

Temporal collections to study invasion biology

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Abstract

Biological invasions represent an extraordinary opportunity to study evolution. This is because accidental or deliberate species introductions have taken place for centuries across large geographical scales, frequently prompting rapid evolutionary transitions in invasive populations. Until recently, however, the utility of invasions as evolutionary experiments has been hampered by limited information on the makeup of populations that were part of earlier invasion stages. Now, developments in ancient and historical DNA technologies, as well as the quickening pace of digitization for millions of specimens that are housed in herbaria and museums globally, promise to help overcome this obstacle. In this review, we first introduce the types of temporal data that can be used to study invasions, highlighting the timescale captured by each approach and their respective limitations. We then discuss how ancient and historical specimens as well as data available from prior invasion studies can be used to answer questions on mechanisms of (mal)adaptation, rates of evolution, or community-level changes during invasions. By bridging the gap between contemporary and historical invasive populations, temporal data can help us connect pattern to process in invasion science. These data will become increasingly important if invasions are to achieve their full potential as experiments of evolution in nature.

KEYWORDS

ancient DNA, herbarium records, historical DNA, invasive species, museum genomics, temporal contrasts

1 | INTRODUCTION

The potential value of invasive species as natural evolutionary experiments has been recognized for more than a century, as illustrated by Grinnell (1919), *The English Sparrow Has Arrived in Death Valley: An Experiment in Nature*.

Grinnell writes:

"How intensely interesting it will be to watch the course of this 'experiment,' now under way, irrespective of human effort, in Death Valley, with 'controls'

vigorously maintaining themselves (against man's wish!) in San Diego, Berkeley and Boston."

Grinnell's suggestion proved to be prescient, with the English sparrow offering an early example of the remarkable speed of contemporary evolution (Johnston & Selander, 1964). This finding has since been replicated for a variety of other biological invasions (Barrett et al., 2016; Lee, 2002; Prentis et al., 2008; Turner et al., 2014), with selection differentials found to be much higher on average than those reported for non-invasive populations (Colautti &

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Lau, 2015; Whitney & Gabler, 2008). An arguably more surprising finding is that population bottlenecks appear to have little impact on short-term evolutionary change, at least for quantitative traits (Dlugosch et al., 2015; Hodgins et al., 2018). Other contributions to our understanding of evolutionary processes from studies of invasive species include evidence of the importance of standing genetic variation in fuelling rapid evolution (Bock et al., 2015; Tepolt et al., 2022), the unforeseen extent to which evolution repeats itself (James et al., 2023; van Boheemen & Hodgins, 2020), and the pervasiveness of ecological constraints on responses to natural selection (Colautti & Lau, 2015).

Despite these advances, an imperfection in many studies of invasive species is that evolutionary change is typically inferred from comparisons of populations from the native and invaded ranges at a single (present-day) timepoint, equating differences across space and time (Hodgins et al., 2018; Lee, 2002; Prentis et al., 2008). This can lead to faulty inferences about evolutionary rates and the origins of adaptive genetic variation if, for example, the exact progenitor populations have been incorrectly identified, no longer exist, or have undergone significant evolutionary change themselves (Dlugosch et al., 2015). Likewise, without data from additional timepoints, it may not be possible to make inferences about the tempo of evolution or the order in which evolutionary changes accumulate. For example, it might be that most evolutionary change occurs shortly after a population is introduced, with slower evolution as the population approaches the optimal phenotype for the new environment (Orr, 1998).

Fortunately, for many biological invasions, additional timepoints can be obtained from historical samples, such as museum and herbarium specimens (North et al., 2021). A burst of recent studies have demonstrated the additional explanatory power offered by temporal information as well as potential pitfalls (Battlay et al., 2023; Bieker et al., 2022; Kreiner et al., 2022). Here, we first review the types of temporal data potentially obtainable for such studies, the temporal scale that can be assayed, and possible biases that may arise when using historical samples. We then describe potential applications, followed by a discussion of promising future directions.

2 | TYPES OF TEMPORAL DATA

Biological invasions are complex phenomena that result from the interplay between ecological and evolutionary processes (Barrett, 2015; Lambrinos, 2004) across distinct timescales. Early processes such as preadaptation, introduction, and establishment may often occur over millennia and centuries-long timescales (e.g., Clavero & Villero, 2013), while the ensuing effects of introduced species on the native community and feedbacks between adaptation and range expansion should continue to play out over more recent timescales. Recent advancements in the fields of evolutionary genetics and ecology have enabled the utilization of not only phenotypic but also genetic and genomic data from across these scales, including archaeological remains that can span thousands of

years, museum and herbarium collections that span the last 2–3 centuries and long-term field collections that can span years to decades (Figure 1). These rich data sources offer a promising pathway for unravelling the dynamic processes driving invasions (Figure 1).

Ancient DNA from archaeological samples has been leveraged to disentangle the invasion biology of humans worldwide (e.g., Rasmussen et al., 2010; reviewed in Slatkin & Racimo, 2016). Plants and animals are often preserved alongside these human remains (e.g., Jiang et al., 2016), providing an opportunity for direct observation of the consequences of human-mediated selection (Abbona et al., 2021; Purugganan & Fuller, 2011). While invasion biologists typically focus on unintentional introductions, humans have knowingly altered the distributions of organisms across the globe for millennia, facilitating introduction and adaptation in new environments (Gravuer et al., 2008). This intentional alteration is evident in domesticated species, where morphological and genetic data from archaeological remains have allowed for tracing their global spread (da Fonseca et al., 2015; Kistler, Thakar, et al., 2020), inferring the timescale of population genetic changes (Pérez-Escobar et al., 2021; Wales et al., 2019), and even reconstructing phenotypes and the degree of local adaptation (Swarts et al., 2017). Such approaches have tremendous promise for invasive species. One such notable example comes from black rats, for which archaeological data spanning 17 centuries revealed the introduction history and source of invasive European populations (Yu et al., 2022). While the quality of degraded ancient DNA is always an important consideration in such studies (Dehasque et al., 2020), a further limitation includes the difficulty of phenotyping due to variable preservation quality. As well, archaeological collections for most organisms are sparsely distributed. Because *a priori* sampling plans cannot be developed for such data, disentangling the role of spatial and temporal heterogeneity remains challenging (see also the discussion of sampling bias for herbarium and museum collections below).

