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Estimating species relative abundances from museum records

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Abstract

1. Dated, geo-referenced museum specimens are a rich data source for reconstructing species' distribution and abundance patterns. However, museum records are potentially biased towards over-representation of rare species, and it is unclear whether museum records can be used to estimate relative abundance in the field.
2. We assembled 17 coupled field and museum datasets to quantitatively compare relative abundance estimates with the Dirichlet distribution. Collectively, these datasets comprise 73,039 museum records and 1,405,316 field observations of 2,240 species.
3. Although museum records of rare species overestimated relative abundance by 1-fold to over 100-fold (median study = 9.0), the relative abundance of species estimated from museum occurrence records was strongly correlated with relative abundance estimated from standardized field surveys (r^2 range of 0.10–0.91, median study = 0.43).
4. These analyses provide a justification for estimating species relative abundance with carefully curated museum occurrence records, which may allow for the detection of temporal or spatial shifts in the rank ordering of common and rare species.

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biodiversity, fishes, invertebrates, mammals, museum records, plants, relative abundance

1 | INTRODUCTION

Standardized field surveys provide critical data on rare and endangered species, hotspots of species richness, and the spread of invasive species (Hallmann et al., 2017; Verheyen et al., 2017). Coupling contemporary records with historical archives provides an essential approach for addressing the effects of climate or land-use change on the distribution and abundance of species, and for helping to identify the 'winners' and 'losers' in changing environments (Alfonsi et al., 2017; Hedl et al., 2017; Kelemen & Rehan, 2021; Moritz et al., 2008; Socolar et al., 2017; Tingley & Beissinger, 2009).

However, relevant field data are not always available because field surveys are labour-intensive, technically demanding, and logistically challenging (Lawton et al., 1998). Moreover, field survey data are patchy even for well-studied regions and taxa (Dornelas et al., 2018). This void is partly filled by dated, geo-referenced specimens in museum collections around the world. Data from museum collections have been used successfully to examine changes in species ranges (Farnsworth & Ogurcak, 2006; Loiselle et al., 2008; Pardi et al., 2020), declines (Case et al., 2007; Habel et al., 2019; Mathiasson & Rehan, 2019; Rowe, 2007; Shaffer et al., 1998) and possible extinctions (Gotelli et al., 2012; Jacobson et al., 2018) of endangered species, expanding distributions of invasive species (Bradley et al., 2015), phenological shifts due to climate change (Burkle et al., 2013; Miller-Rushing et al., 2006), and changes in body size and condition of animals over time (Johnson et al., 2003). At the community level, museum collections have been used to estimate regional species richness (Rahbek & Graves, 2001), the frequency of species associations (Lyons et al., 2016), catastrophic species losses in the fossil record (Raup & Sepkoski, 1982), and the evolutionary diversification and spread of novel traits (Holmes et al., 2016).

Quantitative analysis of museum specimen records, however, poses its own set of challenges. There is uneven geographical and temporal coverage of global biodiversity (Daru et al., 2018; Meyer et al., 2016), as well as taxonomic collecting biases (Prather et al., 2004), such as a preference for species that are easy to collect, process, identify and store. Perhaps the most general source of bias is the tendency for species that are rarely encountered in the field to be sought after and therefore over-represented in museum collections relative to their true abundances. This is a specific manifestation of the general 'rarity-seeking syndrome' prevalent in taxonomy and systematics (Kruckeberg & Rabinowitz, 1985).

The degree to which museum collections reflect the natural abundance of species in the wild likely varies by taxon along a spectrum from random standardized sampling to highly selective cherry-picking of prized species. But where do different taxa fall along this spectrum? If there is a strong correlation between the number of museum specimens of a species or higher taxon and its abundance in the field, then museum records may justifiably serve as proxy variables to estimate their relative abundance in nature. To our knowledge, this relationship has not been empirically tested.

We assembled 17 coupled field and museum datasets representing a diverse array of plant and animal assemblages. Datasets range from 100-year-old botanical records from the area around Concord's Walden Pond to recent citizen science surveys of butterflies from North Carolina and museum studies of springtails from Germany. These analyses verify for the first time a strong, general relationship between the abundance of species in field surveys and the number of museum records in all of the test cases.

