

suggest that non-invasive sampling will provide a reliable DNA template for detailed genetic analyses, and researchers who rigorously tested the method and demonstrated that genotyping errors frequently occur when using hair or feces as a source of DNA⁸⁻¹⁰. In designing a genetic sampling strategy, it is important for researchers to be aware of the following potential drawbacks of using a non-invasive sampling strategy: (1) a substantial proportion of genotyping errors can occur and lead to erroneous conclusions, and (2) the laboratory costs of avoiding these genotyping errors can be 10 to 20 times higher than when using DNA extracted from tissue or blood samples. Non-invasive genetic sampling is a promising new field; however, it could suffer the

fate of many ancient DNA studies – inaccurate results published in leading journals.

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The role of natural history collections in documenting species declines

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Efforts to document the decline of extant populations require a historical record of previous occurrences. Natural history museums contain such information for most regions of the world, at least at a coarse spatial scale. Museum collections have been successfully used to analyse declines in a wide range of plants and animals, at spatial scales ranging from single localities to large biotic and political regions.

Natural history museum collections, when properly analysed, can be an invaluable tool in documenting changes in biodiversity during the past century.

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Nearly a century ago, Joseph Grinnell founded a new natural history museum at the University of California, Berkeley. Rather than promoting the traditional view of a museum as a specimen repository, Grinnell had a fundamentally different vision in which the museum was an ongoing documentation of the faunal composition of a region^{1,2}. In Grinnell's view, the value of his museum '... will not, however, be realized until the lapse of many years, possibly a century ... the student of the future will have access to the original record of faunal conditions in California and the west'. That century has now nearly passed, and profound faunal changes have occurred throughout the world, mostly in the form of species declines and introductions. It therefore seems appropriate to ask whether Grinnell's goal has been realized and to investigate what role natural history museums and other faunal archives play in documenting the decline of species in the new-found science of conservation biology.

At first glance, one might imagine that documenting the decline of a species is a

straightforward task in field biology. However, documenting all but the most extreme declines (for example, complete extinctions) has proved to be extremely difficult. At the heart of this problem is the fact that decline is a comparative concept, and requires knowledge of the status of a species in the past to compare with the present. When a species declines, it experiences reductions in abundance and/or reductions in the area it occupies. While both of these changes can be used to detect declines, there are a number of problems in detecting declines based on changes in abundance that make it particularly difficult to implement. Unfortunately, for most taxa and communities, we do not have the detailed prior information on abundance that we would like, and reconstructing past abundances is usually impossible³. Further complicating the numerical analysis of shifts in abundance is the extreme yearly fluctuation in size that characterizes many natural populations. For example, in pond-breeding amphibian systems, a 12-year study of four species in a relatively pristine

and diverse community at the Savannah River Ecology Lab (SREL)⁴ revealed that patterns of juvenile recruitment may vary by several orders of magnitude between consecutive years from the same pond and that population recovery from low-recruitment years may require one or several years, depending on the biology of individual species, rainfall patterns and other specific factors. In cases such as this, where yearly variance in population numbers is high and may be autocorrelated for years at a time, the characterization of population size is difficult and the statistical power to detect trends is extremely low.

An alternative approach for detecting declines focuses on changes in the distribution (presence and absence) of a species based on comparisons between historic records and current surveys. Here, we summarize some of the ways in which museum collections and related data repositories have been used as a source of historical information in documenting changes in the presence or absence of species. We limit our discussion of declines to the analysis of 'simple' presence/absence data, because (1) these are the vast majority of the historical data that are available, and (2) this confines our discussion to a single set of statistical approaches. Different researchers view both species and sites of occurrence in different ways, and we have categorized these studies into those that either implicitly or explicitly view species and localities as fixed or random effects in their analyses. Our primary conclusion is that although museum data often represent an imperfect match to current sampling programs⁵, they can still provide the critical information necessary to identify declines, and should comprise one of the standard databases in conservation biology.