Herbarium and museum collections are especially well-suited for contemporary invasion dynamics of plants and animals (Alves et al., 2019; Holmes et al., 2016; Lalueza-Fox, 2022; Lang et al., 2019). Unlike archaeological remains, these collections provide ample samples in space and time and abundant opportunities for phenotyping (Heberling, 2022). Also, compared with ancient DNA, which is typically retrieved from archaeological samples that can be thousands or millions of years old (Raxworthy & Smith, 2021), genetic material obtained from herbarium and museum collections that span 2–3 centuries (i.e., historical DNA; Raxworthy & Smith, 2021) displays relatively minimal chemical alteration (e.g., 1%–4% deamination at the first base; Gutaker & Burbano, 2017). As of 2021, over 3500 herbaria and 35,000 museums worldwide house approximately 400 million plants (Thiers, 2021) and over a billion animal specimens (Johnson et al., 2023). These collections thus provide unmatched sampling of genetic, morphological and community states across the contemporary globalized world (Kueffer, 2017), where opportunities for new introductions are constant and invasion into new habitats is facilitated by disturbance through industrialization, agriculturalization, urbanization and changing climate (Figure 1).

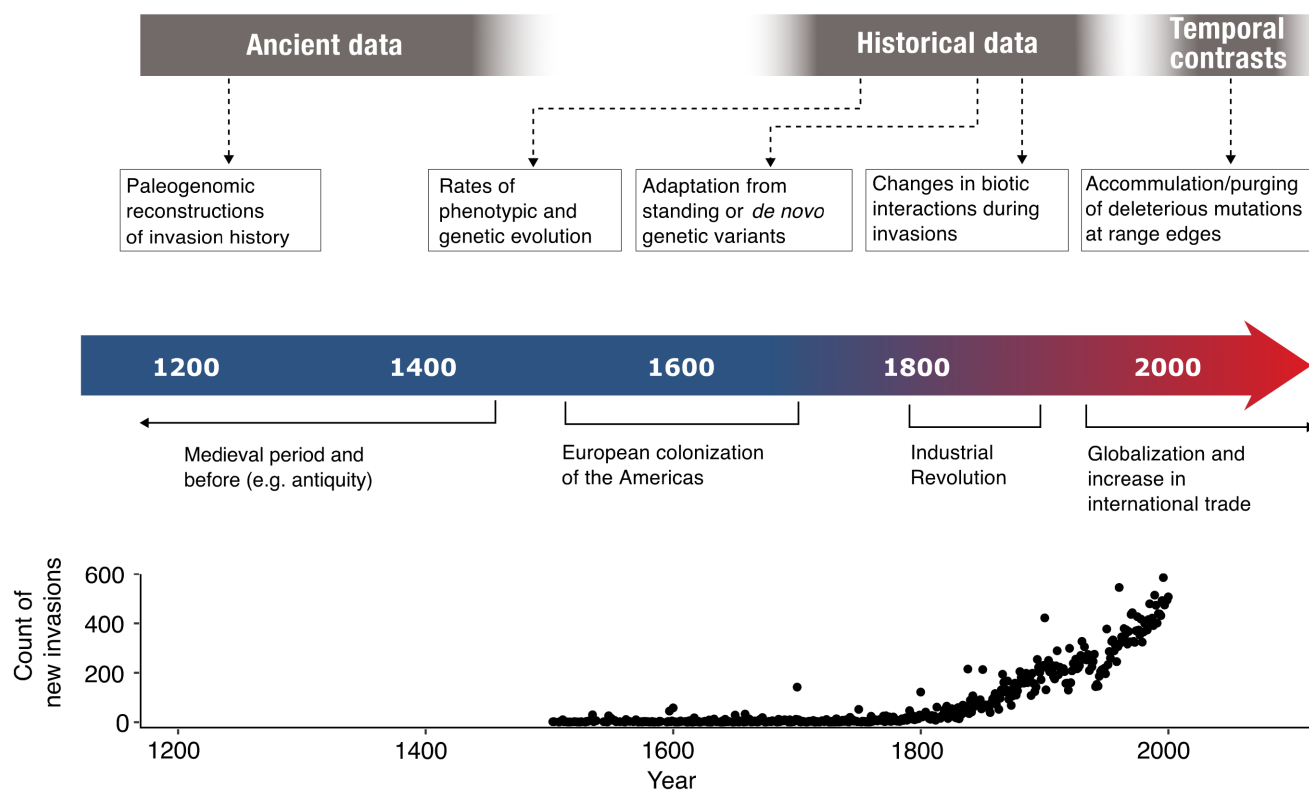


FIGURE 1 The use of temporal data in invasion biology. Ancient data, historical data and temporal contrasts are ordered to reflect the time scale that is typically captured by each approach. Arrows and boxes are used to provide examples of topics in invasion biology that can be investigated using each type of temporal data. The bottom graph shows the increase in the frequency of new invasions, as captured by dates of first record for established invasive species (data obtained from Seebens et al., 2017). No data is available prior to 1500.

Nonetheless, we emphasize that these collections are not uniformly distributed across space and time, and as such, careful curation of focal specimens should be considered to alleviate sampling bias (Daru et al., 2018; Yang et al., 2022). Furthermore, considerations should be taken prior to analysis for both genetic and morphological data: for DNA, either during sample library preparation and/or mapping to account for deamination and relatively short DNA fragments, and for trait data, considering the impact of preservation-related modifications (Maayan et al., 2022). Lastly, recent studies have shown that specimen preparation and storage can also be a source of contamination in DNA obtained from natural history collections (Bieker et al., 2022), and as such, this possibility should also be accounted for.

