

Detecting range shifts from historical species occurrences: new perspectives on old data

Morgan W. Tingley^{1,2} and Steven R. Beissinger^{1,2}

¹ Department of Environmental Science, Policy & Management, 137 Mulford Hall No. 3114, University of California, Berkeley, CA 94720, USA

² Museum of Vertebrate Zoology, University of California, Berkeley, CA, 94720, USA

The difficulty of making valid comparisons between historical and contemporary data is an obstacle to documenting range change in relation to environmental modifications. Recent statistical advances use **occupancy modeling** to estimate simultaneously the probability of detection and the probability of **occupancy**, and enable unbiased comparisons between historical and modern data; however, they require repeated surveys at the same locations within a time period. We present two models for explicitly comparing occupancy between historical and modern eras, and discuss methods to measure range change. We suggest that keepers of historical data have crucial roles in curating and aiding accessibility to data, and we recommend that collectors of contemporary specimen data organize their sampling efforts to include repeated surveys to estimate detection probabilities.

Historical occurrence data: a new opportunity

Documenting range shifts is an integral part of understanding how species and communities have responded to past environmental change and how they might respond to future environmental modifications [1,2]. A key strategy for documenting range shifts is the use and **resurvey** of historical occurrence data, such as those from museum collections and field notes [3]. Here, we define historical occurrence data as any set of information that, through observed detections or **non-detections** (see Glossary), provides evidence on the true **presence** or **absence** of individuals of a species (Box 1). A major obstacle to documenting range change, however, is making valid comparisons between historical and contemporary data [4]. Historical species occurrences are often perceived as untrustworthy, and many rich sources of baseline data have been forgotten, lost, or discarded (e.g. Refs [5,6]). Compared with contemporary data, most historical data were collected using outdated or alternative methodologies, with associated uncertainties and inaccuracies [7] and might not provide strong inference on change when compared naïvely with modern observations. The rapid pace of environmental change, however, necessitates an urgent reexamination of all potential sources of information on range shifts [8].

We describe the types of ecological inference to be gained from historical species occurrence data, and the problems associated with making such inferences. Additionally, numerous recent advances in the estimation and statistical modeling of uncertainty now enable unbiased comparisons between historical and modern data. By minimizing or controlling for many of the problems that have plagued earlier analyses of historical occurrence data, these techniques can aid in understanding range changes that have already occurred. We hope that future studies will ‘rediscover’ historical occurrence data and provide greater inference on how communities, populations and species have shifted over long temporal scales.

Glossary

Absence: a species not occurring at a location (site); difficult in practice to differentiate from a non-detection.

Colonization: an event where a location transitions from being unoccupied to being occupied by a species over time.

Covariate: an explanatory variable that is potentially predictive of the studied outcome. Covariates might be directly related to occupancy (e.g. elevation or habitat) or important nuisance terms affecting detectability (e.g. era or season) that need to be controlled.

Detectability: the probability that a species will be found (detected) during a survey, given its presence.

Extinction: an event where a location transitions from being occupied to being unoccupied by a species over time.

False absence: a non-detection that is treated mistakenly and with certainty as a true absence.

Georeference: a specific reference in a geographical coordinate system that assigns an event (e.g. a detection or occurrence) to a location.

Gradient: a measurable physical quantity or dimension (e.g. elevation, temperature or longitude) that changes gradually in magnitude.

Non-detection: when a species was not detected during a survey by the observer. Non-detections result from the species either being absent or being present and undetected.

Occupancy: the probability of species being present at a set of locations.

Occupancy modeling: an analytical framework that estimates the probability of occupancy while taking into account imperfect detection during surveys; summarized in Ref. [18].

Presence: a species occurring at a location, as affirmed by a positive detection.

Resurvey: a survey that returns to an area that has been previously surveyed. Used to estimate detectability when the time interval between surveys is short, and to make comparisons between two or more time periods (eras) when the interval between surveys is long.

Season: in reference to occupancy modeling, a season refers to any duration of time within which occupancy does not change, but between-seasons occupancy can change [18]. Single-season occupancy models only estimate the probability of occupancy for a single season. Multiple-season occupancy models estimate an initial probability of occupancy for the first season and then estimate concurrent probabilities of extinction and colonization for subsequent seasons.

Corresponding author: Tingley, M.W. (mtingley@nature.berkeley.edu).

Box 1. Defining ‘historical occurrence data’

We define ‘historical occurrence data’ as any set of information that provides evidence for the presence or absence of a species. The term ‘historical’ is relative yet implies that the individual who collected the occurrence records in the past might differ from the person using the records in the present. We also distinguish historical occurrence data from long-term monitoring data, which is often highly standardized, measured and specific in purpose. By contrast, historical occurrence data can be anecdotal, observational and general in nature. To be used in understanding species ranges, historical occurrence data must contain information on at least location and time. Without an assigned geographic locality and temporal reference, occurrence records cannot be compared to contemporary data.

Historical occurrence records originate from a variety of sources. Faunal surveys, such as for breeding atlases (e.g. Ref. [57]), are the most obvious source of data, as they were originally collected with the purpose of estimating species distributions. Historical species accounts and species lists can also be found in the field notes and journals of observers who collected the data without an intentional immediate use. In some cases, photographs of a specific location (e.g. Ref. [58–60]) can be sources of occurrence data for visually unique species, tree species, habitat elements or other aspects of vegetation. Finally, specimen collections from natural history museums are valuable sources of information on species occurrence [61]. Metadata from specimen records are increasingly available over the Internet from global museum databases (e.g. VertNet, <http://vertnet.org/>), which enable rapid access to large amounts of occurrence data from around the world [11].