Alternative strategies for documenting declines

The basic strategy for documenting declines appears simple: if a species' current range is smaller than it was historically, then it has declined. However, several other strategies are in wide use for

Table 1. Representative recent studies using museum specimens or other archival records as historical data to document species declines

Species as:	Sampling sites as:	
	Fixed effects	Random effects
Fixed effects	Cascades frog ⁸ [1, 16] ^a Yosemite frogs ⁶ [7, 40+] Southeastern amphibians ⁴ [4, 1] Colorado montane amphibians ¹⁹ [5, 105] Scandinavian pool frog ²⁰ [1, ~60] California tiger salamander ²¹ [1, 1] Baja California trout ²² [1, 16] Shasta crayfish ²³ [1, 44]	California amphibians ⁵ [6, 315] Oklahoma amphibians ²⁴ [15, many] S. California fishes ²⁵ [38+, many] Australian rainforest frogs ²⁶ [8, 47] California long-eared owl ¹⁸ [1, many] Florida box turtle ¹⁷ [1, 63] Utah boreal toad ²⁷ [1, 71]
Random effects	Pit river fishes ²⁸ [14, 282] New Mexico fishes ²⁹ [21, 23] Boston plants ¹¹ [422, 1] Virginia creek fishes ¹² [32, 6] Panama reptiles/amphibians ³⁰ [100, 1] Rio Grande fishes ³¹ [114, 2] Singapore woody plants ¹⁰ [448, 1]	Western US fishes ³² [>67, many] Iowa amphibians ³³ [7, many] Illinois fishes ¹⁶ [187+, >1500] British butterflies ⁹ [59, many] Illinois prairie birds ³⁴ [16, many] Illinois mammals ³⁵ [27, many] Costa Rican fishes ³ [many, many]

^aNumbers in square brackets are [number of species, total number of sites] in the study.

documenting species declines. We have organized these into two categories, depending on how sites (or localities) or species are resampled (Table 1). In the first approach, historical sites are precisely resampled at some later time to look for changes in species presence/absence. In the second approach, different but presumably equivalent sites are visited in the same region to assess the distribution of a species, and current site occupancy is compared to the historical distribution. We have termed these two strategies as 'fixed' or 'random' sites, respectively, because of the close correspondence to statistical sampling schemes. The two strategies have somewhat different properties and goals. For example, in their analysis of amphibian declines in the Yosemite region, Drost and Fellers⁶ resampled the same ponds that had been sampled 77 years earlier by Grinnell and Storer⁷. Their data provide relatively precise information on these specific sites, but no information on other sites or parts of the geographic distribution of the species. Using the 'random sites' approach, Fisher and Shaffer⁵ provided a more broad-scale view of the declines of many of these same amphibian species over the 28 counties comprising the prairie/grassland ecosystem of central California.

In a similar vein, species may be viewed as 'fixed' or 'random' (Table 1). In the fixed approach the distribution of a limited number of specific species are compared over time [e.g. Fellers and Drost's⁸ study of the disappearance of the Cascades frog (*Rana cascadae*) at historic sites in California]. In the random approach the focus is less on individual species but rather on overall changes in the diversity and composition

of species assemblages, often at a more limited number of sites. For example, in an analysis of British butterflies⁹, the key point was the geographic distribution of species losses rather than declines in individual taxa. Where the goal is to assess patterns of diversity and decline, species are often treated as random sampling units rather than as specific targets of study, particularly when diversity is great^{10,11}.

The relevant data

Resampling programs (sites as fixed effects)

At first glance, the most precise way to document declines may be to precisely resample sites that were studied previously. Two examples of this strategy are Fellers and Drost's analysis of the Cascades frog (*R. cascadae*)⁸ and Weaver and Garman's analysis of fishes in a Virginia stream¹². Based on presence/absence tallies, Fellers and Drost⁸ documented the virtual extinction of the Cascades frog at Lassen Volcanic National Park from 16 sites of previous occurrence. Because each site had an associated date of last sighting, they were also able to demonstrate that much of this decline had occurred during the previous 15 years. The analysis of Virginia fishes¹² sought to replicate an earlier sampling effort to quantify declines and changes in a freshwater fish fauna. The site was selected based on the shift in surrounding habitat use from agricultural in 1958 when the initial survey was collected to urban in 1990, and documents a clear decline in species richness during this period.