Temporal contrasts from field studies are crucial for understanding past invasion history (Blossey, 1999) and for predicting future short-term responses to changing climates (Wallingford et al., 2020). Repeat sampling provides nuanced insights into the factors influencing longer term eco-evolutionary dynamics and spans timeframes longer than a typical experiment (Reinke et al., 2019). Compared to ancient and historical datasets, field studies that rely on temporal contrasts provide insight over much shorter timescales (several years to a few decades; Figure 1), but at much higher resolution and often with better quality. For example, in contrast to historical approaches, temporal field studies can achieve more comprehensive sampling within populations and across the landscape while also

benefiting from uncompromised DNA quality (e.g., Bock et al., 2021; Chen et al., 2019; Rollins et al., 2016). Numerous applications of such in situ temporal studies approaches have demonstrated their eco-evolutionary utility (e.g., Alvarez & Cushman, 2002; Coltman et al., 1999; Haubrock & Soto, 2023) as well as their practical necessity for management (Latombe et al., 2017; Pinsky et al., 2021), and will only increase in their basic and practical importance as invasions become more extreme in future environments and as invasion biologists start to revisit earlier studies on widespread non-native species.

3 | APPLICATIONS OF TEMPORAL DATA IN INVASION BIOLOGY

3.1 | Genetic-level applications

3.1.1 | Demography

Reconstructing invasion histories—a key goal of which is to identify the source(s) of introduction and successive demographic changes that invasive populations experience—is critical to understanding the success or failure of biological invasions (Bock et al., 2015; Cristescu, 2015; Sherpa & Després, 2021). Obtaining this information using contemporary samples of long-established invasive

species is, however, challenging as processes like founder effects, genetic drift, expansion, admixture and selection can all interact throughout invasions, reshaping the genetic composition of introduced populations (Keller & Taylor, 2008; Sherpa & Després, 2021). Temporal data, including ancient and historical DNA, are ideally suited to tackle this complexity because these dynamics can be reconstructed and disentangled through direct observation of these dynamical shifts through time. For example, while multiple introductions and admixtures can often mask the prior occurrence of genetic bottlenecks (Dlugosch et al., 2015; Dlugosch & Parker, 2008; Estoup et al., 2016; Keller & Taylor, 2008), the analysis of historical samples collected during the earliest stages of invasions can mitigate this limitation, allowing researchers to directly evaluate the timing, magnitude, and persistence of genetic bottlenecks (Chan et al., 2006; Slatkin & Racimo, 2016; Wales et al., 2019). Furthermore, reconstructions of the invasion history can be obtained even when only a fraction of the genome can be interrogated. This includes low-coverage (Muhlfeld et al., 2014) or highly degraded DNA (Slatkin & Racimo, 2016), as well as organellar genomes (Abreu-Jr et al., 2020; Wales et al., 2019; Yu et al., 2022). Indeed, some of the earliest demonstrations of the utility of temporal data for reconstructing invasion histories relied on microsatellite markers and first-generation sequencing of organellar genes (e.g., Lees et al., 2011; Rollins et al., 2009, 2011; Saltonstall, 2002).

Temporal datasets have the potential to reshape our understanding of invasive species by revealing cryptic and failed invasions (Grosser et al., 2016; Rawlence et al., 2017). For example, the use of archaeological samples to study New Zealand birds revealed that contemporary lineages of black swans (Rawlence et al., 2017) and Australian little penguins (Grosser et al., 2016) are in fact recent colonizers, while ecologically equivalent native taxa are declining or extinct. As well, historical data have been used to study invasions of the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), a generalist pathogen that has had a devastating effect on amphibian biodiversity worldwide. For instance, museum specimens dating since the 1800s were used to revise the earliest known dates of *Bd* introduction in amphibian populations in Mexico and the Bolivian Andes (Basanta et al., 2021; Burrowes & De la Riva, 2017). Similarly, temporal datasets can offer a unique perspective by allowing us to also study failed invasions (Alaniz et al., 2021; Zenni & Nuñez, 2013), as has now been observed for *Daphnia curvirostris* in the northeastern United States (Duffy et al., 2000).

One evolutionary process that often interacts with demography and is particularly relevant for invasive species is admixture (Ellstrand & Schierenbeck, 2000; Fournier & Aron, 2021). Admixture may disrupt favourable allelic combinations and epistatic gene interactions, leading to outbreeding depression, especially in locally adapted populations (Moran et al., 2021; Todesco et al., 2016). However, admixture may also facilitate biological invasions by alleviating demographic and genetic bottlenecks during introductions and by creating novel genetic combinations that fuel rapid adaptation during establishment and range expansion (Dlugosch & Parker, 2008; Ellstrand & Schierenbeck, 2000; Fournier & Aron, 2021; Pfennig et al., 2016).

Resolving the timing of admixture during biological invasions has remained a major challenge with contemporary data, and therefore its importance for different stages of the invasion is typically unknown. Studying temporal changes in genetic admixture may improve our understanding of the causes and consequences of admixture over the invasion process (Bieker et al., 2022; Kreiner et al., 2022; Muhlfeld et al., 2014). For example, in the rainbow trout (*Oncorhynchus mykiss*) invasion of Montana river systems, the analysis of historical samples revealed that hybridization with the native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) was negligible for almost a century, but it quickly increased in the last 30 years, likely as a result of climate change (Muhlfeld et al., 2014). The analysis of herbarium accessions spanning the last two centuries revealed a complex admixture history in common ragweed (*Ambrosia artemisiifolia*), involving prior admixture in the native area and changes in population structure due to interspecific hybridization in the invaded area (Bieker et al., 2022). Similarly, shifts in the distribution of ancestry across the geographic range in North America were a prerequisite to agricultural adaptation in *Amaranthus tuberculatus* (Kreiner et al., 2022; Figure 2). Excitingly, many cases of invasions involving admixture could be revisited by incorporating historical samples, allowing more general conclusions on the role of admixture during invasions to be developed.