Problems with using historical occurrence data to document range shifts

Variation in the details recorded and methodological characteristics of historical occurrence data largely determine both the problems faced in inferring range change and the solutions available. We group historical occurrence data into four general forms, each differing in the data and the resulting inferences available (Table 1). The simplest form of occurrence data is presence-only data, which are widely available from natural history museum (NHM) collections, are used frequently in modeling distributions and are likely to be the most abundant type of historical occurrence data [9–11]. But presence-only data pose several problems to determining changes to species ranges due to their lack of information on non-detections [12]. Lack of historical non-detections restricts comparisons with modern data to only those locations where species once occurred, enabling an estimate of **extinction** (or its converse, persistence) but not of **colonization** [13]. The use of randomly generated ‘pseudo-absence’ data sets has become popular in modeling distributions from presence-only data [9], but pseudo-absences contain an inestimable number of **false absences** [14], thus biasing comparisons. Although presence-only data are effective in many cases at defining species ranges [15], they can result in vast over-prediction of occurrence [9] and generally do not perform as well as models that include non-detections [15,16].

Other types of historical data include presence and non-detection data, where each site was visited once and all species detected were recorded (Table 1). Presence and non-detection data are more informative than are presence-only data and can enable estimates of changes in occupancy [13]. However, the inability to discriminate non-detections from true absences means naïve use of presence

and non-detection data overestimates colonization events and underestimates extinction events [17]. To yield presence and estimable absence data, historical surveys at sites must have been repeated within short time periods, either by one observer or multiple independent observers. Assuming that survey sites do not change occupancy status over short timescales, repeated surveys or collecting events provide patterns of detection and non-detection, enabling the estimation of the probability of true absence given imperfect detection [18]. Lastly, abundance data enhance simple presence or non-detection data by enabling the estimation of changes in relative abundance, true abundance, or density over time, thus providing a more comprehensive view of range and distribution. Documenting contemporary range change solely through the use of historical abundance data, however, has proven difficult owing to the use of outdated or nonstandard methodologies in collecting most historical abundance data [3].

Regardless of the data format, a notable problem with historical data is the difficulty in differentiating between true absences and non-detections. In particular, the burden of evidence necessary to define ‘extinction’ has been discussed for a variety of taxa [19–21]. In at least one case [22], populations presumed extinct were re-discovered during the publication process because populations were too low during the original survey period for the species to be detected, highlighting the dangers of presuming a non-detection to be equivalent to an absence. Consequently, **detectability** has a key role in interpreting non-detection data [23].

Whereas false absences are a well-documented and consistent problem for interpreting occurrence data, ‘false presences’ or misclassifications of species are generally ignored. False presences are typically associated with survey data, where species identification is related to individual observer skill and experience [24]. However, analyses of range based on physical specimens are not immune from false presences, as misidentifications of specimens in museums [25,26] and herbaria [27] have occurred. Although misidentifications of specimen records can be secondarily validated, correcting for false presences in survey work is more complicated. Meeting this challenge is necessary, however, as even low rates of false presences in occurrence data can bias estimated distributions [28].

A broader problem inherent in all historical data arises from the comparability of surveys done at different times with ‘different underlying properties’ [7]. Comparison of occurrence data from different time periods often suffers from survey-specific differences in methodology, observer skill, weather, effort and other related factors. Thus, comparisons of historical and modern data will often have more inherent bias than will comparisons between samples taken within a single time period [29].

Finally, geographical precision is a problem typically unique to historical occurrence data, yet has been largely ignored. Museum specimens are usually **georeferenced** by specimen tags or collectors’ field notes, but vague accounts, dishonest reporting and human error have led to inaccuracy or imprecision in location [30]. These biases might exist unrecognized, despite new protocols to incorporate estimates of locational uncertainty consistently into

Table 1. Different types of historical occurrence data listed from least informative to most informative

Extent of occurrence data	Data depiction ^a		Non-detection data	Temporal replication	Inference available	Biases to range estimation
Presence-only	<i>Survey₁</i>	<i>Survey₂</i>	No	No	Extinction only	Pseudo-absence data lead to overprediction of historical range and extinction and no inference on colonization
	<i>Site_i</i>	● —				
	<i>Site_j</i>	● —				
Presence and non-detection	<i>Site_k</i>	— —	Yes	No	Extinction and colonization	False absences give underprediction of historical range and extinction and overprediction of colonization
	●	—				
	●	—				
Presence and estimable absence	○	—	Yes	Yes	Extinction and colonization	Probability of occupancy reduces false absence bias
	●	●				
	●	○				
Abundance	○	●	Yes	Yes	Extinction, colonization and change in population size	False absence bias reduced, but abundance comparisons bring new set of biases
	14	20				
	1	○				
	○	3				

^aOpen circles represent sites where a species went undetected during historical surveys, whereas closed circles represent sites with detections. Numbers in the circles represent abundances. Data presented for illustrative purposes only.

georeferencing processes (e.g. [31]). Locational error can create inaccurate distribution maps [26] and can impact estimates of species richness and community composition [32]. In resurvey work, locational error can lead to false conclusions on extinction and colonization events, inflating turnover estimates [27].

Past attempts to account for problems with historical occurrence data

The use of historical surveys for range change comparisons has grown rapidly. Ten years ago, Shaffer *et al.* [3] championed the use of historical data to document declines, citing 15 studies over 38 years that resurveyed species distributions. To illustrate the variety of inferences available from historical data and how they were made, we reviewed recent work published since Ref. [3] that explicitly compared historical and contemporary survey data (Table 2). We found 37 studies published over the past decade that resurveyed species distributions. The time period separating historical and contemporary data varied among studies, depending largely on the data source. Generally, the longest durations were studies of plants

in isolated patches [33,34]. Only one study used historical data to examine colonization [35], despite the existence of a large literature on colonization and species invasions (*c.f.* Ref. [36]). Consequently, many researchers do not appreciate the value of conditioning current presences with probabilistic assessment of past absence.