However, this relationship, by itself, is not useful for quantitative analysis because the units—number of records—are not meaningful for comparisons within or between studies. Instead, the raw counts of field or museum records need to be converted to measures of relative abundance, which can be meaningfully compared. To address this issue, we employed a novel application of the Dirichlet distribution to estimate the relative abundance of each species in both the historical and contemporary collections. The Dirichlet distribution is often used as a prior distribution in Bayesian analysis, and is appropriate for multinomial data, such as integer counts of individuals classified into species or other taxonomic groups.

When comparable field and museum data are available, the Dirichlet distribution can be used to construct a realistic calibration curve (Figure 1) so that estimates of relative abundance from museum records can be converted to approximate estimates that would have been obtained from field samples. We call this procedure of estimation and validation by the acronym FAMA (field abundance–museum abundance).

2 | MATERIALS AND METHODS

2.1 | Field and museum collections

Authors of this paper provided curated datasets of dated, geo-referenced museum specimens and coupled field survey data based on standardized sampling methods appropriate for each taxon. Investigators curated their coupled datasets by removing redundant observations (such as multiple series of ant workers collected from the same nest), addressing synonyms and changes in taxonomy and nomenclature, and, when possible, making sure both the field and museum collections covered comparable time intervals and spatial domains. The final analysis included 17 high-quality plant and animal datasets (Figures 2–4), encompassing vertebrates (small mammals, freshwater fishes, and forest amphibians), invertebrates (ants, bees,

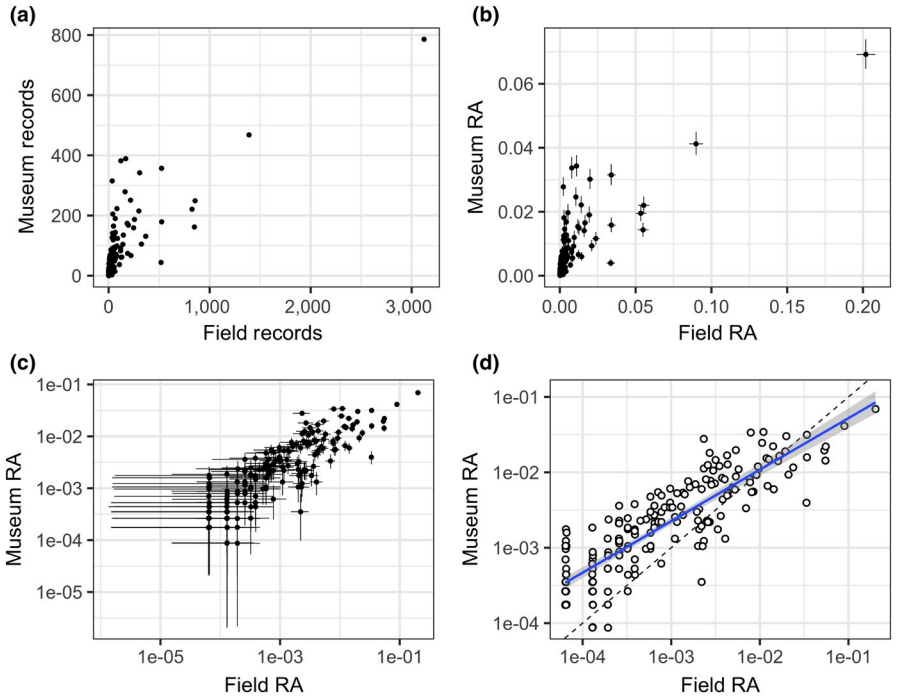

FIGURE 1 Data transformations in FAMA analysis, illustrated with Florida ant data. Each point is a different species ($n = 192$). (a) Raw counts of field occurrences (*x*-axis) and museum records (*y*-axis). (b) Dirichlet transformation of raw counts to relative abundances (RA) for field and museum records. Vertical lines are the asymmetric 95% confidence intervals for the Dirichlet estimate of RA in museum records. (c) Double log-10 transformation of *x*- and *y*-axes, with vertical and horizontal lines depicting 95% confidence intervals for field and museum RA estimates. (d) Ordinary least-squares regression line fitted to relative abundance estimates (blue line) with 95% confidence interval (grey polygon). The dashed line indicates the expected regression line (intercept = 0.0, slope = 1.0) if there is no bias in estimation of RA from museum records compared to field records

butterflies, and springtails) and plants (trees, shrubs, and herbs). The Supporting Information contains meta-data (Table S.1), sampling details and collection information for all datasets.