3.1.2 | Adaptation

Invasive species can display rapid adaptation to new environmental conditions within their introduced ranges, resulting in noticeable genetic and phenotypic changes within short time periods (Colautti & Barrett, 2013; Colautti & Lau, 2015; van Boheemen & Hodgins, 2020; Wu & Colautti, 2022). Analysing DNA changes in populations over time provides a direct means to investigate the genetic mechanisms underlying this adaptation. While this approach has traditionally been challenging for complex organisms in natural environments, evolutionary studies relying on genetic and genomic data increasingly use natural history collections of weedy and introduced species to study "evolution in action" (Alves et al., 2019; Battlay et al., 2023; Bieker et al., 2022; Kreiner et al., 2022; Rollins et al., 2016; Stuart et al., 2022; Vandepitte et al., 2014). These temporally resolved studies are providing a deeper understanding of the genetic architecture of adaptation to environmental change, including the extent of genetic parallelism during adaptation to similar types of environmental change as well as the factors that influence parallelism, such as the source of the adaptive alleles (new mutations or standing variation) and their effect size.

Standing genetic variation, which refers to existing genetic diversity within a population, plays a crucial role in rapid adaptation due to the time required for new mutations to arise (Barrett & Schluter, 2008). Genomic analysis of historical samples has revealed the importance of standing variation in facilitating rapid adaptation during range expansions of introduced species (Battlay et al., 2023; Cohen et al., 2022; Kreiner et al., 2022; Vandepitte et al., 2014).

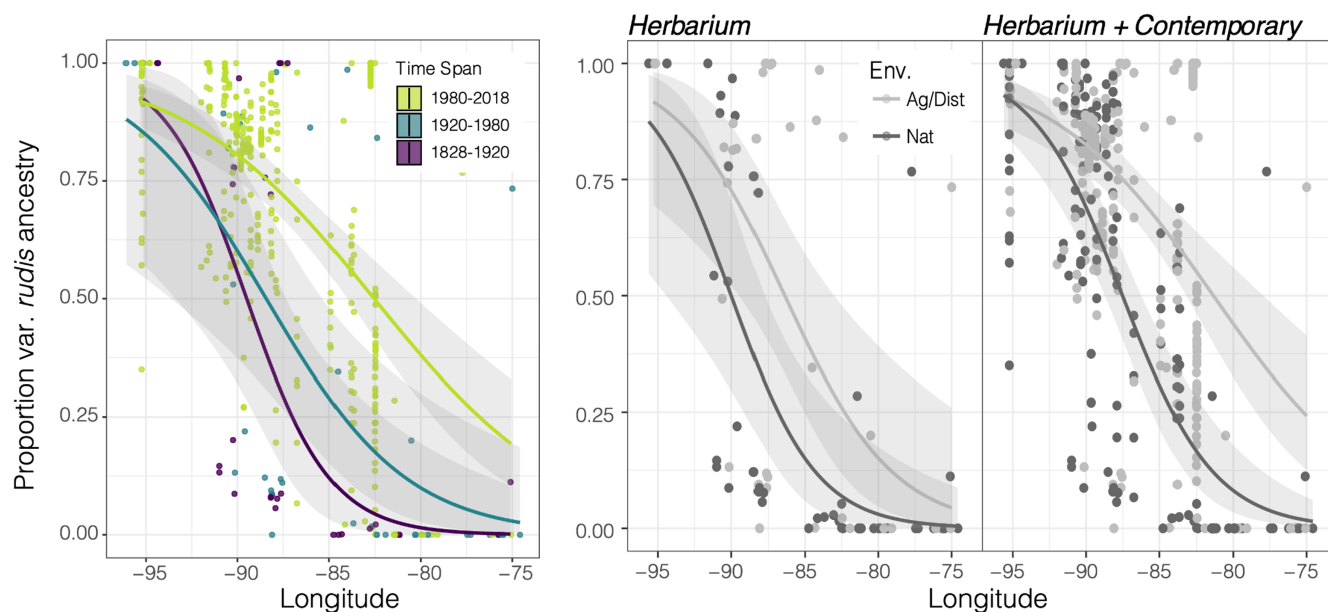


FIGURE 2 Herbarium genomics allows for direct observation of shifting ancestry through time. Left panel depicts an eastward expansion of *Amaranthus* var. *rudis* ancestry, particularly between 1980 and 2018. Right panel demonstrates the effect of the range expansion on the distribution of ancestry in agricultural/disturbed habitats compared to natural habitats. Figure adapted from Kreiner et al., 2022, *Science*, Reprinted with permission from AAAS.

For example, a herbarium-based study identified signals of rapid adaptation in the flowering time genes of *Sisymbrium austriacum* subsp. *chrysanthum*, likely driven by standing variation during the initial stages of introduction (Vandepitte et al., 2014). In *A. tuberculatus*, agricultural selection has drawn on high-frequency variants that tend to historically be found in ancestry mapping to a southwestern lineage (Kreiner et al., 2022). In ragweed, chromosomal inversions associated with adaptive traits and with temporal and spatial signatures of selection predate the European invasion. This points to a key role of standing variation in repeated patterns of climate adaptation between the native North American and introduced European range, likely facilitated by multiple introductions of ragweed into Europe (Battlay et al., 2023; van Boheemen et al., 2017; Figure 3). In contrast to the outcrossing weeds *A. tuberculatus* and ragweed, a single lineage predominates in the introduced range of self-fertilizing *Arabidopsis thaliana* in North America. Genome sequencing of herbarium and modern specimens identified several de novo mutations that had risen to intermediate or high frequencies in this North American lineage. A subset of these changes could explain variation in traits that were thought to be important for adaptation in North America (Exposito-Alonso et al., 2018). These examples highlight the significance of both de novo variation and standing genetic variation in rapid adaptation, likely influenced by factors such as mating systems, invasion history and genetic trait architecture.

