
























Long-term ecological research in freshwaters enabled by regional biodiversity collections, stable isotope analysis, and environmental informatics

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Abstract

Biodiversity collections are experiencing a renaissance fueled by the intersection of informatics, emerging technologies, and the extended use and interpretation of specimens and archived databases. In this article, we explore the potential for transformative research in ecology integrating biodiversity collections, stable isotope analysis (SIA), and environmental informatics. Like genomic DNA, SIA provides a common currency interpreted in the context of biogeochemical principles. Integration of SIA data across collections allows for evaluation of long-term ecological change at local to continental scales. Challenges including the analysis of sparse samples, a lack of information about baseline isotopic composition, and the effects of preservation remain, but none of these challenges is insurmountable. The proposed research framework interfaces with existing databases and observatories to provide benchmarks for retrospective studies and ecological forecasting. Collections and SIA add historical context to fundamental questions in freshwater ecological research, reference points for ecosystem monitoring, and a means of quantitative assessment for ecosystem restoration.

Keywords: environmental stressors, ecosystem restoration, biodiversity collections, freshwater biology, stable isotope analysis

Specimens archived in biodiversity collections are unique to a place and time. Contained within these specimens are elements and molecules that can be interpreted through first principles of biology, chemistry, and geosciences to provide insights into

evolutionary and ecological processes that drive biodiversity accumulation and loss, fundamental shifts in nutrient and material fluxes, and biotic interactions that shape food webs and ecosystems. By examining these attributes within and among

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biodiversity collections, researchers can make comparisons over spatial and temporal scales that encapsulate critically important ecological and societal changes related to an increasingly human-dominated world. In the present article, we explore the potential for assessing ecological change in freshwaters across the continental United States using fish specimens contained in regional biodiversity collections by employing stable isotope analysis (SIA) of the most abundant elements in organic matter. Stable isotope values of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), hydrogen ($\delta^2\text{H}$), and oxygen ($\delta^{18}\text{O}$) provide glimpses into the environmental and physiological state of organisms that can be readily integrated along with other environmental data to assess the drivers of change in abiotic and biotic conditions.

Over the last century, climate change, land-use change (e.g., agriculture, urbanization), hydrologic alteration, habitat fragmentation, invasive species, and pollutants have altered ecosystem function in nearly all freshwaters on Earth, resulting in disproportionately large losses of biodiversity. Using collections to understand the trends, causes, and consequences of radical ecological change is hardly new. Museum collections have long been used to assess trends in the bioaccumulation of mercury, trace metals, and other pollutants across gradients of environmental change, habitat, trophic position, interspecific variation, and physiology (Evans et al. 1972, Gibbs et al. 1974, Hill et al. 2010, Levengood et al. 2013). However, the development of SIA and large-scale environmental databases and observatories, coupled with the digitization and georeferencing of biodiversity collections, expand the spatial and temporal scope of inquiry and permit synthesis across time, place, organismal state, and environmental context using collections from the United States and throughout the globe.

This article emerged from a workshop (organized by HLB, FHM, and TFT) that explored the role of regional fish collections in supporting long-term ecological research in freshwaters. Although the focus of the workshop was the integration of museum specimens with SIA and long-term environmental data, this specimen-centered approach is conducive to other lines of investigation (Lendemmer et al. 2020). New analytical approaches and data sets permit aggregation of specimen-associated data on unprecedented scales that, in turn, allow for retrospective and prospective quantitative analysis of biotic responses to human-mediated and natural changes over time and space.

Regional fish collections and environmental change

Systematic studies of biodiversity are generally focused on research collections at large, free-standing museums because of their age, size, taxonomic breadth, international scope, and the numbers of primary type specimens they hold. However, regional, usually university-based collections are proving to be more important resources for ecological and environmental research because of their focus on local and regional biotas repeatedly sampled over multiple decades. The uniqueness of these collections for use in the research program we are proposing lies in the fact that they often archive large numbers of samples of abundant and ecologically relevant species ideal for robust ecological analysis.

The first university-based biodiversity (i.e., natural history) collections began in the mid-1800s in the United States (table 1), and many experienced exponential growth starting in the late 1940s, peaking in the early 2000s (figure 1). This activity parallels a timeline of major changes to watersheds and a period of unprecedented environmental regulation in the United States (table 1).

Early collections focused on regional watersheds (e.g., Upper Mississippi River, Great Lakes), but roughly 80% of the specimens represent Gulf Coastal drainages in the southeastern United States, southwestern United States, and the upper Colorado River Basin (figure 2). The underrepresented regions of the United States include New England and the Mid-Atlantic states (figure 2). These differences in sample availability will necessarily limit the granularity and temporal depth of inquiry.

Sustaining the value of collections as a continent-wide resource for ecological and environmental research depends critically on continued collection and curation of samples from regional biotas and ensuring the accessibility of this material to the scientific community. Digitization and georeferencing of collection records, and the increasing numbers of online biodiversity data portals (e.g., FishNet2, iDigBio, GBIF) facilitate researcher access to specimens in this context. Specimen records from smaller, more focused collections are also coming online and being integrated with data in existing biodiversity portals, expanding the temporal and spatial breadth of available samples. Another critical issue for sustaining the utility of regional collections as a resource for ecological and environmental research is expanding funding for facilities, staff, and curatorial care of specimens in biodiversity collections (National Academies of Science, Engineering, and Medicine 2021).

Stable isotopes, ecology, and biodiversity collections

SIA has been used for decades by geochemists to study atmospheric, rock, climate, and water cycles on contemporary and geological time scales (Sharp 2017, Bowen et al. 2019). Likewise, biotic processes such as photosynthesis, decomposition, heterotrophic consumption, and organismal metabolism influence the isotopic composition of biological materials in characteristic ways that make them natural tracers for dynamic ecological and environmental processes (Fry 2006). In ecology, SIA builds on biogeochemical principles to provide a means to study primary production, decomposition, consumer resource use, trophic niches, migratory patterns, as well as nutrient and material fluxes through communities and ecosystems.

SIA on fluid-preserved fishes held in biodiversity collections could yield powerful insights into the causes and consequences of natural and human-caused disturbances on aquatic ecosystems over decadal time scales, help identify priorities for restoration, and provide a means for assessing its efficacy. Combining isotopic data from multiple biodiversity collections has the potential to document the historical and contemporary ecological impacts of national and global policies on clean air, water, and endangered species protection at local, regional, and global scales (table 1). Below, we examine possibilities and challenges of integrating the United States (and global) network of biodiversity collections and SIA to study biogeochemical and ecological change over broader spatiotemporal scales than ever before.