Many of the biases inherent in the use of historical occurrence data were not acknowledged in past studies. Almost two-thirds of the recent studies resurveyed specific locations where historical data were collected (i.e. sampling sites as fixed effects; [3]), whereas the remainder resurveyed in the same region, foregoing a direct site-to-site comparison (i.e. sampling sites as random effects; [3]). More than half of the studies (54%) acknowledged that data collection methods differed between the resurvey and the historical survey, and that this might have affected the detectability of species; yet, only one study [37] attempted to correct for this problem. Even fewer studies (35%) discussed the risk of false absences in historical or resurvey data, and these primarily dealt with proving extinctions rather than range change. Only three studies statistically quantified the probability of false absences in occurrence data.

Table 2. Recent studies that have explicitly resurveyed historical data to make different types of inference on range change

Study system	Location	Historical data source	Comparison time span ^a	Addressed biases?			Refs
				Attempted resurvey of specific localities ^b	Addressed differences in methodology or similar factors ^c	Addressed false absences ^c	
<i>Extinction only</i>							
Plants	Oceania	Literature	99–114	Yes	No	No	[62]
	Europe	Specimens	5–127	Yes	No	Verbally	[63]
	Europe	Specimens	88–164	Yes	No	Verbally	[34]
	Europe	Literature	80–100	Yes	Verbally	Statistically	[19]
Beetles	Africa	Specimens	12–131	No	No	Verbally	[64]
Mammals	North America	Specimens, literature, field notes	60–129	Yes	No	Verbally	[65]
<i>Colonization only</i>							
Snails	Australia	Specimens, literature, field notes	110	No	Verbally	No	[35]
<i>Extinction and colonization</i>							
Amphibians	North America	Specimens, literature	27–106	No	No	No	[66]
	North America	Original survey data, pers. commun.	21–29	Yes	Verbally	Verbally	[67]
Birds	North America	Specimens, literature	22–82	No	Verbally	Verbally	[68]
	Africa	Literature	30–47	Yes	Verbally	No	[69]
	Europe	Literature	28–38	Yes	Verbally	Verbally	[70]
<i>Range change</i>							
Algae	Europe	Literature	32–50	Yes	Verbally	No	[71]
Trees	Europe	Literature	45–55	Yes	No	No	[72]
	North America	Original survey data	62–71	Yes	No	No	[73]
Plants	Europe	Atlas	115	Yes	Verbally	No	[74]
	Europe	Original survey data	1–100	No	No	No	[50]
	North America	Original survey data, pers. commun.	28–29	Yes	Verbally	No	[75]
Coral	North America	Field notes, literature	40–183	Yes	Verbally	Verbally	[33]
	Oceania	Field notes, literature	82–85	Yes	Verbally	No	[76]
Bivalves	North America	Field notes, literature	3–42	Yes	Verbally	Verbally	[38]
Lepidoptera	Europe	Atlas	5–35	No	No	No	[77]
	Europe	Pers. commun., literature	31–37	Yes	No	No	[78]
Odonata	Europe	Atlas	15–51	No	No	No	[79]
	Europe	Atlas	15–35	No	Verbally	No	[80]
Amphibia	North America	Specimens, literature, field notes	13–119	Yes	Verbally	Statistically	[81]
	North America	Field notes, specimens	30	Yes	Verbally	No	[82]
	South America	Literature	18–34	Yes	Verbally	No	[83]
	North America	Pers. commun., literature	22–33	Yes	No	No	[4]
Herpetofauna	North America	Original survey data, literature	61–66	No	No	No	[84]
Birds	North America	Field notes, specimens, pers. commun.	51–93	No	Verbally	No	[58]
	North America	Field notes, literature	38–83	No	No	No	[85]
Mammals	Europe	Atlas	7–15	No	No	No	[86]
	Europe	Atlas	16–23	No	No	No	[87]
	North America	Field notes, specimens	83–94	Yes	Statistically	Statistically	[37]
	North America	Field notes, specimens	1–125	No	Verbally	Verbally	[88]
	North America	Field notes, specimens	51	Yes	Verbally	No	[89]

^dRange change was identified as a resurvey study where the goal was to look at the change in geographical range of a species over time. This was considered distinct from an extinction and colonization study where the goal was to look at occupancy dynamics or turnover within a population.

^aTime span calculated as the minimum–maximum number of years between historical and contemporary data. For instance, data collected between 1920 and 1930 and between 2000 and 2005 would equal 70–85 years of time span.

^bDistinction was made between a resurvey at the same location as historical data and resurveying in the same general vicinity but not a direct comparison of occupancy at the site level [3].

^cA verbal address acknowledges the inherent bias and might or might not try to explain how the problem was mitigated; a statistical address attempts to control for the bias through any variety of statistical methods.

In conclusion, although some researchers were aware of problems caused by using historical data, most failed to address them directly. It is likely that the complexity of the problems and the novelty of accessible solutions are mostly to blame for the widespread lack of response to biases in historical data.

