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Symposium

Repeating Historical Studies to Understand Functional Responses to Environmental Change*

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abstract: Heterogeneity and seeming unpredictability in responses to environmental change is driving a push to understand the underlying organismal mechanisms. The 2024 Vice Presidential Symposium of the American Society of Naturalists aimed to catalyze a promising and underutilized approach to extend understanding: repeating historical experiments or otherwise quantifying organism function through time. Many physiological, behavioral, ecological, and evolutionary experiments or observations reported in journal articles and elsewhere offer the potential for repeating the data collection to detect responses to environmental change. The approach extends beyond resurrection studies, which revive organisms to compare function and performance of modern organisms to their historical counterparts but are severely taxonomically and logistically restricted. In this introductory article, we discuss the promise of functional resurveys and highlight exemplar research repeating physiological measurements, behavioral experiments or observations, selection and quantitative genetic experiments, and measurement of ecosystem function. We also feature novel approaches to infer function from both modern and historical specimens and data, including temporal genomics, quantifying composition or energy stores, and genomic reconstruction. The research reveals key organismal mechanisms that mediate responses to environmental changes and can be accounted for to improve ecological and evolutionary forecasts.

Keywords: climate change, experiment, functional trait, plasticity, resurvey, resurrection.

Introduction

Accurately forecasting ecological and evolutionary responses to environmental change is necessary for anticipating and managing changes to biodiversity and ecosystem function (Briscoe et al. 2023; Urban et al. 2023). Currently, predictive approaches largely omit biological mechanisms and exhibit mixed performance (Maguire et al. 2015). Heterogeneity in environmental change responses is promoting a push to understand the underlying organismal mechanisms so as to improve future predictions of climate change responses (Nogués-Bravo et al. 2018). Characterizing how organisms experience their environment (Ergon 2022) and quantifying organismal function through time will assist with identifying the underlying mechanisms (Coulson et al. 2017).

Historical collections and observations have revealed environmental change responses including shifts in phenology, abundance, and distribution (Verheyen et al. 2017). Collections have less often been used to document phenotypic shifts, primarily changes in body size (Woodward 1987; Gardner et al. 2011; Sheridan and Bickford 2011; MacLean et al. 2019). There are extensive opportunities to extend such studies to assess the functional responses that are key to understanding and anticipating responses to climate change (Buckley and Kingsolver 2013).

A promising but underutilized approach to probing responses to environmental change, which we term "functional resurveys," is to repeat historical experiments or otherwise quantify changes in organism function—processes influencing growth, development, survival, or reproduction—through time. The most familiar of this work involves resurrection studies that revive organisms such as

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bacteria, daphnia, or plants to compare environmental sensitivities of modern organisms to their historical counterparts (Weider et al. 2017; Franks et al. 2018). Such resurrection studies are severely taxonomically restricted and rely on scarce historical samples. Long-term continuous experiments and observations have also extended understanding of responses to environmental change (e.g., Rasmussen et al. 1998; Visser 2008; Ozgul et al. 2009; Smith et al. 2015), primarily ecological shifts but increasingly evolutionary changes as well (Cocciardi et al. 2024). But such long-term studies are rare. Our focus is on catalyzing new opportunities to reach back in time—potentially over a century, further than many resurrection or long-term studies—to assess functional organismal responses to environmental change. We focus on studies of climate change responses given their prominence, ubiquity, and relative ease of identifying underlying mechanisms, but the approaches readily generalize to other environmental changes, such as pollution or land use change.

Many physiological, behavioral, ecological, and evolutionary experiments or observations reported in journal articles offer the potential for repeating the data collection to detect climate change responses. Repeating experiments offers greater control that is particularly desirable for detecting evolutionary responses. For example, studies of thermal sensitivity—including thermal performance curves (TPCs), which have rapidly proliferated since the 1980s—are now sufficiently old to offer the potential to detect evolution for organisms with short life cycles, including annual organisms (e.g., see citations of Huey and Kingsolver 1989). A particularly powerful approach, which is rapidly increasing in tractability, is complementing quantifications of organismal function through time with mechanistic information, including shifts in energy stores and gene frequencies (Holmes et al. 2016; Clark et al. 2023). For example, resurrection studies are increasingly probing underlying genomic shifts (Franks et al. 2016). We highlight the potential of functional resurveys by considering questions they are well suited to answer and potential approaches.