The Extended Specimen Network and SIA

Biodiversity collections are in the middle of a scientific renaissance fueled by emerging technologies, digitization and digital data aggregation in biodiversity portals, and big data analytics (National Academies of Sciences, Engineering, and Medicine 2021). Information contained in specimens is extended through materials analysis and links to specimen-derived or related genetic, phenotypic, behavioral, environmental, and physical data.

Table 1. Intersecting timelines of examples of ecosystem change, environmental policy and regulation, milestones in growth and development of biodiversity collections, and environmental and monitoring data sets.

Year	Ecosystem change	Policy change	Biodiversity collections milestone	Environmental data and monitoring	Summary processes
1850		Swamp Land Acts (1850s)	First cataloged specimen UMMZ (1850); Cornell Ichthyology Collection (1867)	US boundary and rail biological surveys (1850s)	Industrialization, water- and land-use transformation
1870		Yellowstone Park Protection Act (1872)			
1880	First fish hatchery in Texas (1881); ditching and draining of Mississippi River (1880s)		Illinois natural history survey collections (1880); Tennessee fish collections (1891); repository established for Alabama specimens (1889)		
1890		Land Revision Act and National Forest system (1891)		Daily stream gage on stage data in the Rio Grande (1898)	
1900	Diversion of Colorado River to Imperial Valley, California (1901)	Reclamation Project Act (1902)			
1910	Haber–Bosch nitrogen fixing (1909), Elephant Butte Dam (1916)				
1920	Urbanization, commercial synthetic chlorinated hydrocarbons (1929)	Colorado River Compact (1928)	Large collections of Michigan inland fishes (1920–1942)		
1930	Hoover Dam (1935), Parker Dam (1938), Dust Bowl (1934–1940)	Tennessee Valley Authority (1933); Bonneville Power Administration (1937)	Rio Grande collections begin (1938)		Large-scale river modification for hydropower, irrigation, flood control, the Green Revolution
1940	End of WWII (1945); Third World industrialization; Intra-coastal Waterway opened (1949)		Michigan DNR specimens added to UMMZ (1949);		
1950	Severe drought in the Great Plains and the Southwest (1950s); St. Lawrence Seaway opened (1959); building of flood control dams on the Mississippi River (1953)	Watershed Protection and Flood Prevention Act (1954)		Contaminant data in the Gulf and South Region (1950)	
1960	Glen Canyon Dam (1963); Flaming Gorge Dam (1964); drying of Comanche Spring (1962); Ross Barnett Dam (1965); Oroville Dam (1968); authorization of Red River Waterway (1968, completed 1994); Cuyahoga River Fire (1969)	Clean Air Act (1963); Wilderness Act (1964); Wild and Scenic Rivers Act (1968)	Lower Pearl River survey (1963–2005);	Publication of Minckley and Deacon (1968)	

Table 1. Continued.

Year	Ecosystem change	Policy change	Biodiversity collections milestone	Environmental data and monitoring	Summary processes
1970	Invasive carp introduced to major US waterways (1970s)	Endangered Species Act (1973), Clean Water Act (1972), Environmental Pesticide Control Act (1972), EPA founded (1970); Safe Drinking Water Act (1974); Great Lakes Fish Monitoring and Surveillance Program (1978); Resource Conservation and Recovery Act (1976); Western Area Power Administration (1977)	Upper Pearl River survey (1973–2005); Red River survey (1976–2000); Alabama River survey (1969–2000);	NASA Landsat (1972); EPA STORET water quality data (1974); industrial and municipal discharge data (1975)	National environmental laws and regulations are authorized and implemented
1980	Zebra mussel invasion (1986); Quagga mussel invasion (1989)	National Acid Precipitation Assessment Program (1980); Comprehensive Environmental Response, Compensation, and Liability Act (Superfund; 1980); Intergovernmental Panel on Climate Change (1988)			
1990		Elwha River Dam removal authorized (1992); Kissimmee River restoration (1995)	Rio Grande surveys (1992–present); San Juan River surveys (1994–present); Tulane collections changed to 70% EtOH (1994–2004)	EPA Environmental Monitoring and Assessment Program (1990); National Land Cover Database (1992); publication of Poiff and colleagues (1997); Water Quality Data Portal (1998)	
2000	Large-scale wildfires throughout the western United States			NRSA (2008); Digitization and Georeferencing of Regional Natural History Collections	Climate change-associated shifts in drought and wildfire
2010	Megadrought in the western United States, increased Permian Basin fracking (2016); warmest years on record (2016–2020); extreme precipitation events up by 55% in US Northeast and 42% in the Midwest (1958–2016)	Mercury and Air Toxic Standards Rule (2011); Minamata Convention on Mercury (2013); Paris Climate Agreement (2016)	South Florida Collections of Invasive Species (2019); UMMZ tissue collection formalized (2019);		
2020	Largest wildfires in California history (2020, 2021)				

Note: The summary processes column is for indexing collections growth in figures 1 and 2. Abbreviations: DNR, Department of Natural Resources; EPA STORET, Environmental Protection Agency Storage and Retrieval Data Warehouse; EtOH, ethanol; NASA, National Aeronautics and Space Administration; NRSA, National Rivers and Streams Assessment; SW US, southwestern United States; UMMZ, University of Michigan Museum of Zoology; WWII, World War II.