Dealing with problems in historical occurrence data: a primer

Some issues with historical data, particularly geographic precision and survey-specific differences, can be addressed simply through careful design of resurvey efforts [38]. For example, sites with extreme uncertainty in location can be

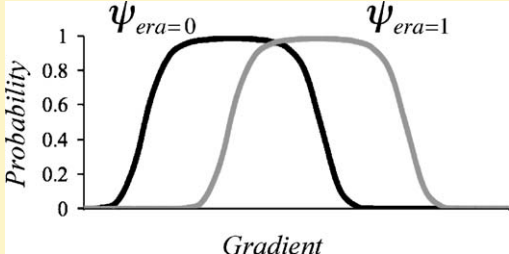
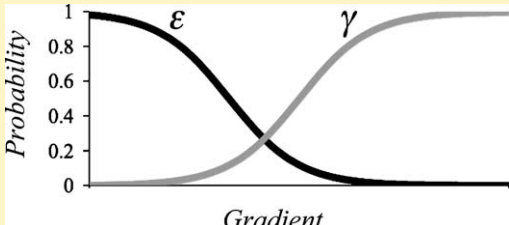
Box 2. Parameterizations of occupancy models for inferring range shifts

The unpaired-site model provides a flexible framework with which to work with occurrence data (Table I). With the unpaired-site model, data from all sites are entered into a single-season occupancy design [18] and ‘era’ (e.g. historical surveys or modern resurveys) is a covariate explored in both models of detectability and occupancy. This configuration does not require matched pairs of sites, but does require occupancy to be related to a defining covariate affecting range (e.g. elevation, precipitation, latitude or longitude). Many different mathematical forms can be used to model the relationship between occupancy and a covariate. Change in the relationship between this defining covariate and occupancy is used to create occupancy profiles and is examined as a proxy for colonization or extinction at sites [37]. Consequently, the unpaired-site model can be used when historical locations are not described well enough to enable a matched pair analysis, and when the relationship between a species and an

environmental gradient is the desired indicator of change over time. It is also useful when the number of paired sites sampled and the number of sites changing occupancy state are small.

The paired-site model can be used to explore occupancy when sufficient numbers of matched pairs of sites are available (Table I). In this specification, a ‘multi-season’ occupancy design [18] is used to compare how the probability of colonization and extinction of sites has changed occupancy between eras. The paired-site model typically estimates the probability of historical occupancy at a site and then models the probability of extinction and colonization between eras [17]. Site-specific covariates (e.g. changes in climate or land use) can be used to explore specific hypotheses related to colonization and extinction estimates. The paired-site model might enable a mechanistic analysis of the factors that affect site-specific occupancy by incorporating covariates potentially associated with range change.

Table I. Model parameterizations for occupancy comparisons along a dominant gradient over two time periods^a

Model	Modeled parameters	Example equations	Range change inference
Unpaired site	Occupancy (ψ) Detectability (p)	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot \text{era} + \beta_2 \cdot \text{gradient} + \beta_3 \cdot \text{gradient}^2$ $\text{logit}(p) = \beta_4 + \beta_5 \cdot \text{era}$	
Paired site ^b	Initial Occupancy (ψ_0) Extinction (ϵ) Colonization (γ) Detectability (p)	$\text{logit}(\psi_0) = \beta_0 + \beta_1 \cdot \text{gradient} + \beta_2 \cdot \text{gradient}^2$ $\text{logit}(\epsilon) = \beta_3 + \beta_4 \cdot \text{gradient}$ $\text{logit}(\gamma) = \beta_5 + \beta_6 \cdot \text{gradient}$ $\text{logit}(p) = \beta_7 + \beta_8 \cdot \text{era}$	

^aTime, or era, is a covariate with which occupancy and/or detectability might vary.

^bExtinction (ϵ) and colonization (γ) probabilities enable calculation of occupancy in future time periods from an initial probability of occupancy (ψ_0) and a probability of detection (p), which might or might not be era specific.

removed from the analysis [39]. Additionally, by conducting modern surveys at the same location, time of day and time of year as the historical data, many potential biases of comparison can be reduced. However, even perfect matching of survey characteristics and methods cannot eliminate large differences in detectability between sampling periods, and these differences must be approached in another way.

Many factors – both controlled (e.g. survey method, time, and date) and uncontrolled (e.g. weather, habitat) – can impact the probability of detecting a species, and the degree of impact can differ on temporal, geographic and taxonomic scales [23,40,41]. Thus, species will often differ in their probabilities of detection, which might be site, era, or survey specific. Expecting differences in detectability between survey eras enables the development of sets of hypotheses that can be tested using occurrence data. The ‘occupancy modeling’ approach simultaneously estimates both the probability of detection and the probability of occupancy, conditioning probabilities of occupancy with the risk of false absences [17,18,42]. This approach can

model covariates of both occupancy and detectability, enabling separate, independent estimates of detection and occupancy for survey eras, or independent probabilities of detection for survey methods [43]. A strength of this framework lies in testing and comparing competing models that represent hypotheses of which covariates best explain the observed patterns of detection or occupancy [44].

Occupancy models cannot use presence-only data but require repeated surveys at the same locations within a time period to estimate detectability [18]. If historical presence and non-detection data without repeated surveys are available, detectability functions derived from modern repeated survey data could be applied to historical non-detections, but it is ill-advised to assume that detectability is constant across survey eras.

Although the application of occupancy modeling is expanding rapidly, it is still used only rarely to compare modern and historical data [37]. Given the complex and variable nature of historical occurrence data, a flexible framework for analysis is needed. We highlight

Box 3. Measuring range changes in practice

We use the montane shrew, *Sorex monticolus*, to illustrate two ways of measuring range change via occupancy modeling. Our data come from Ref. [37], in which small mammal communities were resurveyed along an elevational transect through Yosemite National Park, USA. Historical surveys of small mammals were conducted by trapping at sites on consecutive nights, thus building a record of repeated surveys. Owing to the inability of the resurvey team to locate all historical sites with high confidence and to the addition of new survey sites, the unpaired-site model was used for analyses.

Moritz *et al.* [37] defined and categorized range shifts through the use of P_{fa} tests (Figure 1a). Detectability was estimated using the best of 32 competing models that explored changes in detectability over trap night and survey era, and included trap effort. Historically, *S. monticolus* was not found below 2212 m. During the resurvey, it was found at 18 lower sites, down to 1209 m. The probability that *S. monticolus* was present within that elevational range at one or more of the historical survey sites ($n=17$) and went undetected in the contemporary resurvey was $P_{fa} < 0.001$. Consequently, it was concluded that the lower elevational range limit of the species had shifted downward by 1003 m.