Genomic studies of natural history collections can allow selection coefficients to be estimated over time scales often inaccessible to most evolutionary studies in the field (Alves et al., 2019; Battlay et al., 2023; Kreiner et al., 2022). Spatially and temporally resolved genomic data in common ragweed allowed selection coefficients on

chromosomal inversions to be estimated, including one (hb-chr2) where inversion homozygotes have a 2.4% fitness advantage over the alternative homozygote in the introduced European range, resulting in a large frequency shift over time (Battlay et al., 2023; van Boheemen et al., 2017; Figure 3). Changes in the strength of selection over the course of the invasion can also be captured. A study of European rabbits in France, the UK and Australia identified strong parallel selection on standing variants following the release of the myxoma virus in Europe and Australia. However, as the virulence waned, the strength of selection on those variants declined (Alves et al., 2019). For the invasion of *A. tuberculatus* into agriculture, herbarium data allowed direct observation of shifting selection coefficients imposed over alterations to cropping practices across the last two centuries, the strongest of which were inferred for causal herbicide resistance mutations since the introduction of herbicides in the 1950s (Kreiner et al., 2022; Figure 4). Therefore, temporal data in invasive species offer opportunities to study the strength and tempo of selection over the course of an invasion, which can provide insights into eco-evolutionary dynamics.

3.1.3 | Maladaptation

Aside from adaptive genetic changes, the dynamics of deleterious mutations can also determine invasion success and persistence. For example, the success of invasive species may be hindered by the accumulation of deleterious mutations at expansion fronts, a process known as expansion load (Peischl et al., 2013; Peischl & Excoffier, 2015). Under this model, expanding populations experience extreme genetic drift due to low density

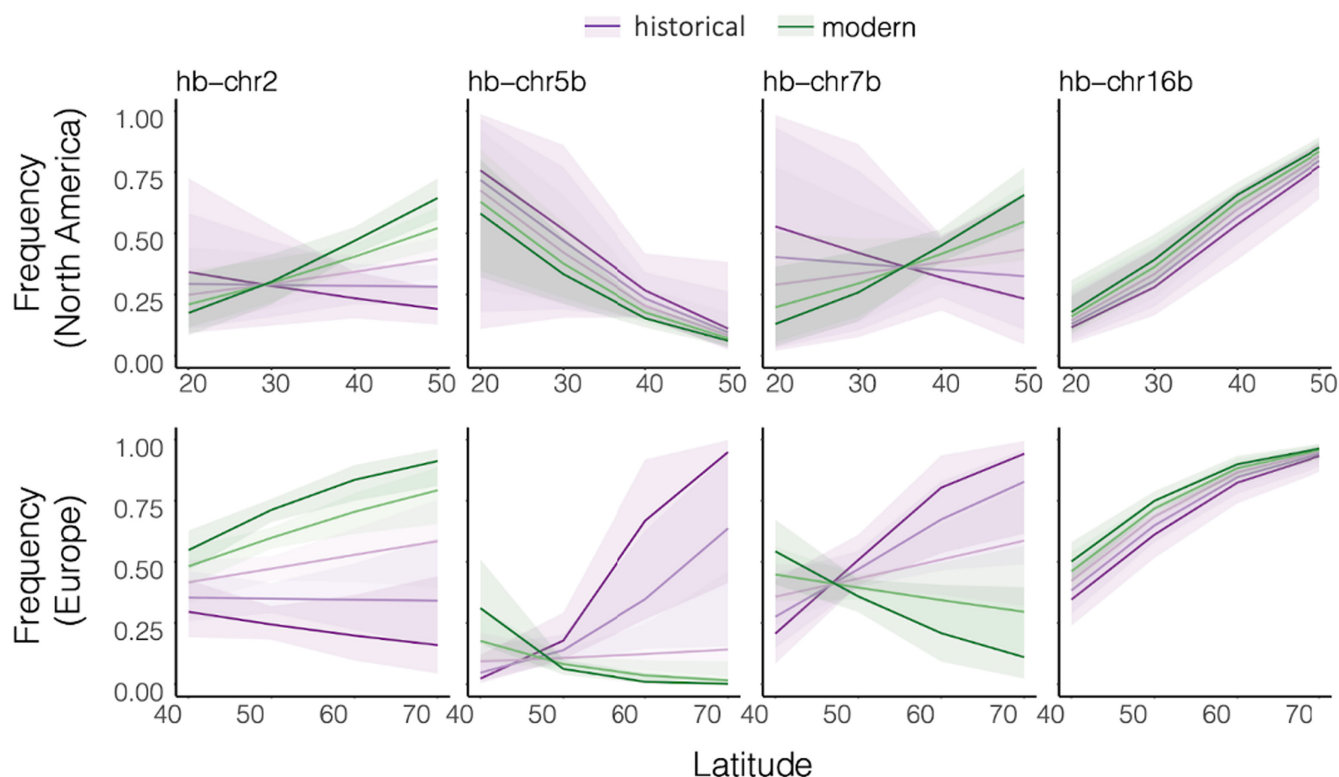


FIGURE 3 Spatio-temporal genomic data allows for inference of the mode of adaptive convergence in latitudinal clines. Each column represents a putatively adaptive inversion, where logistic regression models with error bands represent the 95% CI of haploblock frequency (allele 1) against latitude across five time bins ranging from historical (dark purple) to modern (green) in *Ambrosia artemisiifolia*. Latitudinal clines have formed in Europe (introduced range) from pre-existing adaptive variation present in North America (native range). Figure adapted from Battlay et al., 2023, *Nature Communications*.