2.2 | Independence of field samples and museum collections

Kelling et al. (2019) describe the range of citizen science data that are currently being collected and classify them as 'unstructured', 'semi-structured', and 'structured', depending on the goals of the study and how much primary information is collected. Because our analyses are restricted to both field and museum records that are geo-referenced and dated, they all constitute 'structured' and 'semi-structured' datasets in the system of Kelling et al. (2019). It is important to stress that our analyses have treated museum and field collections ideally as independently derived sources of data, and have used the field collections as estimators of the 'true' relative abundance against which museum data are compared over temporal and spatial domains which are as similar as possible. The Trinidad & Tobago fishes and Massachusetts tree datasets clearly conform to these interpretations because the modern field surveys were completely independent of the museum records. At the other extreme, the small mammal surveys represent historical collections in which the field data are the recorded notes of all mammals that were trapped by a single group of collectors, and the museum records consist of the subset of these trapped mammals that were prepared and deposited as museum specimens. The field and museum mammal records are thus completely non-independent, although they usefully isolate the effect of collector decisions on which material to deposit in a museum. In between these extremes, there are varying degrees of independence of the different datasets. Often the field data consist of subsets of museum records that are the products of standardized sampling surveys by one or a small number of collectors, whereas the museum dataset may be a more heterogeneous summation of smaller collections by individual investigators (see Supporting Information for details on each dataset). Without a detailed knowledge of the nature of the individual collections, naive compilations and analyses of museum records may be distorted by such issues.

For example, for the Connecticut amphibian data, we first compared Mark Urban's field samples from the Yale-Myers Research Forest with historical museum specimen records from the region surrounding the study site. These historical museum specimen records were deposited by different investigators and represent opportunistic collecting. This was one of the few FAMA comparisons in which relative abundances of untransformed specimen counts were not significantly correlated ($r^2 = 0.10$, $p = 0.34$). However, these records initially excluded many of the total specimen records for amphibians in the Yale Peabody Museum from standardized field collections that