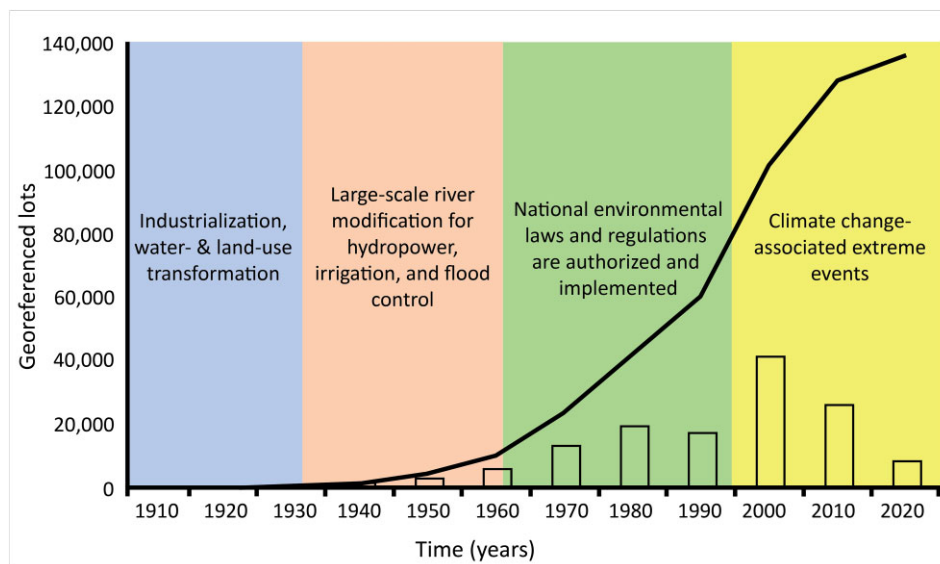


Figure 1. A histogram superimposed on a cumulative distribution (the solid dark line) of georeferenced lots plotted by decade for the 10 most abundant freshwater fish species identified in Fishnet2 (<https://fishnet2.net>), a data portal and aggregator for US fish collections. The term *lot* refers to a sample of specimens of a particular species collected at the same place and time and cataloged as a unit. Important time blocks and transitions are identified by events (text) that correspond to the summary processes column in table 1.

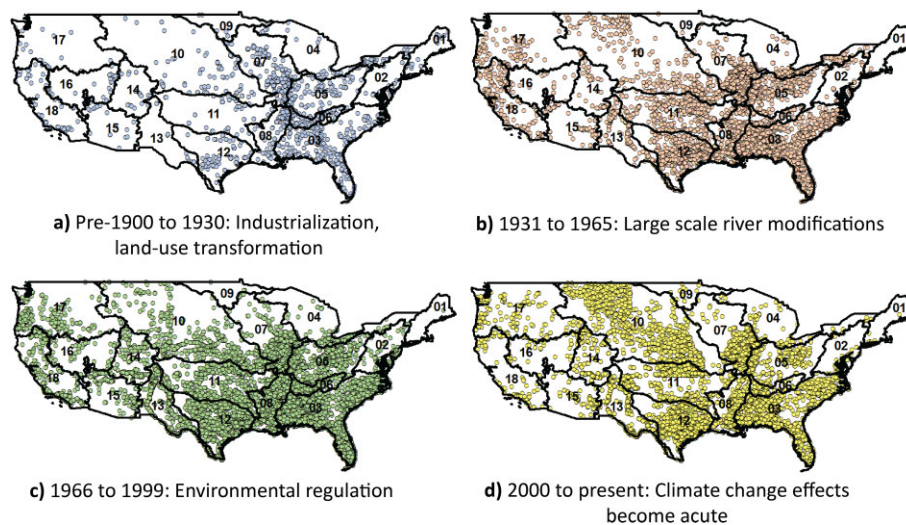


Figure 2. Spatial distributions of georeferenced lots for the 10 most abundant freshwater fish species, aggregated within time frames that correspond to those identified in table 1 and figure 1. The Panels represent time frames (a) from before 1900 to 1930, (b) 1931–1965, (c) 1966–1999, and (d) from 2000 to the present. The dark lines and numbers demarcate major watershed areas of the continental United States. Georeferenced lots were identified in Fishnet2 (<https://fishnet2.net>), a data portal and aggregator for US fish collections.

This concept is articulated in the Extended Specimen Network (ESN; Lendemer et al. 2020), which multiplies the power of SIA as a tool to study biogeochemical and ecological change. Therefore, the ESN proposes that isotopic data obtained from an individual specimen or lot held in a museum collection is a primary extension (figure 3), where isotope values of different elements yield direct insight into sources of food and nutrients ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$, $\delta^{34}\text{S}$), water sources and temperature ($\delta^2\text{H}$, $\delta^{18}\text{O}$) and migration history ($\delta^2\text{H}$, $\delta^{18}\text{O}$, $\delta^{87}\text{Sr}$) of a particular specimen (figure 3). Tissues experience different rates of isotopic turnover, depending on their physiology, such that accretionary mineralized structures (e.g., otoliths or vertebrae) continuously record information over a lifetime, whereas more metabolically active tissues (e.g., liver

or muscle) integrate isotopic change over weeks to months. Beyond bulk tissues, SIA of individual compounds such as amino and fatty acids provide deeper insights into physiological (e.g., nitrogen balance) and ecological (e.g., food chain length) processes (McMahon and McCarthy 2016, Ohkouchi et al. 2017, Whiteman et al. 2019, and see below). Morphometrics and specimen imaging link the “isotopic niche” (Newsome et al. 2007) to morphological and anatomical variation within and among species in a community. SIA of bycatch and gut contents (e.g., invertebrates) could provide insight into trophic structure of other community constituents.

Field notes, environmental data collected at the time of capture, photographs, and other documentation aid interpretation of