Questions

Functional resurveys afford opportunities to test predictive approaches and to resolve questions such as the ones outlined below.

Question 1. How do environmental exposure and organismal sensitivity shape responses to environmental change?

Question 2. How do environmental conditions and traits determine whether organisms respond to change via stasis, environmental tracking through space or time, plasticity, or evolution?

Question 3. How are levels of biological organization differentially sensitive to environmental means, variability, and extremes?

Question 4. What are the timescales of environmental changes relative to those of biological responses?

Question 5. What is the interplay of individual, population, community, and ecosystem responses to environmental change?

Approaches

We outline six nonexhaustive classes of functional resurveys. We expect organisms to shift through time to better tolerate warmer and more variable conditions, avoid energy depletion, and minimize phenological mismatches with interacting species and resources (fig. 1). The complexities of organismal-environment interactions and their influence on multiple fitness components will drive exceptions to these expectations (Buckley et al. 2021; Srivastava et al. 2021). Such exceptions highlight the need for approaches such as functional resurveys to reveal the mechanisms by which organisms are actually responding.

Approach 1: Resurrection. Resurrecting historical organisms offers a direct assessment of evolutionary shifts over time (reviewed in Franks et al. 2008, 2018; Weider et al. 2017). Resurrection studies have found shifts in plant drought tolerance (Dickman et al. 2019; Wooliver et al. 2020); in *Daphnia*, thermal tolerance (Geerts et al. 2015); and in bacteria, fitness responses to water chemistry (Fox and Harder 2015). Monkeyflower (*Mimulus*) responses to recent drought include earlier seedling emergence, potentially to avoid dry conditions along with other associated outcomes (Dickman et al. 2019; fig. 2*A*). In this special section, Sheth et al. (2026; see table 1) extend *Mimulus* resurrection studies examining evolution in response to drought and heat. They quantify differences in traits and fitness for ancestors and descendants for populations across the species' range in common gardens at differing range positions, which provides insight into the interplay between evolutionary rescue and range dynamics (question 2). Closely related to resurrection approaches are synthetic strategies such as re-creating proteins (see approach 6 below).

Approach 2: Repeating physiological measurements. Abundant opportunities exist to repeat physiological measurements, including TPCs, thermal limits, metabolic rates, enzyme activities, and heart rates. The methods for these measurements are usually sufficiently standardized and well described in articles to reliably repeat the experiments. For example, an exceptionally long-term physiological resurvey found that intertidal flatworms were able to regenerate at lower salinities and may regenerate well over a broader range of salinities than a century prior (Clayton and Spicer 2020; fig. 2*B*).

Developmental plasticity in response to environmental cues is a central mechanism by which organisms respond to climate change (question 2). In this special section,