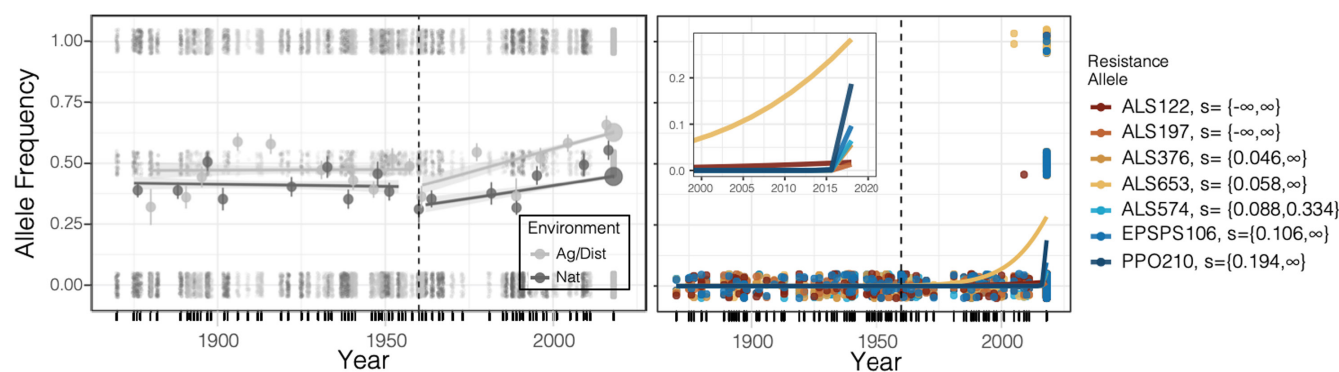


FIGURE 4 Direct inference of selection coefficients, along with their change through time, from temporal herbarium genomic data. Left panel depicts the allele frequency trajectories of contemporary agricultural alleles based on logistic regression of genotypes (smallest dots) observed in herbarium samples from natural (dark grey) or agricultural/disturbed (light grey) habitats. A segmented regression approach provided evidence for a shift in selection, as depicted by the vertical dashed line. Right panel depicts the strengths of selection governing herbicide resistance alleles across the landscape (all habitat types), with the logistic fits visualized and the maximum likelihood 95% CI provided for each segregating resistance allele (see legend). Figure adapted from Kreiner et al., 2022, *Science*; Reprinted and adapted with permission from AAAS.

(Edmonds et al., 2004), which in turn enables existing and new mutations to “surf” to high frequencies (Klopfstein et al., 2006; Travis et al., 2007). This can restrict range expansion (Peischl et al., 2015; Willi et al., 2018), particularly when deleterious mutations have small to intermediate effects (Henry et al., 2015; Peischl & Excoffier, 2015). Alternatively, range expansion post-introduction

could facilitate the purging of deleterious alleles. Increased inbreeding due to population bottlenecks during range expansion allows strong selection to remove deleterious alleles, reducing the genetic load (Barrett & Charlesworth, 1991; Barringer et al., 2012; Pujol et al., 2009). Simulations using invasive wild populations of *Brachypodium sylvaticum* showed that intermittent gene flow

among isolated, inbreeding populations during range expansion can increase genetic purging (Marchini et al., 2016), improving the fitness of range-edge populations. However, the prevalence of expansion load versus purging in invading populations is, to a large extent, unknown, and most evidence to date comes from historical expansions of human populations (Henn et al., 2016; Lohmueller et al., 2008; Peischl et al., 2013; 2018) or domesticated species (e.g., Renaut & Rieseberg, 2015). Future studies could utilize natural history collections and historical DNA from the early stages of invasions and from the native range to help resolve the dynamics between expansion load and genetic purging towards the range edge. Furthermore, historical DNA could also offer a potential avenue to study the role of deleterious variants in failed invasions where species are now extirpated in their non-native ranges (Duffy et al., 2000). Similarly, historical genomes could provide insight into the genetic factors contributing to long demographic lags that precede invasions (Aikio et al., 2010), advancing our understanding of maladaptation and genetic load during biological invasions.

3.2 | Epigenetic-level applications

Another fascinating avenue for exploration involves the development of techniques for studying historical epigenomics. Indeed, there has long been speculation that epigenetic mechanisms may be one resolution for the genetic paradox of invasion (Mounger et al., 2021). Given that epimutations occur at higher rates than DNA mutations and can be stable over time (Schmitz et al., 2011; Xu et al., 2020), it is possible that epimutations could contribute to adaptation over short time scales, particularly in cases where genetic variation is limited, such as clonal invaders (Mounger et al., 2021). Employing sequencing approaches to identify DNA methylation patterns and changes in chromatin architecture in historical samples of invasive populations could allow the timing of epimutations in relation to DNA changes to be identified and their role, if any, in rapid adaptation to be explored. Further, epigenetic modifications can mediate environmental effects on phenotypes through gene expression and historical epigenomics may therefore allow ancestral patterns of gene expression to be inferred (e.g., Hahn et al., 2023; Rubi et al., 2020). These analyses could be coupled with direct reconstruction of gene expression profiles from natural history specimens (e.g., Marmol-Sanchez et al., 2023), which is now possible, thanks to the development of protocols for extracting RNA from preserved specimens (e.g., Speer et al., 2022). DNA methylation patterns have already been investigated in ancient and historical specimens (e.g., Gokhman et al., 2014; Gokhman et al., 2016; Hahn et al., 2020; Niiranen et al., 2022; Orlando et al., 2015; Pedersen et al., 2014; Rubi et al., 2020; Smith et al., 2014), indicating that this approach holds promise for unravelling the role of heritable epigenetic modifications in facilitating rapid adaptation to environmental shifts. However, the effects of sample age, preservation method, contamination and the sensitivity of epigenetic marks to the environment mean their feasibility will be

dependent on the specimen type and preservation method (Hahn et al., 2020; Raxworthy & Smith, 2021).