Occasionally, historical abundance data are available from old surveys or museum records, which makes it possible to analyse changes in abundance between two time points^{3,6}. Such efforts are appeal-

ing for the increased numerical detail that they offer on the dynamics of declines, but they must be approached cautiously. Changes in sampling methods¹², sampling effort³, weather⁶ and many other factors influence the quantitative estimates of population size, often making it extremely difficult to compare studies across time. To take one example, in a recent resampling of frogs at Yosemite National Park⁶, the sampling techniques were roughly equal to those used historically⁷, but the expertise and effort were not. (As Drost and Fellers⁶ discuss, their survey was only aimed at amphibians, whereas the original one was a broad vertebrate survey with much less sampling emphasis and expertise on amphibians.) Controlling for biotic and abiotic factors is much more complex, particularly because it is not always clear whether a factor is something to be controlled for or whether it is responsible for an observed decline. For example, rainfall has a clear effect on abundances of amphibians at a site⁴, and variation in precipitation among sampling years is generally corrected for either statistically¹³ or in the resampling design^{5,6}. However, if rainfall patterns have changed historically (in association with deforestation, for example), then this represents a deterministic change in habitat that should be included in the comparison of abundance data across time.

Sites as random effects

When collections are pooled and analysed over a larger geographic region, individual localities are no longer the focus of attention. Rather, of all of the sites that could have been sampled, a subset (which, it is hoped, is random with respect to variables affecting the distribution and abundance of species) is represented in museum collections, and a new random sample is used to determine current distributions. For example, in our evaluation of six species of amphibians from the grassland/oak woodland habitat of central California⁵, we used the county (partial or entire) as our sampling unit, and tallied the presence of species in each county in museum records and in our own sampling efforts as a measure of decline. A somewhat different approach was used in the extraordinary documentation of the Illinois fish fauna between the end of the 19th century¹⁴ and the 20th century^{15,16}. Although the sampling program was intensive (over 1500 localities sampled in the first survey, over 2000 in the second), Burr¹⁶ essentially chose the state of Illinois as a single unit of analysis with multiple, random sites serving as the primary data to document disappearances, range expansions, and new species invasions. In doing so, the likelihood of misinterpreting a trend is reduced, although a great deal

of potentially detailed information at a smaller spatial scale is ignored as a consequence. Obviously these same data could be used at a county or smaller scale, although such an analysis has not been performed to our knowledge.

Species as fixed or random effects

Species may also be considered as fixed or random sampling units. Here, the distinction is less clear than for sites and may have to do as much with the emphasis of the researcher as with the actual data collected. However, certain cases are unambiguous and emphasize the difference in the strategies. For example, if only a single species is studied (e.g. Florida box turtle, *Terrapene carolina*¹⁷; long-eared owl, *Asio otus*¹⁸), then that species is the only target of analysis, and it is clearly a 'fixed' effect. At the other extreme, some studies use past data collections and current surveys to document shifts in the diversity of a community of organisms, with relatively little emphasis on individual taxa. This is a particularly useful strategy when species diversity is very high, many taxa are uncommon, and there is little hope of constructing an exhaustive species list for an area. For example, one temperate¹¹ and one tropical¹⁰ survey of plant diversity at a single site each documented the apparent local extirpation of a large fraction (about 1/3 to 1/2) of the species present a century ago. Although the species lists on which these studies are based could be used to evaluate individual taxa, the approach of both investigations was instead to examine the patterns of loss and turnover of broad classes of taxa (native, introduced, weedy, etc.) to look for general patterns of decline. In so doing, detailed inferences on each taxon are sacrificed, but the broad patterns of change in biodiversity can be quickly assayed even if different sampling protocols were used in the historical and recent surveys.

Null expectations

Several biases and assumptions (Box 1) impinge on any resampling effort and must be considered in the interpretation of changes in species ranges over time. Two that are of particular importance when museum collections are used to document historical records are the inherent variability of a species and the spatial scale over which localities are pooled to document a decline.