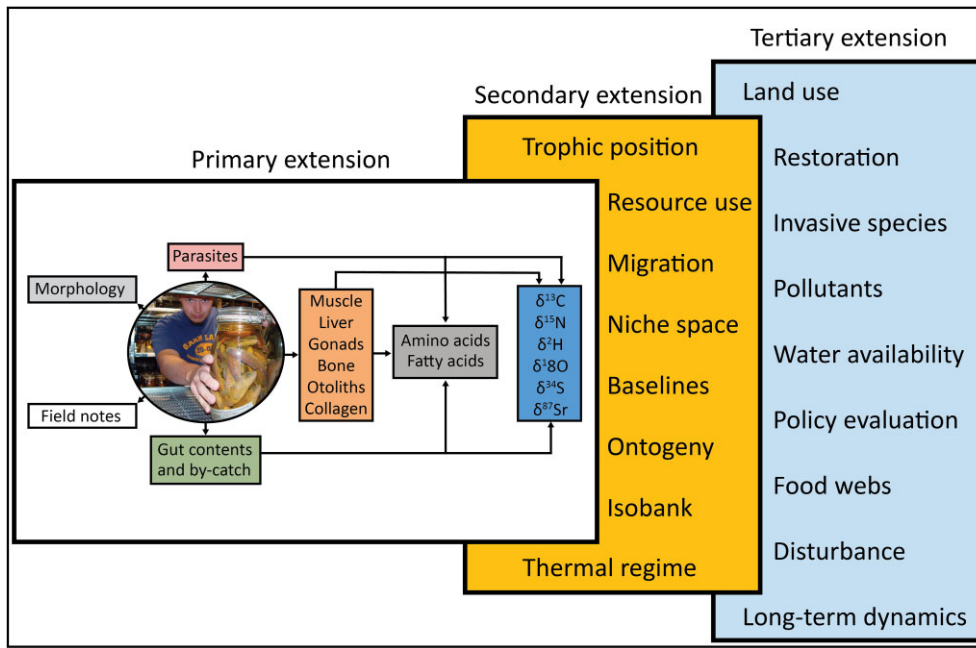


Figure 3. The Extended Specimen Network multiplies inferential and explanatory power of stable isotope analysis (SIA), and SIA contributes fundamental insight into community and ecosystem changes that can be integrated with other data inherent to the specimen. The extensions represent changes in scale of inference and additions of other data. Because SIA provides a record of change in units (e.g., delta values, δ) linked explicitly with biogeochemical processes, it can be directly integrated into other hydroclimatic data sets. The primary extension is stable isotope ratios of various elements that can be used to infer ecological processes and the physiological state of the specimen at the time and place of capture. The secondary extension puts isotopic data into the biological context of the population or community. The tertiary extension maps isotopic ratios of organisms, communities, and other biotic and abiotic drivers onto spatial landscapes with a time axis that can span decades.

isotopic data. Therefore, individual specimens and their associated data (i.e., the extended specimen) reveal tremendous information about multiple processes at a particular time and place. For example, external and internal parasites can be analyzed to understand trophic interactions in host–parasite associations (Kanaya et al. 2019) and gut content data can be integrated with SIA to quantify isotopic baselines and ontogenetic and seasonal dietary changes (Davis et al. 2012). Biological context and interpretation are derived from analyzing many specimens across populations, species, time, and space to produce a secondary extension of the preserved material. Linking aggregated isotopic data with other physical data sets, such as river discharge, pollutant emissions, appearance of invasive species, or climate data, permits the evaluation of ecosystem processes and their trajectories over large spatiotemporal scales and represents a tertiary extension of specimen data (figure 3).

Long-term perspectives for aquatic ecosystem change

The power of combining SIA and biodiversity collections is that it captures changes in ecosystem processes that can take decades or centuries to manifest. Retrospective analyses provide the kinds of multidecadal perspective necessary to identify environmental stressors or releases that may generate time-lagged, nonlinear, or gradual ecological responses to examine major drivers of change that occurred historically and persist into the present day. Once they are developed, these ecological timelines serve as a basis for developing targets for environmental policy or specific restoration actions and create a means to forecast and assess progress toward intended goals and outcomes. Longer timelines provide better information for predicting the impacts of continued environmen-

tal change and informing more mechanistic models of climate change effects.

Local processes

Central to understanding the impact of disturbances over time is the study of energy flow pathways and trophic interactions among species (Rooney and McCann 2012, Sagouis et al. 2015) and species–environment relationships (DeLong and Thoms 2016). For example, Pruell and colleagues (2003) used SIA to characterize archived scale samples collected between 1982 and 1997 to identify the mechanisms underlying a dietary shift in striped bass (*Morone saxatilis*) in the Chesapeake Bay. Increasing $\delta^{13}\text{C}$ values in both striped bass and their benthic prey coincided with decreases in pelagic prey availability (Overton et al. 2000). Similarly, wall-eye (*Sander vitreus*) shifted its diet in response to extirpation of its primary prey, pelagic gizzard shad (*Dorosoma cepedianum*) in Nebraska reservoirs (Bethke et al. 2012). SIA is also a powerful tool for understanding the complex ecological effects of invasive species (for a review, see McCue et al. 2020). Vander Zanden and colleagues (2003) used SIA of fishes and invertebrates sampled over a 120-year time series to document how eutrophication and introductions of nonnative lake trout (*Salvelinus namaycush*) and mysid shrimp changed the Lake Tahoe food web, ultimately leading to the extirpation of a native cutthroat trout. Similarly, historical fish collections (1974–2008) were used to track changes in the diets, biomass, and trophic structure of the native fish assemblage in the Wabash River prior to and during establishment of invasive carp in the 1990s (Schaus and Vanni 2000, Sampson et al. 2009). SIA and stomach contents data refuted the hypothesis that direct negative interactions with invasive carp led to a collapse of gizzard shad in this waterway (Pyron et al. 2017). Instead, increased nutrient loading and disturbance forced the decline of the gizzard shad

population, leaving a vacated niche that facilitated expansion of invasive carp (Pyron et al. 2017).

Regional processes

Local stream reaches and lakes are nested within watersheds, the spatial scale at which species and communities respond to environmental changes (i.e., flow regime, land use; Poff 1997, Fausch et al. 2002). Comparisons using SIA of serial collections within and across river basins yield insight into ecological responses that are missed by documenting changes in species composition alone (e.g., Ruhí et al. 2016). For example, Delong and colleagues (2011) found that the trophic diversity of Missouri River fish assemblages decreased following the onset of dam operations in the 1950s, likely because of resource limitation imposed by diminished river connectivity. Turner and colleagues (2015) found that community-wide trophic niche space declined with river incision and sediment deprivation over 70 years of river regulation in the Rio Grande, New Mexico. Reduced flooding and urbanization facilitated a shift toward greater reliance on instream energy sources (i.e., benthic algae) for the entire fish community. Similar work in Australian rivers documented homogenization of resource use by aquatic consumers following extensive water development (Thoms and Delong 2018). Bowes and colleagues (2020) used compound-specific SIA of individual amino acids to demonstrate long-term changes in trophic positions of fishes driven by changes in habitat structure after addition of low-head dams and levees in the Ohio and Mississippi Rivers.