Another way to examine range shifts is through species optimums, by determining the covariate value where the probability of occupancy is highest [50,51]. Moritz *et al.* [37] built a candidate set of 112 occupancy models per species using the best 14 detection models combined with eight competing occupancy models that incorporated era, elevation (represented as linear or quadratic functions) and interactions. Model-averaged occupancy curves [44] were created for *S. monticolus*, illustrating how the probability of occupancy changed over the elevational gradient and how this relationship changed over time (Figure 1b). Historically, the optimum elevation was at 2870 m, whereas the modern optimum increased to 3190 m, an increase in optimum elevation of 320 m. *S. monticolus* occupancy also increased throughout its range.

At first glance, these two measures seem to provide contradictory conclusions from the same data. However, they describe different aspects of the complex process of range change. Looking at either the range margins (P_{fa}) or the optimum partially describes range change, yet neither measure describes change to the entire range. Lack of a standard technique to compare full range distributions hinders our ability to understand how species have responded to large-scale environmental change.

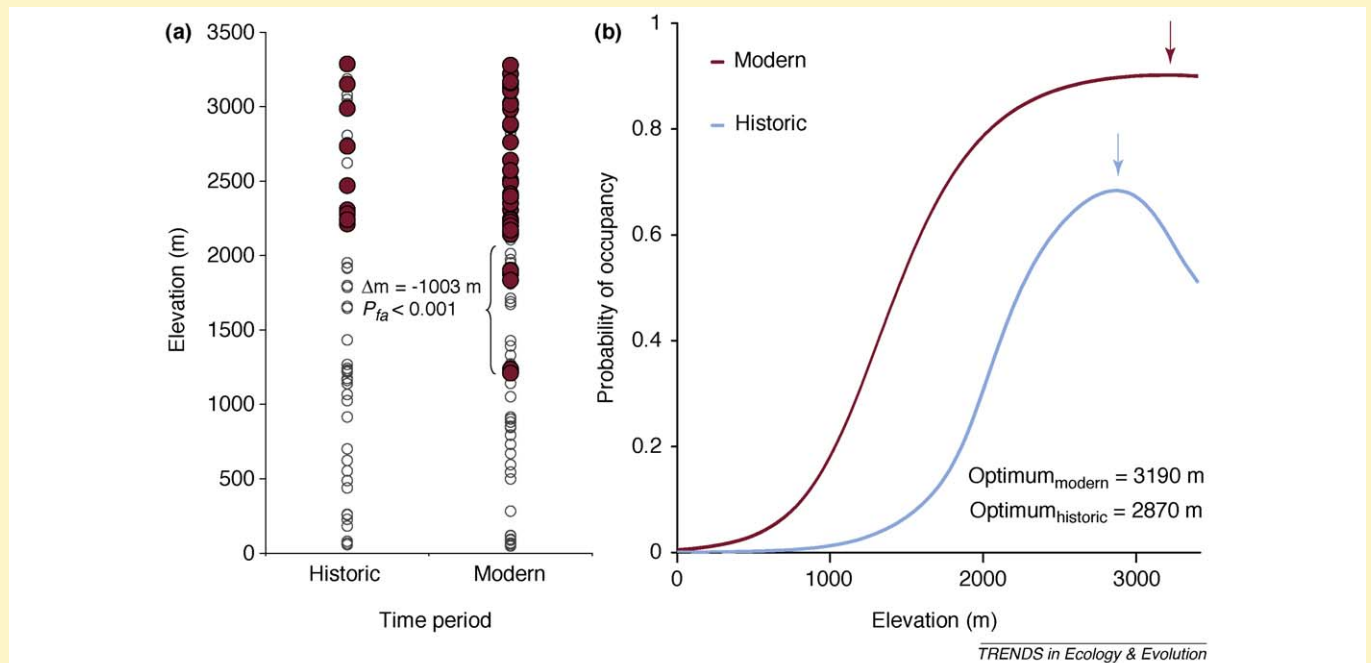


Figure 1. Methods of quantifying range change using modeled probabilities of detection and occupancy for the species *Sorex monticolus* [37]. Raw presence (solid circle) and non-detection (open circle) data (a) can be used to calculate the probability of false absence (P_{fa}) for a set of sites along an elevational gradient. The modeled probability of occupancy curve (b) can be used to find the 'optimum' elevation (denoted by arrows) for each time period. Figure adapted from the Online Supplementary Material in Ref [37].

two different methods ('unpaired' and 'paired' site models, Box 2) for comparing occupancy at sites in both historical and modern eras. Each asks slightly different questions of occurrence data, yet both facilitate the estimation of range shifts while accounting for risks of false absence.

Although both models consequently solve many issues in using historical data, neither addresses the problem of false presences. At least one modification to occupancy models enables incorporation of false positives [28] by estimating the probability of a false positive at a site where a species is not present. Modeling the probability of false positives reduces inflated estimates of occupancy when false positives are abundant [28]. Consequently, models

incorporating the risk of false positives should be strongly considered when analyzing occurrence data. However, this is a developing field and methods that further integrate false positive risks into the occupancy modeling framework are needed.

Measures of range change

Estimating the probability of occupancy for a species in both historical and present eras accounts for many of the biases in historical data, yet a method is also needed to measure range change. Defining the range of a species is a complex and often controversial task [45]; consequently, we provide multiple methods for comparing ranges across time. The first method requires a modeled

probability of detection function, whereas the second method could be applied to any occupancy distribution.