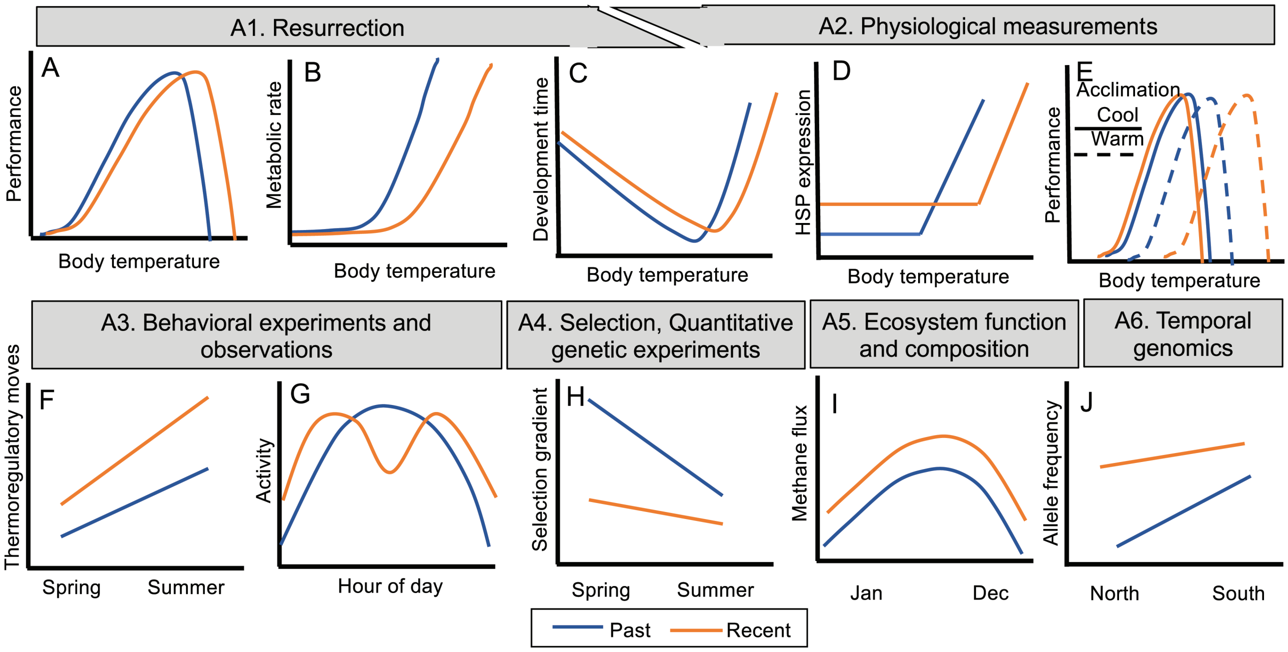

Figure 1: Shifts in many types of functional responses can be detected via resurrection experiments (*A1*) or repeating past experiments (*A2*). Expected responses to warming between past and recent time periods include shifts in thermal performance curves toward warmer temperatures (*A*), depression of metabolic rates and their temperature dependence (*B*), declines in developmental rates to limit phenological mismatches and shifts in the thermal optima of development (*C*), higher levels of constitutive heat shock protein (HSP) expression and induction at higher temperatures (*D*), and evolution of increased plasticity in thermal sensitivity (*E*). *A3*, Behavioral experiments and observations are expected to reveal shifts including more movement to enable thermoregulation and differential responses across seasons, such as phenological shifts (*F*), and increased activity during cooler time periods and activity restrictions during warm periods (*G*). *A4*, Shifts in selection, including reduced seasonality and changes in direction (*H*), are expected with warming. Quantitative genetic experiments can reveal additional changes, such as changes in genetic variances and covariances. *A5*, Repeating experimental and observational studies of ecosystem function and composition of functional members such as microbes provide a robust means of detecting functional changes (*I*). *A6*, Genomic shifts through time are increasingly feasible to detect, generally along spatial gradients (*J*).

Buckley and Kingsolver (2026) address how the interplay of butterfly plasticity and evolution is mediated by environmental exposure (questions 1 and 2). They use mechanistic models to generate predictions that are then tested by repeating historical experiments and measuring specimen phenotypes. An additional butterfly example resurveyed development rate to contrast responses across life stages: evolutionary shifts were detected for photoperiod-cued butterfly

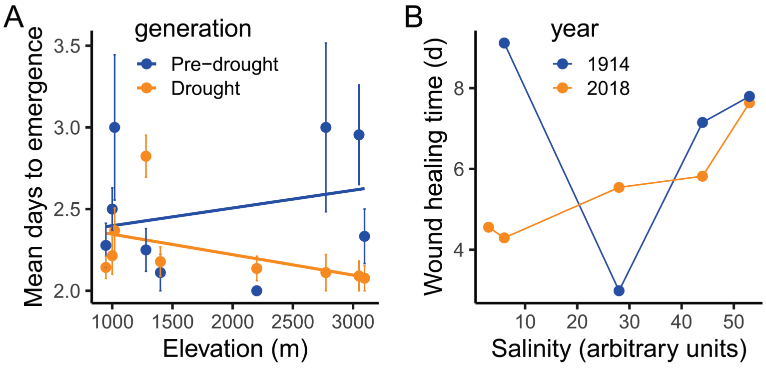

Figure 2: *A*, Time to emergence for resurrected *Mimulus* seeds was less for those collected after the drought (2014) than for those collected before it (2006; data from Dickman et al. 2019). *B*, The regeneration ability of flatworms at low salinities increased between 1914 and 2018 (data from Clayton and Spicer 2020).