3.3 | Trait-level applications

Characterizing the traits that facilitate the invasive spread of populations and species has been a fundamental goal of invasion biology for over six decades (Baker, 1955; Baker & Stebbins, 1965). While some patterns have emerged for particular traits since then (reviewed in Hodgins et al., 2018), the role of morphological, physiological and reproductive traits in invasion resoundingly shows strong dependence on taxonomic, spatial and temporal contexts (Hamilton et al., 2005). Leveraging temporal data across scales will therefore provide key insights into the dynamics of traits during the process of invasion, from establishment to spread. Indeed, the combination of contemporary field studies with museum collections has been instrumental in disentangling the link between leg-length evolution and the capacity for range expansion in a near 100-year invasion of cane toads in Australia (Phillips et al., 2006). However, a major challenge to the utility of museum and herbarium collections for evolutionary inference is plasticity—that specimens have not experienced the same environments and thus trait differences through space and time do not necessarily reflect evolutionary change. Wu and Colautti (2022) provide one path forward, implementing a modelling approach to explicitly control for phenotypic plasticity in phenological observations to highlight the importance of the early evolution of flowering time in purple loosestrife during its invasion across North America. Lang et al. (2022) provide another possible path, using functional genetic information to predict the genetic component of traits and thus their evolution through time and space. We expect that the further integration of modelling and genetic approaches with phenotypic data, herbarium and museum data will be key to future investigations of trait evolution during invasions and changing environments.

3.4 | Community-level applications

During biological invasions, introduced species may lose or gain enemies such as competitors, herbivores, or parasites (Cappuccino & Carpenter, 2005), as well as mutualists such as mycorrhizal fungi, pollinators or seed dispersers (Tedersoo et al., 2007). These changes in biotic interactions may determine whether invasive populations can successfully establish and spread in a new region (Richardson et al., 2000; Traveset & Richardson, 2014), and they may also prime invasive populations for rapid evolutionary change (Blossey & Nötzold, 1995). As such, understanding how invasive species interact with other members of biological communities is critically important. Specimens maintained in herbaria and museum collections have proven useful for understanding such interactions and their temporal dynamics (e.g., Beaulieu et al., 2018; Iverson et al., 2022; Schilthuizen et al., 2016; Zangerl & Berenbaum, 2005). In wild parsnip (*Pastinaca sativa*), for example,

Zangerl and Berenbaum (2005) relied on 152 years of herbarium records to document initial enemy loss and subsequent enemy gain during a biological invasion. Specimens from before 1889, when invasive populations of *P. sativa* were still free from interactions with a major native-range webworm herbivore, had no evidence of herbivory damage. As well, these early specimens showed reduced investment in chemical defence, consistent with a metabolic cost of defence traits and with selection favouring

less costly genotypes. After 1889, however, these patterns were reversed once the webworm herbivore was introduced, and the antagonistic interaction between these two species was re-established (Zangerl & Berenbaum, 2005).

Methods to quantify species interactions at the trait or organismal level can, however, be laborious and typically permit the study of only a small number of species (Banerjee et al., 2022). As an alternative, studies have highlighted the possibility of reconstructing