The first method examines naïve estimates of change in occupancy and tests for statistical support by calculating the probability of false absence (P_{fa}). This measure comes from Ref. [37], and is reformulated as Equation 1:

$$P_{fa} = \prod_{j=1}^m (1 - p_j^*) = \prod_{j=1}^m \prod_{i=1}^n (1 - p_{ij}) \quad (1)$$

where p_{ij} is the probability of detection at the i th survey of site j , and p_j^* is the probability of detecting the species over n surveys at site j . The probability of false absence can be calculated across m sites with non-detections to estimate the chance the species was present at all of those sites and escaped detection. The P_{fa} test uses only the modeled probabilities of detection to test the likelihood of absence across a set of unoccupied sites. Consequently, it gives a confidence estimate as to whether a naïve range shift is significant.

P_{fa} tests have many uses, one of which is to test for changes in the limits of distributions (Box 3) [37]. However, inferences focusing solely on the limits or extremes of a distribution could be biased by vagrant or single ‘out-of-range’ individuals that temporarily exist outside the boundary of the fundamental niche [46]. These individuals might signify ‘sink’ populations that cause an apparent expansion of range boundaries [47], or result in observed high rates of turnover and local extinction at range boundaries [48]. Although individuals or populations at the limits of a distribution might be most responsive to environmental change, occupancy changes across the whole of a species distribution might be more indicative of a population-level response to environmental change [49]. In simulations, analyses of range change based on entire distributions have been shown to be more sensitive to detecting expansions or retractions than have analyses focused on range limits [7].

In attempting to infer change from the entire distribution, several authors [50,51] have used a ‘maximum probability’ approach, where the maximum probability of occupancy in a species distribution along a gradient (elevation) was chosen as the species ‘optimum’ (Box 3). Changes over time can be calculated as shifts of the species optimum [50]. Although this approach provides inference on the distribution as a whole, it is difficult to interpret when there is no single maximum value (e.g. when occupancy is maximized over many continuous values or the distribution is multi-modal). The development of further measures for estimating range shift from probabilistic occupancy functions should be a priority for future research in applying these analytical methods.

Conclusions: an eye to the past and an eye to the future

Many of the problems with using historical data can now be explicitly accounted for through occupancy modeling [18] and other quantitative techniques [37]. To avoid bias, however, these techniques require, at a minimum, occurrence data with some repeated visits within survey periods, and data from enough sites to achieve sufficient

statistical power (c.f. Ref. [52]). Consequently, occupancy modeling is not a ‘one-size-fits-all’ solution and additional approaches will need to be developed to deal with all types of occurrence data (Table 1). The recent development of ‘multi-state’ occupancy models [53] might provide a useful framework for comparing historical and resurvey abundance data.

The tools presented here provide important implications for those who both store and use historical data, as well as those who collect contemporary data. Foremost, observational and occurrence data should be given greater value by NHMs, field biologists and other holders of original historical records. In particular, field notes often hold key occurrence metadata, including information on non-detections, location and effort, that individual records do not contain. When possible, occurrence data, including field notes, should be made publicly available and important metadata, such as geographic location and specificity, should be refined and uncertainty quantified. NHMs have led the way in making specimen-based occurrence data available publicly [11], but have been slow to do the same with historical observation records.

To estimate probabilities of detection, museums or database managers might have to modify how occurrence records are related to each other in a structured database [54]. Most specimen-based occurrence databases are currently structured around localities, with specimens attached to localities, and items such as collection date and collector are unrelated metadata [55]. To estimate detectability, occurrence records need to be assembled into survey periods, with resurveys at localities. Thus, date of collection and details of the collector become crucial organizational levels of occurrence data rather than unrelated metadata. Incorporating this extra structural level into databases might be difficult to populate with data correctly, particularly as most occurrence databases are organized around known objects (e.g. specimens or observations) rather than non-detections. Designating occurrence data as part of a specific ‘survey’ or ‘collection event’ requires detailed historical records and the effort must be made to obtain them [11]. Conversion from presence-only occurrence data to presence and estimable absence data [56] would be a burden on NHMs, which have other important missions. Yet, this endeavor would expand the value of museum specimens and records for measuring the influence of environmental change.

To increase the future value of contemporary occurrence or specimen data, researchers could organize their sampling efforts to include repeated surveys to estimate detection probabilities. Repeatedly surveying locations during a single collecting trip conflicts with conventional museum collecting methods, which sample as many habitats and locations as possible to maximize diversity of collections. Yet, changing methods to include repeat surveys is necessary if researchers are to infer absence successfully and thus accurately estimate occupancy. If resampling specific transects is not possible, sampling similar habitats within the same locality can facilitate estimation of detectability at a local level.

Historical data represent an underused but valuable source of data that can provide novel insights into how the natural world has changed over human life spans. The rapid pace of human-mediated alteration of the global environment requires that ecologists turn to innovative methods for identifying impacts [8]. By enlarging established baseline data sets to include historical data, researchers can expand both the geographic and the temporal scale of inference on change. Not to do so would forfeit countless opportunities to gain reliable knowledge about biological processes on largely undiscovered time-scales

Acknowledgements

This work was supported by funding from the National Science Foundation (DEB 0640859) and benefited from discussions with members of the Grinnell Resurvey Project. We are grateful for helpful comments from C. Moritz, K. Winker, the Beissinger Lab and three anonymous reviewers on earlier drafts of this article.