Table 1: Questions addressed and approaches employed by articles in the special section

Article	Questions	Approaches
Sheth et al. 2026	1–3	1 (resurrection), 4 (repeating selection and quantitative genetic experiments)
Buckley and Kingsolver 2026	1–3	2 (repeating physiological measurements), 4 (repeating selection and quantitative genetic experiments)
Zoller et al. 2026	5	3 (repeating behavioral experiments or observations)
Braga et al. 2026	4, 5	5 (repeating measurement of ecosystem function and composition)
Fitz et al. 2026	2, 4	6 (temporal genomics)

larval development time but not pupal diapause (Nielsen et al. 2023). Pond frog populations have also evolved to develop faster, potentially to avoid accelerated pond drying, in response to 17 years of climate change (Arietta and Skelly 2021). Repeating measurements of how growth and developmental rates respond to environmental conditions and other factors, such as nutrition, can likewise help interpret and anticipate phenotypic changes.

Measuring functional trait values over time from museum specimens and using modeling to infer functional changes over time is a less direct, but broadly feasible, approach to study function over time (Briscoe et al. 2023). Riddell et al. (2019) used museum specimens to quantify traits influencing heat retention in birds and mammals. Using the traits to parameterize energy budget models revealed that water requirements for cooling likely accounted for the greater decline in Mojave Desert bird communities compared with mammal communities over recent decades. While phenotypic changes over time have been detected (MacLean et al. 2019), other studies suggest evolutionary constraints or unaccounted for complexities (question 2). For example, phenotypic and demographic stability was observed over decades for salamander populations (Evans et al. 2018; Giery et al. 2021).

Approach 3: Repeating behavioral experiments or observations. Repeating behavioral experiments and observations is another readily conducted type of functional resurvey, but one prone to observer differences and other inconsistencies through time. Behavioral resurveys appear to be scant, but observation of behaviors including habitat choice, temporal and spatial partitioning of activity, the incidence of species interactions, and thermoregulatory behaviors offer abundant opportunities for functional resurveys (Johansson et al. 2024). Behavioral resurveys can provide important insight since behavioral buffering is a primary response to climate change and an alternative to evolution (Huey et al. 2003; Muñoz 2022; questions 1 and 2). For example, a resurvey of microclimates available to pikas suggests that the availability of cool microclimates has declined over 50 years (Monk and Ray 2022). Pikas behaviorally thermoregulate by using subsurface microclimates in taluses and rocky habitats, where temperature fluctuations are moderated. Changes in these microclimates could reduce the effectiveness of their thermoregulation.

Exemplar studies include the observation of novel migratory behavior in birds that was linked to heritable genetic variation in migration direction (Berthold et al. 1992). Otero et al. (2015) resurveyed the microhabitat selection and body temperatures of Puerto Rican *Anolis* lizards to examine the implications for reproduction. The resurvey ultimately revealed counterintuitive downward shifts in the distributions of montane lizards through a period of warming due to the influence of reforestation on microclimates (Battey et al. 2019). Other research infers function through species' associations, such as quantifying parasite loads in museum collections (Wood and Vanhove 2023).

Functional resurveys build on influential work using resurveys of occurrences of interacting species to infer function, such as pollination (Burkle et al. 2013; Rafferty et al. 2013; Zoller et al. 2023). Variability in phenological responses in interacting species, such as plant flowering and pollinator activity, could shift overlapping phenophases such that opportunities for interaction are reduced and become mismatched (Kharouba et al. 2018; Visser and Gienapp 2019). In this special section, Zoller et al. (2026) resurveyed observations of plants, pollinators, and their interactions from a study conducted over a century earlier on Pikes Peak, Colorado, a classic research site of the plant ecologist Frederic Clements (Resasco et al. 2024). They found that the onset of pollinators and flowering started significantly earlier in the present, with plants showing a larger shift than pollinators. They also found that greater temporal overlap predicted a higher probability of persistence of the interactions, emphasizing the potential for climate-induced phenological mismatches to result in interaction loss (question 5).