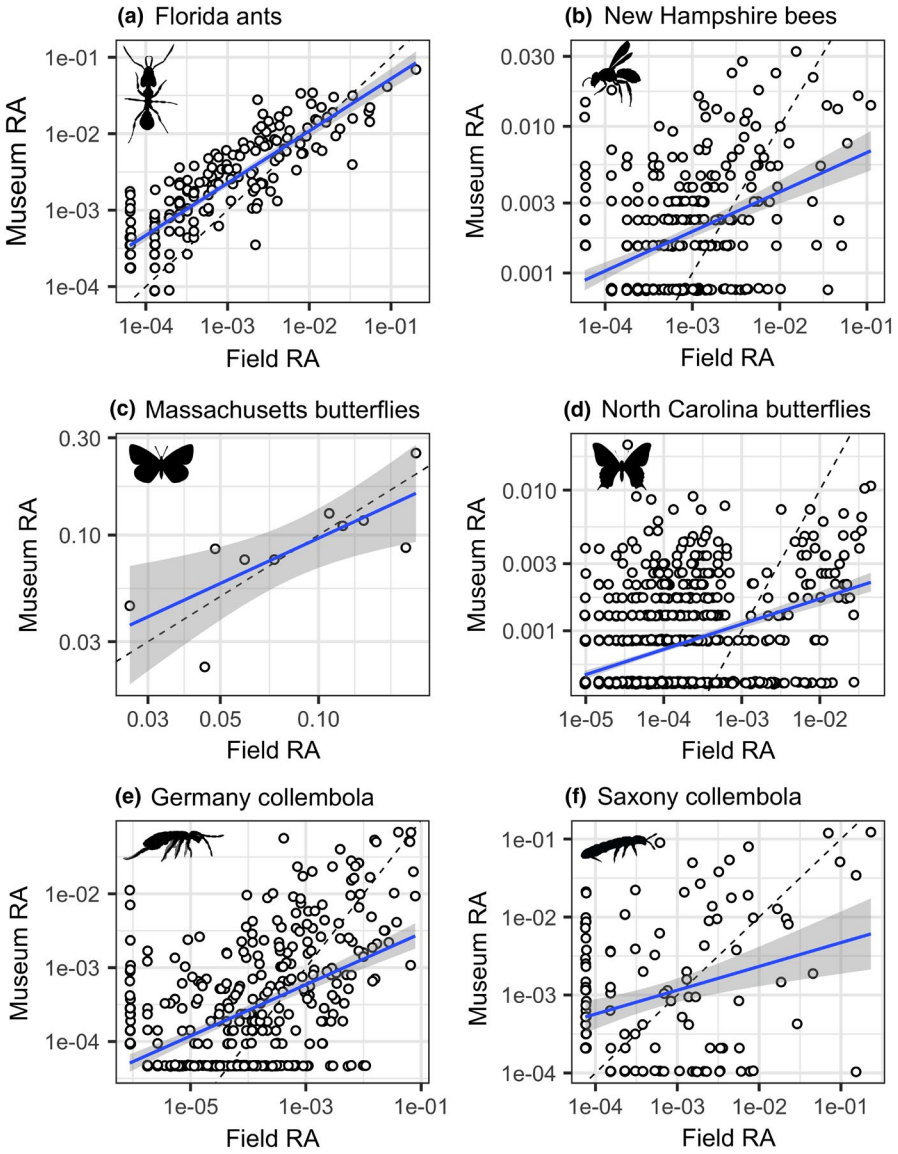

FIGURE 2 (a–f) FAMA analysis for six coupled invertebrate datasets of field and museum Records. Details as in Figure 1d. Regression statistics in Table 1

were deposited by Dave Skelly and others using similar field methods. When the total amphibian records of the Yale Peabody museum are used (i.e. the standardized collections and opportunistic records), the FAMA comparison is more typical of the other datasets we analysed ($r^2 = 0.48$, $p = 0.018$), despite the small number of species ($n = 11$). Although historical collectors under-collected common species, museum collectors for many taxa are now more likely to use standardized methods and deposit entire collections. Thus, the distinction between field and museum records may become less important for recently deposited material, which could cause problems for comparisons of recent versus older museum records.

2.3 | Estimating relative abundance

For each study, the data structure is a matrix in which each row is a species, and the two columns are for the field records and museum records. The entries are the abundance (or count of incidences for presence–absence field data recorded from multiple sub-plots) of each species in the two collections. We first calculated a simple correlation between the counts of field and museum records within each study. These data were untransformed, so they include zeros for species that were represented in field records but not museum records or vice versa.

Next, we estimated the relative frequency of each species in the field and museum collections by fitting the Dirichlet distribution to the underlying count data. At large sample sizes, the Dirichlet estimate converges on the familiar frequentist estimate $p_i = n_i/N$, where p_i is the relative frequency of species i, n_i is the number of specimens counted for species i (in either the field or the museum collection) and N is the total number of specimens counted (in either the field or the museum collection). For rare species, the Dirichlet estimate of relative abundance is slightly smaller than n_i/N, which compensates for the fact that the frequentist calculation overestimates the true relative abundance of rare species when sampling is incomplete (Chao et al., 2015).