References

- Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42
- Root, T.L. *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60
- Shaffer, H.B. *et al.* (1998) The role of natural history collections in documenting species declines. *Trends Ecol. Evol.* 13, 27–30
- Skelly, D.K. *et al.* (2003) Estimating decline and distributional change in amphibians. *Conserv. Biol.* 17, 744–751
- Matthews, P.E. and Heath, A.C. (2008) Evaluating historical evidence for occurrence of mountain goats in Oregon. *Northwest Sci.* 82, 286–298
- Thorne, J.H. *et al.* (2008) Vegetation change over sixty years in the central Sierra Nevada, California. *USA. Madroño* 55, 225–239
- Shoo, L.P. *et al.* (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecol.* 31, 22–29
- Sparks, T. (2007) Lateral thinking on data to identify climate impacts. *Trends Ecol. Evol.* 22, 169–171
- Lütolf, M. *et al.* (2006) The ghost of past species occurrence: improving species distribution models for presence-only data. *J. Appl. Ecol.* 43, 802–815
- Pearce, J.L. and Boyce, M.S. (2006) Modelling distribution and abundance with presence-only data. *J. Appl. Ecol.* 43, 405–412
- Graham, C.H. *et al.* (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends Ecol. Evol.* 19, 497–503
- Zaniewski, A.E. *et al.* (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol. Model.* 157, 261–280
- Parsons, B. *et al.* (2008) Contraction in the range of Malleefowl (*Leipoa ocellata*) in Western Australia: a comparative assessment using presence-only and presence-absence datasets. *Emu* 108, 221–231
- Chefaoui, R.M. and Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecol. Model.* 210, 478–486
- Elith, J. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151
- Brotons, L. *et al.* (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27, 437–448
- MacKenzie, D.I. *et al.* (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207
- MacKenzie, D.I. *et al.* (2006) *Occupancy Estimation and Modeling*. Academic Press
- Kery, M. *et al.* (2006) How biased are estimates of extinction probability in revisitation studies? *J. Ecol.* 94, 980–986
- La Marca, E. *et al.* (2005) Catastrophic population declines and extinctions in neotropical harlequin frogs (Bufonidae: Atelopus). *Biotropica* 37, 190–201
- Newmark, W.D. (1996) Insularization of Tanzanian parks and the local extinction of large mammals. *Conserv. Biol.* 10, 1549–1556
- Britten, H.B. *et al.* (1994) The pending extinction of the Uncompahgre fritillary butterfly. *Conserv. Biol.* 8, 86–94
- Kery, M. (2002) Inferring the absence of a species - A case study of snakes. *J. Wildl. Manage.* 66, 330–338
- Southgate, R. *et al.* (2005) An evaluation of transect, plot and aerial survey techniques to monitor the spatial pattern and status of the bilby (*Macrotis lagotis*) in the Tanami Desert. *Wildl. Res.* 32, 43–52
- Townsend, H. *et al.* (1999) DNA identification of museum specimens of the *Anopheles gambiae* complex: an evaluation of PCR as a tool for resolving the formal taxonomy of sibling species complexes. *Syst. Entomol.* 24, 95–100
- Graham, C.H. *et al.* (2008) The influence of spatial errors in species occurrence data used in distribution models. *J. Appl. Ecol.* 45, 239–247
- Miller, B.P. *et al.* (2007) Record error and range contraction, real and imagined, in the restricted shrub *Banksia hookeriana* in south-western Australia. *Divers. Distrib.* 13, 406–417
- Royle, J.A. and Link, W.A. (2006) Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* 87, 835–841
- Hilden, O. (1981) Sources of error involved in the Finnish line-transect method. *Stud. Avian Biol.* 6, 152–159
- Peterson, A.T. *et al.* (2004) Detecting errors in biodiversity data based on collectors' itineraries. *Bull. Br. Ornithol. Club* 124, 143–151
- Guo, Q.G. *et al.* (2008) Georeferencing locality descriptions and computing associated uncertainty using a probabilistic approach. *Int. J. Geogr. Inf. Sci.* 22, 1067–1090
- Rowe, R.J. (2005) Elevational gradient analyses and the use of historical museum specimens: a cautionary tale. *J. Biogeogr.* 32, 1883–1897
- Primack, R.B. *et al.* (2009) Changes in the flora of Thoreau's Concord. *Biol. Conserv.* 142, 500–508
- Stehlik, I. *et al.* (2007) Floral free fall in the Swiss lowlands: environmental determinants of local plant extinction in a peri-urban landscape. *J. Ecol.* 95, 734–744
- Loo, S.E. *et al.* (2007) Freshwater invasions: using historical data to analyse spread. *Divers. Distrib.* 13, 23–32
- Mack, R.N. *et al.* (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710
- Moritz, C. *et al.* (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322, 261–264
- Strayer, D. and Fetterman, A. (1999) Changes in the distribution of freshwater mussels (Unionidae) in the upper Susquehanna River basin, 1955–1965 to 1996–1997. *Am. Midl. Nat.* 142, 328–339
- McPherson, J.M. *et al.* (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *J. Appl. Ecol.* 41, 811–823
- Allredge, M.W. *et al.* (2007) Factors affecting aural detections of songbirds. *Ecol. Appl.* 17, 948–955
- Bailey, L.L. *et al.* (2004) Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecol. Appl.* 14, 692–702
- MacKenzie, D.I. *et al.* (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255
- Nichols, J.D. *et al.* (2008) Multi-scale occupancy estimation and modelling using multiple detection methods. *J. Appl. Ecol.* 45, 1321–1329
- Burnham, K.P. and Anderson, D.R. (2002) *Model Selection and Multimodel Inference*. Springer-Verlag
- Brown, J.H. *et al.* (1996) The geographic range: Size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* 27, 597–623
- Grinnell, J. (1922) The role of the 'accidental'. *Auk* 39, 373–380
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *Am. Nat.* 132, 652–661
- Doherty, P.F., Jr *et al.* (2003) Local extinction and turnover rates at the edge and interior of species' ranges. *Ann. Zool. Fenn.* 40, 145–153
- Archaux, F. (2004) Breeding upwards when climate is becoming warmer: no bird response in the French Alps. *Ibis* 146, 138–144
- Lenoir, J. *et al.* (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320, 1768–1771