Global processes

For decades, environmental scientists have used biodiversity collections to study ecological effects of pollutants (Suarez and Tsutsui 2004). The earliest studies in the 1970s compared mercury concentrations in contemporary fish with those in specimens collected in the late 1800s (Barber et al. 1972, Evans et al. 1972). Since that time, biodiversity collections have been employed to examine changing pollutant emission histories over decades to more than a century (Drevnick et al. 2007, Lepak et al. 2019) on a global scale. This is because specimen archives expand spatial coverage to undersampled regions globally and permit the evaluation of how concentrations relate to regional variation in contaminant loads or transport (Tanabe and Ramu 2012). For example, specimen archives allowed researchers to infer the distributions of persistent organic pollutants and contaminants of emerging concern from coastal waters in southern India to central Japan (Tanabe and Ramu 2012). This information identified where modern contaminant sources persist and permitted the identification of contaminant-specific transport mechanisms. In freshwater ecosystems, combining environmental contaminant analyses with SIA has been used to identify the mechanisms and pathways of contaminant accumulation and transport. For example, Drevnick and colleagues (2007) used SIA with mercury data from northern pike to challenge the hypothesis that changes in trophic position were related to observed declines in fish mercury concentration. Lepak and colleagues (2019) used similar methods to demonstrate that invasive mussels in Lake Michigan facilitated shifts in energetic and trophic pathways to lake trout that, in turn, led to altered rates of mercury accumulation in that species. Using mercury SIA, Lepak and colleagues (2019) also showed how US policy-driven reductions in mercury emissions resulted in rapid changes in the mercury isotope ratios measured in lake trout. These examples illustrate how species interactions, including invasive species, water flow regulation, and pollutants,

have effects that are mediated through ecosystem change, environmental policy, and biotic interactions.

Ecological restoration

Retrospective analysis with biodiversity collections and SIA identify important changes to ecosystem processes. Purposeful specimen collections made before, during, and after restoration projects can be used to evaluate outcomes. The underlying goals for many restoration programs are endpoint based and aim to recover historical conditions of an ecosystem (Osenberg et al. 2006, Vander Zanden et al. 2006). The selection of appropriate restoration endpoints is hampered by the lack of relevant historical data, which often leads to speculation about predisturbance or reference conditions (Vander Zanden et al. 2003, 2006). SIA-enabled reconstruction of food webs provides insight into predisturbance conditions, historical trophic links, and pathways of energy flow (Palmer et al. 1997). Other restoration programs aim to produce an effect of a specified magnitude (e.g., increase population size by 30%; Osenberg et al. 2006) and are effect-size based, where effect sizes are quantified using before–after–control–impact (BACI) approaches (Osenberg et al. 2006, Conner et al. 2016). Although the BACI method is a powerful tool for quantifying restoration effects, it is difficult to implement because of the post hoc nature of many restoration monitoring efforts (Osenberg et al. 2006, Palmer et al. 2014). Biodiversity collections can provide the pretreatment data required to complete BACI analysis. For projects that aim to restore ecosystem processes by reestablishing biodiversity through functional redundancy (Palmer et al. 1997), biodiversity collections and SIA provide information on species-specific habitat use in an historical ecosystem context. In all cases, SIA and biodiversity collections can provide the historical reference or pretreatment conditions critical for understanding the full effect of ecological restoration.

Challenges and uncertainties

To reconstruct ecological timelines, preserved specimens must be physically comparable (species, size, and age), the effects of preservation on response variables should be well documented, and there must be sufficient data for valid statistical inference (Evans et al. 1972). There are important effects of chemical fixation and preservation on sample integrity for both SIA and the characterization of pollutants. Preservative media may be changed over the life of a specimen (e.g., exchanging isopropanol for ethanol), which could impose additional effects. Experimental studies report alteration of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chemically preserved bulk tissue samples relative to fresh or frozen tissues (e.g., Arrington and Winemiller 2002, González-Bergonzoni et al. 2015), although consensus across studies is difficult to reach because of the variability in preservation and experimental methods. Biodiversity collections often hold tissues in different conditions (e.g., frozen versus fixed in formalin), potentially allowing for direct examination of preservative effects on pollutant concentrations and stable isotope values on a case-by-case basis. Broader comparisons will be important for combinability of isotopic data across collections, but preservation-induced shifts are often small (at least 1 per thousand) relative to isotopic shifts driven by ecosystem changes or trophic fractionation (Edwards et al. 2002). Moreover, shifts in carbon (C) and nitrogen (N) ratios were realized immediately and remained stable following formalin fixation and ethanol preservation (Edwards et al. 2002).

Interpretation of bulk tissue isotopic data in a food web or ecosystem context usually requires information about $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary producers, referred to as *baseline values* (e.g., Peterson and Fry 1987, Post 2002, Fry 2006). SIA on identifiable gut contents from museum specimens can be used to establish such baselines (Bishop et al. 2014), but fixation and preservation may differentially affect isotope values in plants and invertebrates. In cases in which historical baselines are not available, essential amino acid (e.g., isoleucine, leucine, valine, threonine, phenylalanine, lysine) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses can help constrain isotopic variation in primary producers through space and time. This is because heterotrophic consumers cannot synthesize essential amino acids *de novo*; they must acquire them directly from their diet, such that the essential amino acid $\delta^{13}\text{C}$ values of consumer tissues closely mirror those of basal producers (McMahon et al. 2015) or symbiotic gut microbes (Newsome et al. 2011, 2020). Primary producers display variable isotopic discrimination during *de novo* essential amino acid synthesis, providing distinct multivariate essential amino acid $\delta^{13}\text{C}$ fingerprints (Scott et al. 2006, Larsen et al. 2013) that are spatiotemporally conserved (Elliott Smith et al. 2022) and can reliably distinguish among distinct autochthonous (algae) and allochthonous (terrestrial plants) primary producers (Besser et al. 2022). Because of low frequencies of transamination during nitrogen metabolism (O'Connell 2017), the $\delta^{15}\text{N}$ values of some essential amino acids (phenylalanine and lysine), also known as *source amino acids*, in consumer tissues are minimally altered as they move up food chains, providing a metric for baseline $\delta^{15}\text{N}$ values (McMahon and McCarthy 2016, Ramirez et al. 2022). Source amino acid $\delta^{15}\text{N}$ values can be used in conjunction with the $\delta^{15}\text{N}$ values of *trophic amino acids*, which undergo substantial transamination during consumer metabolism and therefore display significant trophic discrimination moving up food chains, to estimate consumer trophic level from a single tissue sample (Popp et al. 2007, Choy et al. 2012). Tissue fixation and preservation also affect the isotopic composition of individual compounds, but some studies reported no differences in amino acid values between frozen and fluid-preserved fish (Hetherington et al. 2019, Chua et al. 2020, Durante et al. 2020), whereas others reported stabilization of differences between frozen and preserved samples (e.g., Welicky et al. 2021). Other sources of temporal isotopic variation, such as changes in atmospheric $\delta^{13}\text{C}$ values caused by increased fossil fuel emissions, known as the *Seuss effect*, can be corrected in a systematic fashion over time (e.g., Dombrosky 2020).