Approach 4: Repeating selection and quantitative genetic experiments. Repeating selection experiments allows for assessing the mechanisms of evolution and whether the strength and direction of selection have changed over time (question 4). For example, selection to capitalize on warming by evolving traits to extend function spatially and temporally may reverse over time with the onset of thermal stress (Buckley and Kingsolver 2019, 2026). Seasonal and interannual fluctuations in selection may be amplified or reduced with warming depending on the onset of thermal stress and role of plasticity (Bitter et al. 2021). An increased magnitude of environmental variation and incidence of extremes may also alter selection (Kingsolver and Buckley 2017; question 3). How genetic correlations or genetic variation have shifted through time can reveal the extent to which they have constrained evolution (Urban et al. 2023). A compilation of long-term studies found high additive genetic variance, indicating capacity for adaptation to environmental changes (Bonnet et al. 2022).

Evolutionary resurveys are complementary to approaches examining evolution via experimental evolution, genomic tracking of populations (Campbell-Staton et al. 2021; Rudman et al. 2022), or spatial comparisons. For example, shifts in *Drosophila* phenotypes related to reproductive output and stress tolerance corresponded to genomic shifts aligned with seasonal environmental changes (Rudman et al. 2022). At decadal timescales, shifts in chromosome inversion frequencies corresponded to environmental changes for clinal *Drosophila* populations (Balanya et al. 2006). Studies using spatial comparisons have provided important insight into thermal adaptation to urban heat islands (Campbell-Staton et al. 2021; Diamond et al. 2022; Verrelli et al. 2022). Studies of selection over time directly assess the mechanisms of environmental change responses and clarify how environmental and biological timescales align (question 4).

Approach 5: Repeating measurement of ecosystem function and composition. Repeating measurements of ecosystem fluxes (or inferring function from composition or genetics) can demonstrate how ecosystem composition and function have changed in response to climate change (question 5). Examples include measuring carbon and methane storage and production. Studies of microbes in ancient permafrost have revealed shifts in the abundance of enzymes involved in carbon and nitrogen cycling through long-term environmental changes (Rivkina et al. 2016). Studies of diatoms and other algae from lake cores have afforded insight into evolutionary responses to changing environmental conditions (Benoiston et al. 2017; Ellegaard et al. 2020; Behrenfeld et al. 2021). Satellite observations have revealed shifts—often increases—in net primary productivity over recent decades (Xu et al. 2024).

Shifts in ecosystem function can also be demonstrated or inferred from other functional resurvey approaches. Resurrected coastal marsh plants allocate fewer resources into belowground growth, consistent with increasing pollution making nutrients more available (Vahsen et al. 2023*a*). Analyses of ecosystems consequences suggest that the shifts may reduce resistance to marsh flooding (question 3). The resurrection studies also revealed the evolution of plasticity in additional plant traits (Vahsen et al. 2023*b*).

In this special section, Braga et al. (2026) outline how recent advances in ancient environmental metagenomics can be used to reconstruct temporal dynamics in ecosystem functioning. The authors show that the role played by microbes in ecosystems changes during climate change over geological timescales has been overlooked. Their exploration of past ecosystem shifts in light of plant-microbe interactions suggests that climate change may have triggered bottom-up effects by controlling microbial diversity and functioning, which produced plant-soil feedbacks that restructured entire ecosystems (question 5). Braga et al. (2026) argue that this approach can be used to test mechanisms for ecological state shifts over evolutionary timescales.

Approach 6: Temporal genomics. The promise of temporal genomics, involving either sequencing historical specimens or comparing modern sequencing to past data, to reveal changes in individual genes or population and community structure has been reviewed elsewhere (Jensen and Leigh 2022; Clark et al. 2023; question 5). Insight is stemming from both studies focused on particular alleles and those considering full genomes. A study (Des Roches et al. 2020) of temporal shifts in sticklebacks (which required inferring past allele frequencies from phenotypes) found decreases in the frequency of an allele for defensive bony plates, consistent with hotter and drier conditions that created still-water habitats. Fixation of the allele without many defensive plates is spreading north along a latitudinal gradient, which may hinder future adaptation because genetic variation is reduced (Des Roches et al. 2020).