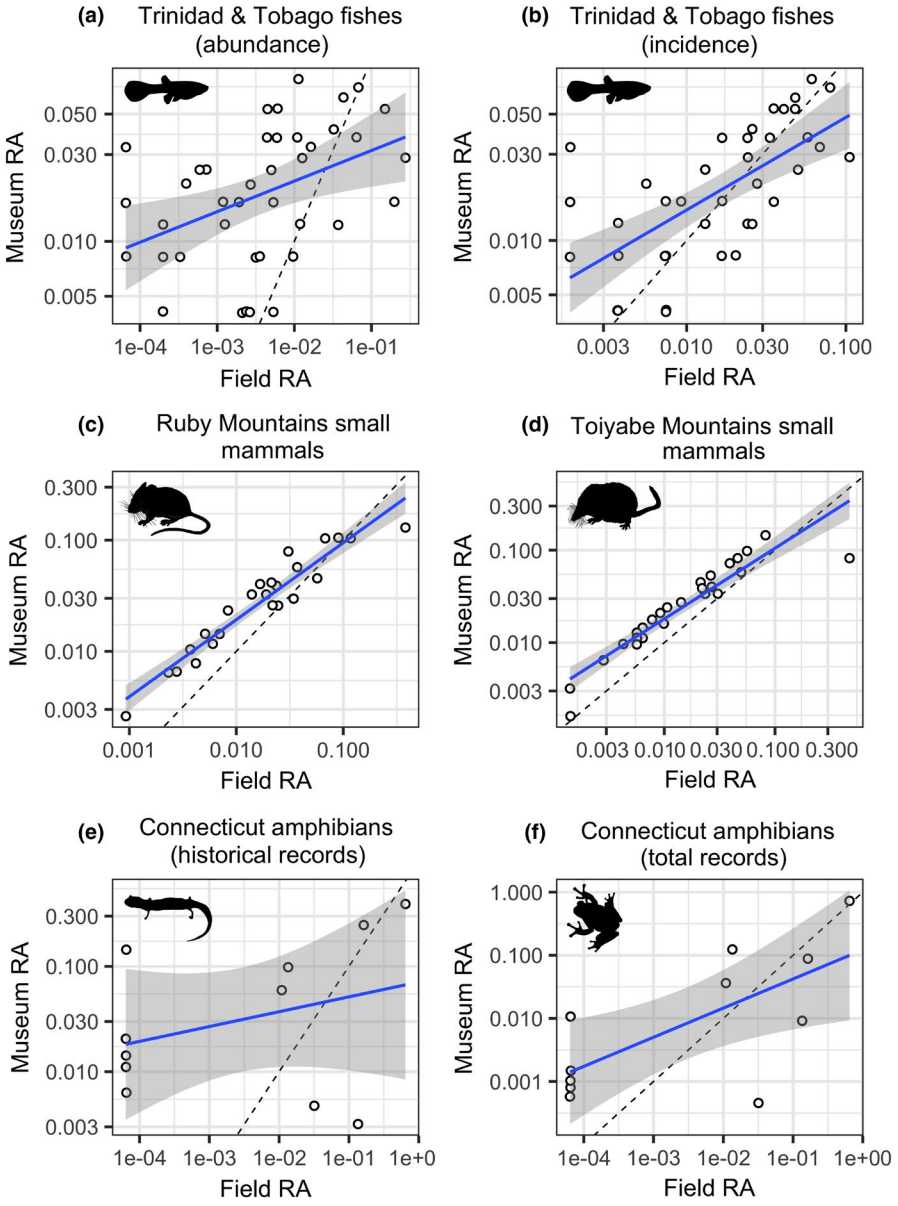

FIGURE 3 (a–f). FAMA analysis for six coupled vertebrate datasets of field and museum records. Details as in Figure 1d. Regression statistics in Table 1

The Dirichlet distribution also sensibly handle zeroes—cases in which a species was either not recorded in the local field sample or not found in the collection of museum records. For these cases, the Dirichlet estimate is a small positive value of p_i that is close to zero, whereas the frequentist estimate p_i/N yields precisely 0.0, which is not strictly true. Finally, the Dirichlet distribution incorporates uncertainty due to both total sample size and the commonness or rarity of individual species. For each species, it generates positive asymmetric confidence intervals for relative abundance (see Supporting Information for more details, and Tables S.1 and S.2 for comparisons with frequentist estimates).

We assumed the union of the species lists for the museum and field collections represents the common source pool of species that could be represented in either field or museum. However, we applied the Dirichlet distribution separately to the counts of the museum and field records. This distribution treats the counts in each collection (museum or field) as a random sample from the pooled list of species present in the coupled dataset. In theory, the source pool could be broadened by adding species from regional checklists. If an added species was absent from both museum and field datasets, then double zeroes would be entered into the matrix (which would have little effect on the overall outcome). A similar approach is used in occupancy modelling to construct an augmented species occurrence matrix that includes rows for species that were not represented in any of the samples (e.g. Dorazio et al., 2011).