Sparse and uneven sampling in time and space

Inferential power of SIA is positively related to replication and balance within and among groups to be compared across space and time. Regional biodiversity collections can be sporadic in coverage of space or time because historical sampling events were opportunistic, and contemporary sampling can be limited by the availability of collections space and resources. Pooling samples into functional groups or guilds offers some ability to balance sample sizes across groups given that SIA provides robust information on functional roles and trophic diversity. Meta-analysis of SIA data could be used to compare groups where data are temporally sparse (Ishikawa and Finlay 2012, Orton et al. 2014). Estimated marginal means can adjust for unbalanced data sets by weighting (e.g., Stets et al. 2020). Geospatial interpolation methods (e.g., spatiotemporal regression kriging, Ruybal et al. 2019; random forest machine learning, Oczkowski et al. 2016; integrated nested Laplace approximation, St. John Glew et al. 2019) can be applied to

fill spatiotemporal data gaps. Another approach to inferring ecological change in freshwater systems with sparse data might be to create a post hoc BACI design by selecting samples that bracket a disturbance in space and time. Although sampling may be unbalanced, establishing pre- and postdisturbance measurements can be informative even if traditional statistical analysis is limited by sample size or sampling design.

Integration of SIA and environmental data

The key to harnessing the power of SIA and museum collections is a centralized, searchable repository for isotopic data that links to digitized data. The IsoBank Database Project (<http://isobank-qa.tacc.utexas.edu>) is developing this resource to enable a broad SIA community to capitalize on data analytics (Pauli et al. 2017). It is especially useful for studies using biodiversity collections because it allows extensive searches for samples with similar time and space identities that can improve inferential power of specimen-specific isotope data. IsoBank will also be linked directly with spatiotemporal metadata in established collection management tools (e.g., Arctos). Much like the Genbank database for DNA sequence data, IsoBank is expected to accelerate interactions across collections, museums, and scientific disciplines with a common chemical language and facilitate the same diverse, interdisciplinary approaches that have resulted in some of the biggest and most creative advances in science. IsoBank will also establish and enhance standards for data quality assurance and control by creating a network among core isotope laboratories that are currently producing millions of new data points per year (Oliver Shipley, University of New Mexico, Albuquerque, New Mexico, USA, personal communication, 12 March 2023). Finally, IsoBank is poised to address growing initiatives of publication and funding agencies for data accessibility and transparency, standards that biodiversity collections have been developing for decades.

Once it was populated, the IsoBank database can be queried in the context of temporal and spatial trends by integrating SIA data with environmental data. Environmental data, including remote sensing data, are abundant and accessible but underused in conservation monitoring because of a lack of simple tools that can be used to identify and quantify land-cover changes and habitat loss (Willis 2015, Evans and Malcom 2020). With advances in remote sensing technology, data-intensive cloud computing and advanced statistics, artificial intelligence and machine learning, analyses of large data sets allow exploration of important ecological questions associated with species distributions, differences between fundamental and realized niches, and species interactions along disturbance and climate gradients. Data science approaches can facilitate inquiry across disciplines such as ecology, hydrology, geomorphology, and biogeochemistry on the effects of changing climate, anthropogenic stressors, and natural disturbance regimes on biodiversity. Open-source GIS and automated analytical tools could accelerate the application of remote sensing to monitoring and identification of underlying factors in biodiversity declines (Evans and Malcom 2020).

River discharge, water temperature, nutrient composition, and contaminants are fundamentally important to the distribution, persistence, and behavior of freshwater organisms. Accordingly, organismal responses tend to covary with these environmental conditions, with SIA proving valuable in documenting organism and ecosystem responses to environmental variation (Finlay 2001, Turner et al. 2015). Because of the historical nature of natural history collections, museum specimens provide a unique and powerful opportunity to investigate species responses to both

Box 1. Inference models for SIA and biodiversity collections.

A commonly used isotopic niche method (Newsome et al. 2007) was initially developed by Bearhop and colleagues (2004) and extended into a hypothesis-testing framework using geospatial statistics (Layman et al. 2007), resampling (Turner et al. 2010), Bayesian (Jackson et al. 2011), and kernel density (Eckrich et al. 2020) approaches. Isotopic niche is measured as dispersion of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values in bivariate space, and was expanded to accommodate more dimensions with additional isotopes (e.g., $\delta^2\text{H}$; Cucherousset and Villéger 2015, Bowes et al. 2017), to allow explicit consideration of physiological processes (Yeakel et al. 2016), and to provide metrics to quantify and compare trajectories change in multidimensional isotopic niches in time and space (Sturbois et al. 2022).

Natural and anthropogenic disturbances sometimes cause ecological conditions to shift through a threshold to one or more alternative stable states, creating a situation where a different ecological state exists for the same environmental conditions (Delong et al. 2021). Change-point or breakpoint analyses can detect changes that occur in a time series (Zeileis and Hortorn 2002). Sudden, distinct changes in the direction or sign of the slope in the cumulative sum plot indicates potential change points that are confirmed by resampling (bootstrapping) (Taylor 2000).

For network models, because the fundamental dynamic qualities of natural communities, trophic interactions can be highly variable through time (Holme and Saramäki 2012), and this should be reflected in the topology of networks (Boccaletti et al. 2006, Morueta-Holme et al. 2016, Scholtes et al. 2016, López et al. 2018). One solution is to create a trophic network model where the in-degree represents the number of prey consumed by each predator (also called generality), whereas the out-degree represents the number of predators attacking each prey (also called vulnerability; Newman 2003, Lurgi et al. 2012, López et al. 2018). Another approach is the use of nondeterministic network dynamics models that are based on combinations of chance (randomness) and necessity (system constraint; Mullon et al. 2009, Planque et al. 2014).