Separately, analysis of historical songbird specimens revealed both that admixture increased adaptive potential over time and that the direction of allele frequency shifts were consistent with climate adaptations (Turbek et al. 2023). Another study integrated historical herbarium genomes and knowledge from gene function experiments to determine that plant stomatal density evolved in response to climate change (Lang et al. 2024). In this special section, Fitz et al. (2026) apply whole-genome sequencing to historical and modern coral reef fish samples that span the last century as part of the *Albatross* Re-collection Project. They uncover evidence for stronger selection and greater population declines in a population exposed to greater human influence. More generally, the declining cost of DNA sequencing and improvements in genomic methods are allowing the application of temporal genomic approaches to a wider range of species.

Genomics also enables re-creating and manipulating proteins to understand their function compared with modern forms (Hochberg and Thornton 2017). Ancestral sequence reconstruction suggested how thermostability evolved in microbes living in extreme thermal environments (Hart et al. 2014). Research reconstructing heat shock protein evolution is relevant to understanding selection in stressful environments (Starr et al. 2018). Similar approaches can be applied to investigate more recent evolutionary responses to environmental changes.

Opportunities and Challenges

The selection of resurvey approaches should be informed by the types (stasis, tracking through space or time, plasticity evolution), biological levels (genomic, physiological, organismal, population, community ecosystem), and timescale(s) of the anticipated responses. Experimental tractability, including the potential for resurrection, and the availability of genomic resources are other considerations. Combining resurvey approaches can be particularly powerful. A tractable combination is uniting resurveys of abundance or distribution with modern experiments probing outcomes such as ecosystem function. Using resurvey experiments to test model forecasts of responses such as evolution can assess mechanistic understanding of underlying mechanisms (Vahsen et al. 2023*a*; Buckley and Kingsolver 2026).

Integrative biology approaches that scale across levels of organization, time, and space are likely to be important for resolving underlying biological mechanisms (Wake 2003, 2008). The potential to supplement repeating past, often organismal, research with modern molecular tools or instrumentation may resolve open questions from the initial publications and provide insight into mechanisms underlying observed changes (Kültz et al. 2013; Gligorijević and Pržulj 2015; Stillman and Armstrong 2015). For example, greater accessibility of sensitive respirometry equipment could allow testing past hypotheses of metabolic depression driving seasonal differences in the temperature dependence of growth and development rates. Metabolomic and proteomic assessments may resolve hypotheses regarding shifts in energy and resource allocation.

Genomic approaches can substantially enrich the mechanistic insight gleaned from other resurvey approaches. For example, the Grinnell Resurvey Project, which included extensive resurveys of occurrence, also documented declines in genetic diversity as an alpine chipmunk shifted upslope in response to warming (Rubidge et al. 2012). Genomic analysis of historical specimens detected population genetic fragmentation through time for the retracting species coupled with positive selection and shifts in the frequency of a gene linked to environmental responses (Bi et al. 2019). A stable species did not show corresponding genomic changes. Repeating multiple studies conducted on research teams' long-term study systems can afford opportunities to combine approaches.

Understanding the interaction of responses to environmental change is an important research objective that can be aided by combining research approaches. Integrating studies of plastic responses including behavior and evolution can help resolve long-standing questions of whether plasticity tends to facilitate or hinder evolution in response to environmental change (Ghalambor et al. 2007; Hendry 2015; Buckley and Kingsolver 2026). Functional resurveys can also help resolve when the absence of responses is an indicator of robustness or fragility.

Replicating methodology based on published descriptions can be challenging, but functional resurveys can benefit from lessons learned from resurveys of occurrences (Stuble et al. 2021). The challenge may be reduced for functional resurveys: experiments tend to use more standard methods, which are more thoroughly reported, than observational studies. However, information such as how to collect and maintain organisms, the environmental or resource conditions other than the focal condition(s) experimentally varied, acclimation procedures and durations, and the methodological pitfalls that were overcome in implementing the past research are often insufficiently reported in publications for straightforward replication. Repeating measures of relative function in different conditions, such TPCs, can lessen the impacts of any changes in methodology. Communicating and collaborating with researchers who conducted the initial work can provide important details to facilitate resurveys (Martínez et al. 2023).

