links for birds. For example, ornithological museum specimens have been used to study environmentally induced changes in colour and plumage over time (Galeotti *et al.* 2009; Alström *et al.* 2015). In one elegant study, Karell *et al.* (2011) used museum specimens and field observations to show that in less snowy years, brown-morph tawny owls, *Strix alco*, have a survival advantage over grey morphs. Using field data, they demonstrated a high heritability of these plumage types. Finally, they found that as annual snow cover decreased over a thirty-year period due to increasing temperatures, the frequency of brown-morph individuals increased in comparison with the grey morphs (Fig. 5). An exciting direction for potential future study could be to assay the large number of previously identified candidate pigmentation genes to make direct links between genes, phenotypic response and environmental change.

Body size is another morphological trait in avian species that has been linked to environmental change. For example, Gardner *et al.* (2009) examined specimens of eight species of passerine birds collected from 1860 to 2001 and documented a decrease in body size of 1.8–3.6%, which the authors attribute to global warming. They suggest the observed decrease in body size represents evolutionary change and is not a result of diet-induced plasticity. These results are consistent with other studies showing a decrease in body sizes of birds that may be correlated with increased local temperatures (Yom-Tov 2001; Yom-Tov & Yom-Tov 2006).

Habitat modification has also been linked to phenotypic changes in birds studied in NHCs. Desrochers (2010) examined 21 species of temporal and boreal forest passerines collected between 1900 and 2008. He found a direct correlation between habitat fragmentation and an increase in the projections of outer wing feathers. Fragmented habitats lead to a more pointed wing shape, which is generally observed in birds with longer migratory distance and movement (Winkler & Leisler 1992; Senar *et al.* 1994). In contrast, birds that were found in habitats with less fragmentation showed a decrease in primary project length, suggesting reduced long-distance movement. Although the authors did not directly explore whether these changes were genetic or plastic, previous studies in other bird species have identified genetic contributions to wing length and
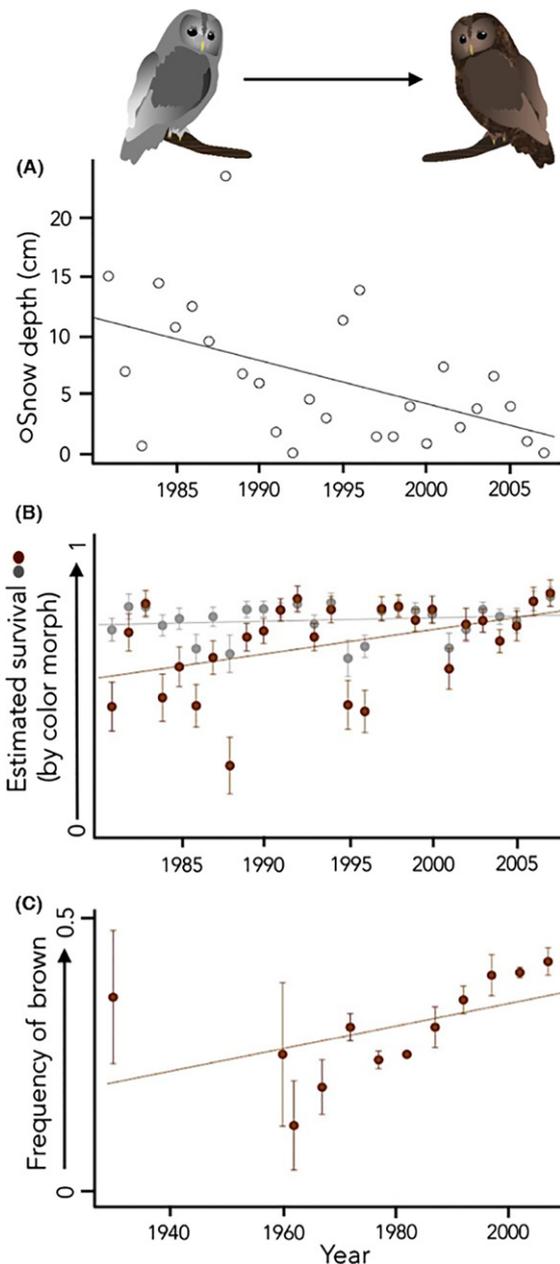

Fig. 5 Work on tawny owls using museum and field-identified specimens indicates that plumage coloration can be affected by changes in climate. Brown owls are poorly camouflaged against snow, thus, selection against the brown morph is typically strongest in heavy-snow winters; this selection has been relaxed as snow levels have decreased due to climate change. (A) A decrease in snow depth (open circles) over a 27 year period was documented. (B) Using mark-recapture modeling, survival estimates for grey and brown morphs were modeled. Graph shows estimated survival for grey (grey circles) and brown (brown circles) morphs, illustrating increased survival for brown morphs in years with less snow. (C) Using museum specimens and field-collected data, the frequency of the brown morph in the wild was found to have increased over time. Note that the *x*-axis for (C) differs from (A) and (B). Figure based on data from Karell *et al.* (2011).

shape (Schielzeth *et al.* 2012), including one study that found a single QTL that explained over one-third of the phenotypic variation in wing length in great reed warblers (Tarka *et al.* 2010).