If a species has an extremely fluctuating population or metapopulation structure, then the null expectation for resampling fixed historic sightings is a decline. For example, consider a simple model of frequent extinction and recolonization of local populations, in which subpopulations in a hypothetical metapopulation blink on

and off every ten years. If the region is surveyed over enough time (museum records often include repeated collections from sites spanning many decades), at least one positive sighting will be recorded at each site. However, a resurvey would expect to find only half of the sites occupied. Different assumptions regarding the average persistence and recolonization time for subpopulations will change the expected resurvey probability (following a binomial distribution), but in all cases the null expectation is a decline. This problem can be overcome by considering sites as random effects and pooling over an appropriately large sampling area⁵, or by surveying additional random localities in the vicinity of fixed historical sites⁶. The same problem results from fluctuating populations⁴ if one assumes that a population regularly falls below a minimum detectable level for a survey technique.

The scale over which samples are pooled is an extremely important component of resampling random sites. The trade-off here is between the size of the grid or unit over which samples are pooled and the scope of one's inference. For example, in our analysis of Californian amphibians⁵, we used the 28 partial or complete counties in our survey region as sampling units, based on both the density of our own sampling and what we inferred was the coverage in museum collections. Had we taken the more conservative strategy of using only the three broad ecological regions in our analysis (Coast Range, San Joaquin Valley, Sacramento Valley) we would have found only one species (*R. aurora*) in decline, rather than all six. A trade-off exists between sample unit size, the inference that can be drawn and the scope of sampling both in the current and the historical data. If sample unit size is very large, then only widespread declines can be detected; however, historic and current sampling can be relatively sparse and uneven and still be informative³. The flip side is that when sample unit size is very large, more subtle (and often more interesting) patterns may be missed in the data. For many of the very oldest museum collections that were amassed over previous centuries, the grid size may, by necessity, be extremely large because very few voucher specimens were collected. However, even these collections may provide insights into large regional patterns of species extirpations.

Conclusions

Although they are certainly not perfect, museum and other historic locality archives offer a rich source of material for the analysis of species declines. In many ways, we favor the approach of treating sites as random rather than fixed, primarily because more general statements of

Box 1. Important assumptions

In using historical museum data to document declines, different assumptions come into play for each of the strategies identified in Table 1. The distinction that we have drawn between species as random and fixed effects is to some extent a biological decision rather than a methodological one, and we do not consider it in detail here. However, the assumptions involved in considering sites as fixed or random effects differ dramatically.

Sites as fixed effects

Key assumptions of this strategy center on the new survey data being directly comparable to the historical data. The importance of these assumptions varies with individual species and the goals of a study: for common species, these assumptions may not affect the determination of presence/absence, because the species will generally be above a detection threshold even if the assumptions are violated. However, if a species is rare or detection is difficult, these assumptions become increasingly important. They include the following:

- The same sampling techniques were used.
- The expertise of both teams was equal.
- The sampling effort was the same in both surveys.
- Normal biotic and abiotic factors regulating population fluctuations were the same during the sampling periods.
- Detectability (the detection threshold) of the target species has remained the same. [This may change due to natural effects (such as succession) or anthropogenic effects (such as eutrophication).]

Sites as random effects

The historical data (usually pooled museum collections) and the current data (usually an organized survey) often differ dramatically. Key assumptions center on whether these two data sets differ in such a way as to bias the resulting trend and on the extent to which the data sets represent random samples from the same pool of potential sites. They include the following:

- Historical and current sampling should be sufficient so that a lack of occurrence in a region is meaningful.
- The size of the region over which the sampling sites are pooled should include enough sites to be statistically rigorous, but should not be so large as to be biologically trivial (e.g. considering an entire continent as a single unit).
- The size of the sampling unit over which sites are pooled should be larger than the scale of the biotic and abiotic forces affecting population fluctuations.

decline over ecologically or geographically relevant spatial scales can be made. Assessments of changes in abundance over time are very problematic, and should be interpreted with great caution. However, by judiciously using museum collections as a source of historical data, changes in the presence/absence of individual species and communities can successfully be evaluated across a wide range of plant and animal taxa in habitats ranging from single-species temperate habitats to complex tropical systems (Table 1). Several outstanding issues still need to be addressed, including the effect of increasing or

decreasing the spatial scale (or 'grid size') over which sites are pooled and the quantitative impact of natural population fluctuations on the null expectations of re-sampling schemes. However, we feel that Grinnell's original goal of the natural history museum as a repository of historical distributional data is beginning to be realized, and that museum collections offer an important source of data for a meaningful evaluation of species declines.

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