Structural equation modeling (SEM), or path analysis, is a multivariate technique that can test for the nature and magnitude of direct and indirect effects of multiple interacting factors (Grace et al. 2010, Lefcheck 2016). SEM is an approach that interprets information about observed variables and hypothesized causal pathways in order to evaluate complex causal relationships (Shipley 2000, Grace 2008). SEM is particularly well suited for large-scale observational community or population data sets, like those of museum specimens' metadata and associated stable isotope signatures. Its intuitive connection to how we conceive of our study systems makes it a powerful and useful technique for ecologists and evolutionary biologists (Mitchell 1992).

spatial and temporal environmental variability. Although environmental data from lotic systems are not as widely available as terrestrial systems, field-based data collection infrastructure and more-recent advances in informatics resources now provide a reasonable amount of information for spatially and temporally robust analyses of lotic species distributions and diversity.

US-government-maintained river gaging stations that collect discharge, water temperature and nutrient data are likely the most accessed and temporally robust resources of riverine environmental data. For example, the US Geological Survey maintains approximately 10,000 stream gages across the United States and associated territories (<https://waterdata.usgs.gov/nwis>), with the first gage established on the Rio Grande basin in 1889. These types of gages often provide useful environmental data at high temporal resolutions, but their localized nature constrains the application of these data to biodiversity data collected near an actual gage. However, a recent influx of remote sensing observations includes data on surface water quantity (e.g., the NASA Surface Water and Ocean Topography mission) and water quality (e.g., Landsat- and MODIS-based water temperature, clarity, color). The Monitoring Trends in Burn Severity Program (www.mtbs.gov) maps the burn severity and extent of large fires across all lands of the United States from 1984 to the present and can be used to predict the effects of wildfire on surface water conditions. These data sources are more continuous in space than in situ observations, but they generally have less frequent sampling in time and limitations on the basis of what can be observed from above (e.g., gaps under clouds and canopy).

Computational advances facilitated development of watershed- to global-scale models that estimate river flows, water temperatures, sediment, and nutrients in riverine systems (Chien et al. 2013, van Vliet et al. 2013, Krause et al. 2019).

For example, the NorWeST project (Isaak et al. 2016) depicts historical, spatially discontinuous stream temperature data and climate scenarios for streams and rivers across the western United States. Interpolation methods that can fill data gaps in space and time (Ver Hoef et al. 2014) can be applied to water quality data to model historical stream conditions. A particularly appealing aspect of these models is retrospective characterization and forecasting of freshwater environmental conditions across spatially contiguous areas, overcoming the constraints of localized stream gages and other sparse observations (in time or space). These models can also help identify trends and change points (box 1) within and beyond the observational record and can be used to discern cooccurring and frequently compounding factors influencing freshwater habitat quality, such as land cover change and climate change. Historical climate and land use data are generally used to develop models, but they can incorporate projected changes in climate and land use to estimate future environmental conditions, providing the ability to investigate potential species' responses to environmental change (e.g., Andres et al. 2019).

Physically based, spatially distributed hydrological models are now being implemented within the real-time forecasting systems traditionally dominated by weather models, with examples including the US NOAA National Water Model and the European Flood Awareness System (see review in Emerton et al. 2016). Developed from long-term retrospective model integrations, these operational hydrological modeling systems provide new research and forecasting opportunities by predicting a more complete and detailed water cycle, including the high-resolution, rapid, first flush processes that can dominate contributions to constituent transport and water quality changes. For example, the NOAA National Water Model provides real-time estimates and forecasts out

to 10 days of high-resolution (250-meter) shallow water table, surface inundation, and surface runoff as well as water stores and fluxes through 5,000 lakes and 2.7 million stream reaches across the United States (NOAA 2016, Gochis et al. 2020). With the addition of water quality predictors, these models could transition into ecological forecasting applications that predict harmful algal blooms and degraded thermal regimes alongside floods and water supplies.

Ongoing development of environmental informatics resources allows the dissemination of large data sources from hydrological models, in situ measurement networks and remote sensing observations, and these can then be integrated with isotopic data from museum specimens. These informatics resources are varied and provide an array of relevant environmental data for contemporary and retrospective analyses (reviewed in Dow et al. 2015). Moreover, future riverine environmental estimates based on global climate model projections are becoming available for integration with biodiversity data to investigate potential responses of biodiversity to changes in climate. For example, the GIS-based Hydroclim data set (hydroclim.org) was developed, in part, for integration with data from biodiversity collections and provides monthly river discharge and water temperature estimates for river sections in all major watersheds in the United States and Canada from 1950 to 2099 based on 40 global climate model projections. Modern data science leverages the fields of both mathematics (e.g., statistics, probability) and computer science (e.g., artificial intelligence, machine learning). These techniques show promise for meaningful joint analysis of data sources that vary widely in quality, frequency, scale and type, as are common in environmental science and management (for a review, see Blair et al. 2019, Sun and Scanlon 2019). SIA data-model synthesis activities can improve our understanding of the processes that influence freshwater species habitat and health, which, in turn, can inform better resource management.

Synthesis: Regional biodiversity collections, SIA, and environmental data

How and why populations, communities, and ecosystems change are fundamental questions in ecology. Hortal and colleagues (2015) identified persistent gaps in ecological knowledge, including uncertainties regarding the role of functional trait variation and ecological performance, organismal responses and tolerances to abiotic shifts in ecological conditions, and the roles of species (i.e., biotic) interactions for driving change. Regional biodiversity collections are poised to help fill these knowledge gaps, owing to coincident advances in discoverability enabled by digitization and georeferencing, the development of ecologically relevant conceptual and analytical approaches for SIA (see box 1), and emerging long-term data sets and infrastructure that document change in ecosystem attributes (see the section above). A comprehensive effort to measure stable isotope values of museum specimens offers the potential for discovering process-based insights into the drivers of biodiversity change over decadal time and continent-wide spatial scales.

The ESN (Lendemer et al. 2020) is the conceptual framework we use to address these ecological knowledge gaps. We highlighted examples of the link between environmental change and community response viewed through the lens of food webs that explicitly incorporate trophic interactions, thereby translating biological diversity into ecosystem function and vice versa (Alp

and Cucherousset 2022). For example, variation in functional traits within and among species can be determined by examining covariation of morphometric traits and resource use in the context of the isotopic niche (Layman et al. 2007, Newsome et al. 2007), especially for abundant and widespread species. Abiotic stressors, such as pollutant accumulation or climate-forced changes in temperature and precipitation are expected to affect resource availability to consumers. Likewise, ecological responses and tolerances can be visualized by comparing changes in biodiversity losses through extirpation and gains through species introductions with shifts in resource use (determined through gut content analysis) and trophic positions of constituent species determined by isotopic values (e.g., Vander Zanden and Rasmussen 1996). Coupling stable isotope timelines with changes in abiotic conditions identified in environmental data provides inferential power about the roles of changing stressors on community function over decades (e.g., Vander Zanden et al. 2003, Turner et al. 2015).