- 51 Wilson, R.J. *et al.* (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* 8, 1138–1146
- 52 Bailey, L.L. *et al.* (2007) Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. *Ecol. Appl.* 17, 281–290
- 53 MacKenzie, D.I. (2009) Getting the biggest bang for our conservation buck. *Trends Ecol. Evol.* 24, 175–177
- 54 Porter, J.H. (2000) Scientific databases. In *Ecological Data: Design, Management and Processing* (Michener, W.K. and Brunt, J.W., eds), pp. 48–69, Blackwell Science
- 55 Canhos, V.P. *et al.* (2004) Global biodiversity informatics: setting the scene for a 'new world' of ecological modeling. *Biodiv. Inform.* 1, 1–13
- 56 Jones, M.B. *et al.* (2006) The new bioinformatics: Integrating ecological data from the gene to the biosphere. *Annu. Rev. Ecol. Syst.* 37, 519–544
- 57 Hill, J.K. *et al.* (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. Lond. B* 269, 2163–2171
- 58 Martin, K. *et al.* (2004) The historic and current distribution of the Vancouver Island White-tailed Ptarmigan (*Lagopus leucurus saxatilis*). *J. Field Ornithol.* 75, 239–256
- 59 Miller-Rushing, A. *et al.* (2006) Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *Am. J. Bot.* 93, 1667–1674
- 60 Danby, R.K. and Hik, D.S. (2007) Evidence of recent treeline dynamics in southwest Yukon from aerial photographs. *Arctic* 60, 411–420
- 61 Suarez, A.V. and Tsutsui, N.D. (2004) The value of museum collections for research and society. *Bioscience* 54, 66–74
- 62 Duncan, R. and Young, J. (2000) Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology* 81, 3048–3061
- 63 Lienert, J. *et al.* (2002) Local extinctions of the wetland specialist *Swertia perennis* L. (Gentianaceae) in Switzerland: A revisitation study based on herbarium records. *Biol. Conserv.* 103, 65–76
- 64 Hanski, I. *et al.* (2007) Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biol. Lett.* 3, 344–347
- 65 Larrucea, E. and Brussard, P. (2008) Shift in location of pygmy rabbit (*Brachylagus idahoensis*) habitat in response to changing environments. *J. Arid Environ.* 72, 1636–1643
- 66 Bradford, D.F. *et al.* (2005) Distributional changes and populations status of amphibians in the Eastern Mojave Desert. *West. N. Am. Nat.* 65, 462–472
- 67 Gibbs, J.P. *et al.* (2005) Changes in frog and, toad populations over 30 years in New York State. *Ecol. Appl.* 15, 1148–1157
- 68 Hossack, B. *et al.* (2005) Lack of significant changes in the herpetofauna of Theodore Roosevelt National Park, North Dakota, since the 1920s. *Am. Midl. Nat.* 154, 423–432
- 69 Azeria, E. *et al.* (2006) Temporal dynamics and nestedness of an oceanic island bird fauna. *Glob. Ecol. Biogeogr.* 15, 328–338
- 70 Foulfopoulos, J. and Mayer, G.C. (2007) Turnover of passerine birds on islands in the Aegean Sea (Greece). *J. Biogeogr.* 34, 1113–1123
- 71 Lima, F.P. *et al.* (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? *Glob. Change Biol.* 13, 2592–2604
- 72 Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.* 90, 68–77
- 73 Franklin, J. *et al.* (2004) Change over 70 years in a southern California chaparral community related to fire history. *J. Veg. Sci.* 15, 701–710
- 74 Lavergne, S. *et al.* (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *J. Biogeogr.* 32, 799–811
- 75 Kelly, A.E. and Goulden, M.L. (2008) Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci. U.S.A.* 105, 11823–11826
- 76 Cornish, A.S. and DiDonato, E.M. (2004) Resurvey of a reef flat in American Samoa after 85 years reveals devastation to a soft coral (Alcyonacea) community. *Mar. Pollut. Bull.* 48, 768–777
- 77 Franco, A.M.A. *et al.* (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Glob. Change Biol.* 12, 1545–1553
- 78 Wilson, D.M. and Bart, J. (1985) Reliability of singing bird surveys – effects of song phenology during the breeding-season. *Condor* 87, 69–73
- 79 Konvicka, M. *et al.* (2003) Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Glob. Ecol. Biogeogr.* 12, 403–410
- 80 Hickling, R. *et al.* (2005) A northward shift of range margins in British Odonata. *Glob. Change Biol.* 11, 502–506
- 81 Davidson, C. *et al.* (2001) Declines of the California red-legged frog: Climate, UV-B, habitat, and pesticides hypotheses. *Ecol. Appl.* 11, 464–479
- 82 Lips, K.R. *et al.* (2004) Amphibian population declines in montane southern Mexico: resurveys of historical localities. *Biol. Conserv.* 119, 555–564
- 83 Ron, S.R. *et al.* (2003) Population decline of the Jambato Toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *J. Herpetol.* 37, 116–126
- 84 Brodman, R. *et al.* (2002) Historical changes of reptiles and amphibians of northwest Indiana fish and wildlife properties. *Am. Midl. Nat.* 147, 135–144
- 85 Winker, K. *et al.* (2002) The birds of St. Matthew Island. *Bering Sea. Wilson Bull.* 114, 491–509
- 86 Brommer, J.E. (2004) The range margins of northern birds shift polewards. *Ann. Zool. Fenn.* 41, 391–397
- 87 Thomas, C.D. and Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature* 399, 213–213
- 88 Myers, P. *et al.* (2009) Climate-induced change in the small mammal communities of the Northern Great Lakes Region. *Glob. Change Biol.* 15, 1434–1454
- 89 Rowe, R. (2007) Legacies of land use and recent climatic change: The small mammal fauna in the mountains of Utah. *Am. Nat.* 170, 242–257