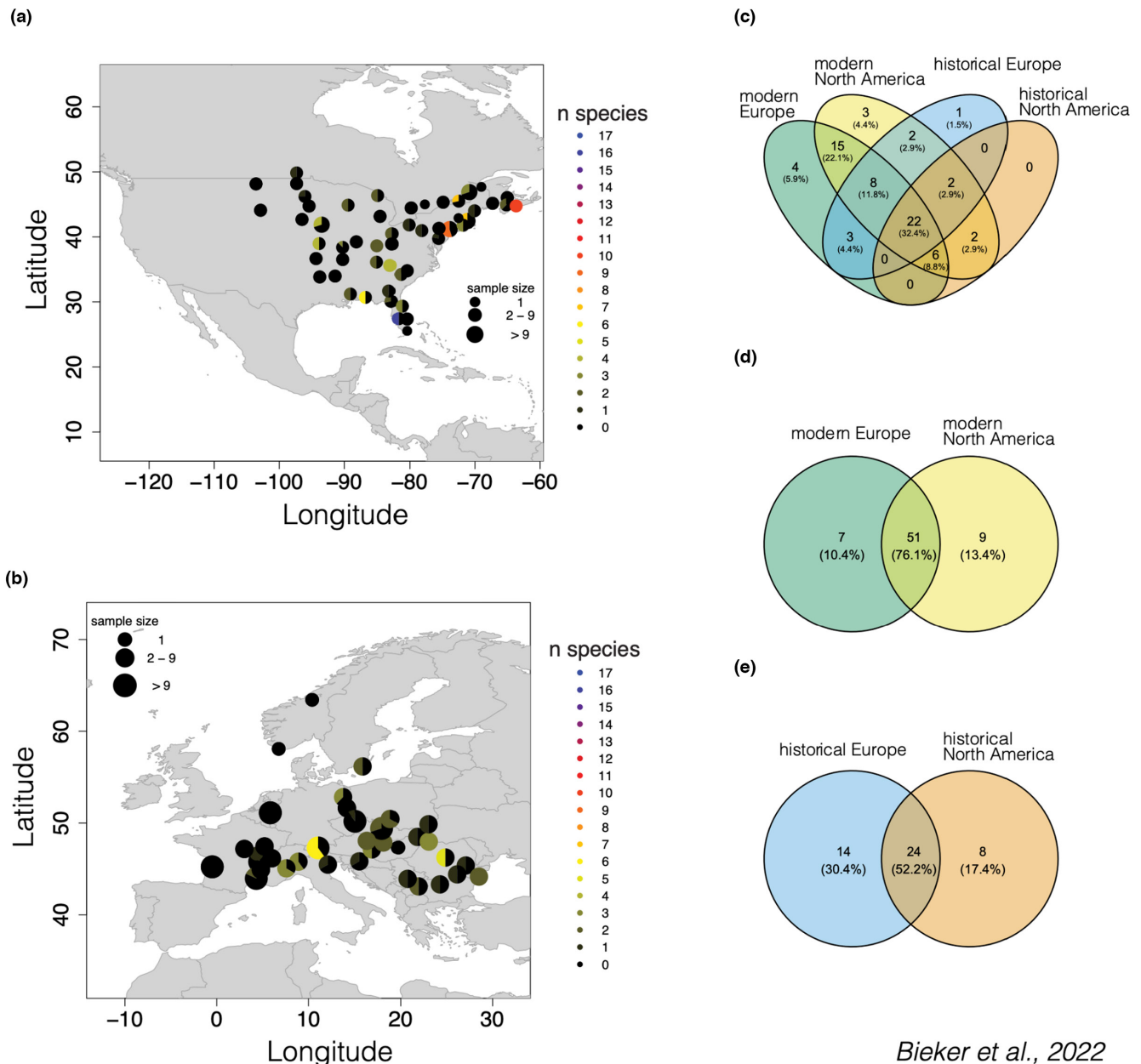


FIGURE 5 Pathogen presence over time in native and introduced common ragweed populations. (a, b) Prevalence of *Xanthomonas* spp., a bacterial pathogen of common ragweed, in modern genomic samples. The pie chart indicates the fraction of samples in which *Xanthomonas* spp. are present, with black indicating no *Xanthomonas* species being identified. The colour indicates how many different *Xanthomonas* species were identified at a location. (a) Modern North America. (b) Modern Europe. (c) Venn diagram of pathogens identified in modern European (green), modern North America (yellow), historical European (blue), and historical North America (orange) samples. (d) Venn diagram of pathogens identified in modern European (green) and modern NA (yellow) samples. (e) Venn diagram of pathogens identified in historical European (blue) and historical NA (orange) samples. Figure from Bieker et al., 2022 *Science Advances*.

interaction networks in complex biological communities using DNA (e.g., Banerjee et al., 2022; Valentini et al., 2009). Importantly, this technology can also be applied to ancient and historical samples. After properly accounting for the possibility of contamination related to the preparation or storage of specimens (Bieker et al., 2022), these methods can be used to reveal the diet of extinct animal species (Poinar et al., 1998) or to quantify pathogenic microbes from plant specimens that are maintained in herbaria (Kistler, Bieker, et al., 2020; Malmstrom et al., 2022; Yoshida et al., 2014). In invasive species such as the common ragweed, for example, metagenomic analyses of herbarium specimens helped reveal how pathogen dynamics shape invasion success (Bieker et al., 2022; Figure 5). In this species, escape from microbial pathogens that are common in the native range may have facilitated the early success of introduced populations. Novel pathogens that were subsequently encountered during invasive range expansion then represented a new source of natural selection that likely shaped genomic variation (Bieker et al., 2022). In support of this possibility, the genome of common ragweed was found to retain the signature of natural selection on genes known to be associated with defence response (Bieker et al., 2022). We anticipate that similar studies, which successfully connect changes in community composition to adaptive genetic variation, will become more common as DNA information is increasingly used to study species interactions in historical and contemporary populations.

4 | CONCLUSIONS

In this review, we have highlighted how temporal collections can be leveraged to study biological invasions. Early studies predominantly used herbaria and museums to obtain occurrence data, with the goal of reconstructing the temporal and spatial progression of invasions (e.g., Reznicek & Catling, 1987; Sauer, 1957; Stuckey, 1980; Suarez et al., 2001). More recent studies have highlighted how these collections, as well as repeated sampling available from earlier research, can be used to obtain much more detailed, time-stratified information on genetic, epigenetic, phenotypic, and community-level changes that occur during invasions. This was made possible due to progress on two fronts. First, technologies for ancient and historical DNA have advanced tremendously since the earliest demonstration, nearly four decades ago, that genetic material can be retrieved from ancient specimens (Higuchi et al., 1984); reviewed in (Raxworthy & Smith, 2021; Willerslev & Cooper, 2005). These methods now allow entire genomes to be interrogated, with the potential to provide a detailed spatiotemporal record of genetic and epigenetic change (Hahn et al., 2020; Raxworthy & Smith, 2021; Rubi et al., 2020). Second, the digitization of temporal collections is accelerating, along with the development of data aggregators that facilitate analysis (Davis, 2023; Hedrick et al., 2020; Soltis, 2017). Thus, image data from a rapidly expanding number of specimens is available for research.

These temporal datasets have been effectively applied to answer long-standing questions on the origin of invasive species (e.g., Yoshida et al., 2013), on mechanisms of adaptation during novel-range colonization (e.g., Alves et al., 2019; Bieker et al., 2022; Vandepitte et al., 2014), or on the rate of genetic and phenotypic evolution during invasions (e.g., Alves et al., 2019; Kreiner et al., 2022; Wu & Colautti, 2022). Despite this progress, the potential of temporal collections in invasion biology has yet to be fully achieved. For example, while temporal data can reveal whether alleles derive from standing variation or new mutations (e.g., Alves et al., 2019; Exposito-Alonso et al., 2018), most studies to date have focused on adaptive variants, and more work is needed to explore the origin of deleterious variants. In this context, invasion genomics lags behind conservation genomics, where temporal collections are used to obtain baseline levels of genetic load (e.g., Feng et al., 2019; van der Valk et al., 2019). Also, screens for epigenetic marks in the genomes of archived specimens can provide clues on gene expression and epigenetic re-patterning (Hahn et al., 2020; Rubi et al., 2020), an area that has received limited investigation in the context of invasions (Mounger et al., 2021). Lastly, temporal collections can reveal changes in interspecific interactions during invasion (Bieker et al., 2022). In turn, this information is required to understand if rapid adaptation in invasive populations tends to occur more often in response to abiotic or biotic factors (Hodgins et al., 2018). With increased incorporation of temporal data across a range of invasive taxa, broad analyses on these topics will increasingly become possible, ultimately unlocking the full potential of invasions as natural evolutionary experiments.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Not applicable.

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