Anthropogenic environmental change, particularly climate change, can also be expected to affect migratory behaviours in birds (Guttal & Couzin 2010), and some changes in migratory patterns have already been observed (e.g. Pulido & Berthold 2010). While migratory phenotypes are not directly discernible in museum specimens, collection dates assign individuals to particular locations at particular times and thus can provide indirect information about migratory patterns. Moreover, it may be possible to assay historical and contemporary NHC specimens for candidate migratory genes (Liedvogel *et al.* 2011; Mueller *et al.* 2011; Kuhn *et al.* 2013).

Mammals

Like birds, mammals tend to be highly represented and well studied in museum collections. For example, mammal specimens have recently been used to study changes in body size in response to climatic shifts (Eastman *et al.* 2012; Sonne *et al.* 2013). In contrast to expectations based on thermal ecology, mammals do not show a consistent decrease in body size in response to increasing temperature. Pergams & Lawler (2009) examined rodents from 28 NHCs representing 25 species from four continents. Rapid phenotypic changes were detected in skull and body size, but changes varied by region and were uncorrelated with climate variables and human population impact. Whether these changes are genetically or plastically controlled is often unclear, and in general, exploring the genetic underpinnings of body size is challenging since it is typically a highly polygenic trait (Allen *et al.* 2010; Perola 2011; Chan *et al.* 2012; Kemper *et al.* 2012) and susceptible to environmental influences (Boutin & Lane 2014).

Changes in mammalian cranial morphology have recently been studied in a number of species using museum specimens (Snell-Rood & Wick 2013; Tomassini *et al.* 2014; Holmes *et al.* 2016). However, the genetic basis of skull shape is complex (Burgio *et al.* 2012; Maga *et al.* 2015), and skull shape is also known to show considerable plasticity during development (Gonzalez *et al.* 2011; Noback & Harvati 2015). Changes in dentition have also been studied using museum collections. For example, Szuma (2003) examined changes in dental traits of the red fox, *Vulpes vulpes*, collections of which spanned over 70 years. Significant changes in dentition were found in occlusal surfaces of premolars and incisors, which the authors suggested might be driven by an increase in the types of food available for *V. vulpes* due to historical land-use changes. Although tooth development appears to be polygenic (Thesleff 2006), studies in both humans and mice have associated anomalous dental phenotypes with specific mutations; for example WNT10A mutations result in supernumerary molars, molars with fewer cusps, and incisors with distinctive apical–lingual wedge shapes (Yang *et al.* 2015). Candidate gene approaches would be useful for linking changes in dental phenotypes over time to specific mutations.

Conclusions and future directions

Evolution is rarely directly observable, but comparisons of specimens collected at different points in time enable us to document and understand evolution in a way that is typically not possible in the lifetime of a single researcher. Understanding the genetic basis of evolutionary change requires that we make links from genotype to phenotype and from phenotype to environment. We envision a number of important future directions for making these links in the context of museum collections.

First, repeated sampling of populations that have been well sampled in the past will help identify specific phenotypic changes. Detailed historical records of biotic and abiotic conditions can be compared with current conditions to assess changes in the environment that may have driven changes in phenotype. For example, the PRISM climate data (http://prism.oregonstate.edu) contains climate records from 1895 to the present. Second, candidate genes can now be surveyed for many traits, and some of these will lead to specific genotype–phenotype links, which can then be followed through time. Although the relevance of genes identified from laboratory mutants to natural populations has been questioned (Palopoli & Patel 1996), it is clear that there have been many successes of this approach, especially for traits that are not highly polygenic (Barrett & Hoekstra 2011). Third, the ability to generate sequence data across the genome from historical specimens (Bi *et al.* 2013; Suchan *et al.* 2015) opens up many exciting areas. The obvious drawback of a candidate gene approach is that it focuses on a particular phenotype and limits discovery to genes that are already known. In contrast, genome scans are blind with respect to phenotype and can help identify genes that may have been under selection but were not previously suspected. Such genes may then point to phenotypic differences that may be important in evolution. In this way, museum specimens may provide a natural counterpart to the increasingly common 'evolve-and-resequence' studies that have been carried out in the laboratory.

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