A research program based on SIA and biodiversity collections can be applied to any group of organisms. We focused on freshwater fishes because they are nearly ubiquitous and important in freshwater communities and are well represented in biodiversity collections in the United States and worldwide. Patterns of fish biodiversity differ across biomes and reflect large-scale biogeographical processes and ecological gradients in precipitation and temperature and smaller-scale longitudinal patterns within stream networks (Matthews 2012). Moreover, fishes are sensitive indicators of ecosystem transformation from natural and human activities. As mobile and heterotrophic consumers, fishes are integrators of primary and secondary production and therefore record resource use and nutrient availability in their tissues. Within a community, fish species vary substantially in functional diversity in relation to traits such as body size, trophic position, morphology, life history, migration propensity, and other attributes. Samples can be partitioned across life stages (ontogeny), individuals, populations, species, and communities to address ecological hypotheses at all levels of biological organization (Ross 2013) in aquatic ecosystems to address multiple questions about nutrient sources and cycling through a food web.

Regional fish collections in the United States provide access to millions of specimens, tissues, and metadata (e.g., field notes and other digitally captured records) to inform retrospective ecological studies employing SIA. The collections described in this article hold specimens from long-term monitoring of sensitive aquatic systems, endangered species, and important fisheries for most major systems in the United States, with well-sampled regions in the Great Lakes, Mississippi, Colorado, Rio Grande, and Gulf Coastal waterways (figure 2). Survey timelines bracket disturbances (table 1, figure 1) such as habitat degradation, hydrologic alteration, pollution, invasive species, and climate change that originate at multiple scales from point sources to landscape or catchment and regional or global scales (Fausch et al. 2002, Allan 2004, Dudgeon et al. 2006, Olden et al. 2010). Combining specimens across large, repeated collections facilitates analysis of stressor effects across levels that represent temporally relevant ecological connections with other specimens collected at the same time (Lane 1996, Hilton et al. 2021). The application of SIA to widely distributed taxa at basin-wide, multiregional, or continental scales over time facilitates the development of dynamic isoscapes (Bowen 2010) that serve as a template for more spatially and temporally focused research efforts.

Socioeconomic considerations

In addition to filling basic ecological knowledge gaps, a collections-based SIA research program provides another means of assessing coupled interactions and feedbacks of social, economic, and natural systems. For example, the contamination of fishes by mercury and other pollutants has been studied since the mid-1970s using museum specimens, including some specimens dated to the late nineteenth century. The application of SIA and long-term environmental data to these samples could illuminate the effectiveness of pollution control measures implemented under the Clean Water and Clean Air Acts that were intended to protect the environment and human health. By extension, the analysis of contaminants in specimens, when coupled with SIA and environmental risk analysis, could be used by federal, tribal, and state agencies to address the disproportionate exposure burdens often faced by Native Americans, minorities, rural residents, immigrant, and low-income communities (Harris and Harper 1997, 2004, Sechena et al. 2003, Gochfeld and Burger 2011, Lauber et al. 2017). Billions of dollars have been spent on freshwater restoration projects in the United States (Bernhardt et al. 2005), but there is still substantial debate about how to monitor and quantify restoration outcomes. In major waterways such as the Great Lakes, the efficacy of restoration is tied, at least in part, to whether the locations had the capacity to provide key ecosystem services historically or whether services are suppressed by current stressors (Allan et al. 2013). The long-term perspective provided by biodiversity collections provides an important line of evidence to assess these alternatives and allow for better investment in restoration locations and activities.

Future directions

We propose a concerted and large-scale research agenda that extends the utility of biodiversity collections for ecological inquiry at broad temporal and spatial scales. We envision these steps to developing this program: First, isotopically characterize fish specimens within and across collections selected to span multiple water resource regions along similar timelines to address broadscale hypotheses of disturbance effects (table 1). Next, deposit georeferenced materials from ongoing studies in biodiversity collections and implement specimen collection as part of restoration monitoring. Then, link museum records explicitly to stable isotope ratios recorded in the Isobank database to allow aggregation of SIA data across space and time that includes details of tissue type and other primary metadata associated with sample preparation, preservation history, and analysis. Next, connect temporal and spatial patterns of isotope ratios to environmental databases characterizing land use change, atmospheric, point and nonpoint source pollution, and water quality. Then, associate SIA data from fish collections with isotopic data of other organisms they depend on for food (aquatic invertebrates). Next, couple renewed or sustained specimen collection of frequently sampled sites with deliberately curated tissue samples. Then, use freshly collected tissue samples in comparative studies to develop technologies to extract more SIA data from archived museum material. Finally, identify biodiversity collections with extensive international holdings to compare hypotheses of community responses to environmental change at global scales.

The utility of this approach depends on regular resampling of the most repetitively sampled sites or watersheds represented by specimens in regional fish collections and continued archiving of specimens from these sampling efforts in museums. The numbers of specimens deposited in museums have dropped precipitously

in recent years (Colella et al. 2021). Rare species are the traditional focus of current collecting efforts, but abundant species are most relevant for ecological study. It should also be possible to expand the scope of SIA studies involving biodiversity collections globally by comparing specimens from US collections with extensive international holdings (e.g., the extensive Robert Rush Miller collections from Mexico archived in the fish collection at the University of Michigan) with specimens from collections in Mexico, other parts of Latin America or other parts of the world.

In conclusion, there is enormous potential for a transformative research using biodiversity collections, SIA, and environmental informatics that could stimulate ecology akin to the impacts museum genomics has made in evolutionary biology (Card et al. 2021). Like DNA, isotope ratios are a fundamental currency interpreted in the context of biogeochemical and ecological principles. Long time series, extensive spatial sampling, and archived metadata and other extended attributes of museum specimens could be further developed and explored in a research program that interfaces museum resources, stable isotope laboratories, and ecological observatory networks such as the Long Term Ecological Research Network and NEON (the National Ecological Observatory Network). Marshaling resources in regional fish collections in the United States and worldwide will provide important historical context to fundamental needs in freshwater biodiversity research that include bolstering data infrastructure, providing baselines for monitoring and scientifically reproducible means for assessing effects of disturbance and measures of restoration success.

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