When methodological tools and approaches have advanced since the initial resurvey, it is often possible to use the new methods by examining correlations with the past approaches (Nielsen and Kingsolver 2020). Statistical approaches can account for methodological changes (Tingley and Beissinger 2009). Statistical comparisons of historical and current data can also pose a challenge, particularly when the errors or sample sizes of the initial experiments are not thoroughly reported. One viable approach is to generate surrogate historical datasets using means, errors, and sample sizes to then use in statistical analyses (Larson 1992; Nielsen and Kingsolver 2020). Bootstrapping analyses and comparing historical values to modern confidence intervals can also aid comparisons.

Shifts toward making raw data and code available should facilitate repeating experiments in the future. In addition, archiving tissue or other samples from modern population genomic studies will enable future temporal genomic research, as long as appropriate metadata are also included (Deck et al. 2017). Many of the researchers who conducted studies of thermal sensitivity in the 1980s, when they began to proliferate, or earlier are retiring or emeritus. The initial publications generally did not include raw data, but we are finding that researchers are able to track down raw data from old notebooks and files, and there is potential to preserve data by publishing them in public repositories. Opportunities to utilize natural history collections to understand function through time are rapidly expanding with new methodology, reinforcing the value of such collections (Sanders et al. 2023).

Selecting studies with methods that can be reliably replicated ensures that either finding changes or not is interesting and valuable to understanding responses to environmental change. Such research reinforces the importance of reproducible methods. Although the past studies offer an excellent road map, additional but feasible work is needed to design resurvey experiments. Functional resurveys thus provide an excellent orientation to a system or field for beginning investigators. Repeating historical research in the context of environmental change can also be an engaging and effective element of graduate seminars or course-based undergraduate research experiences. Interactions between beginning and senior researchers who initially conducted experiments or museum studies will enable knowledge transfer and mentoring. The practice of science and composition of scientists has changed considerably since the baseline studies. The changes provide opportunities to reflect on past progress and pathways toward more equitable and inclusive science.

Conclusions

We were able to locate only a few examples of functional resurveys through time relative to the number of published functional studies. Given increasing emphasis on functional and environmental change research and accelerating environmental change over recent decades, opportunities to repeat functional experiments and observations will only increase. Despite being limited to date, functional resurveys are already helping to resolve key questions regarding how organisms and ecosystems will respond to environmental change. Initial studies indicate that extreme environmental conditions can be a stronger evolutionary driver than means, with observed shifts such as broadening TPCs (Buckley and Kingsolver 2026). Performance over a broader range of environmental conditions has also evolved, consistent with increases in environmental variability (Clayton and Spicer 2020). Accelerated development may allow organisms to avoid unfavorable or variable environmental conditions (Dickman et al. 2019; Arietta and Skelly 2021). We await with interest whether more studies will find accelerated development or the converse, which would be expected to avoid phenological asynchrony.

The American Naturalist and other long-standing journals are troves of functional research to potentially repeat. We envision a repository where researchers can contribute suggestions for functional studies with the potential for resurvey and any available resources for the resurveys. We encourage junior researchers to keep in mind the potential for functional resurveys when reviewing literature. We encourage more senior researchers to consider their past functional research and contemplate repeating the research themselves or mentoring a junior researcher to repeat the research. Areas that have long concentrated research, such as field stations, offer potential for integrated understanding of climate change responses across communities and ecosystems. Researchers should remain on the lookout for unexpected resurvey opportunities, such as specimens preserved in unusual ways (e.g., fish in rum; Fitz et al. 2026) or extensive compilations of historical data (Zoller et al. 2026). Repeating historical functional experiments or observations is a promising approach to help solve the problem of unpredictability in environmental change biology.

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Statement of Authorship

L.B.B. conceptualized the special section and led article writing and figure creation. All other authors contributed ideas and editing.

Data and Code Availability

Data and code are available in GitHub (https://github.com/lbuckley/ASN_FunctionalResurveys) and Zenodo (https://doi.org/10.5281/zenodo.14895104; Buckley 2025).

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