In our formulation, the Dirichlet distribution ensures that all species—whether found in field samples, museum collections or both—have an estimated probability of occurrence that is greater than zero. However, for species that were represented by zero specimens, the estimated occurrence probability is very small, and becomes even smaller as the total sample size increases. For each vector of abundance, we used the *rdirichlet* function in the *gtools* library (Warnes et al., 2020) of R (R Core Team, 2020) to simulate 10,000 relative abundance vectors, from which we calculated the

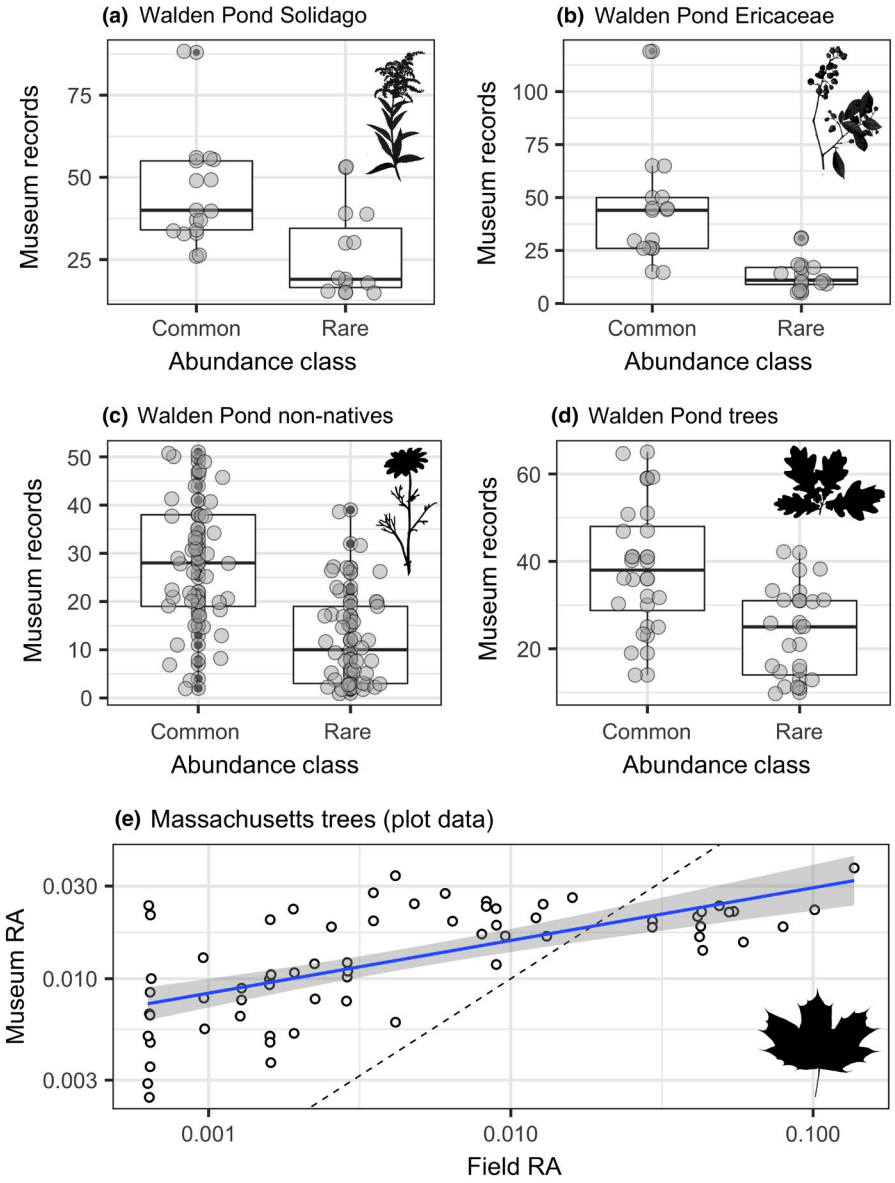

FIGURE 4 FAMA analysis for five coupled plant datasets of field and museum records. (a–d) Box plots of historical plant survey data from Walden Pond. Each point is a species, and the *y*-axis is the number of museum records. The groups 'Common' and 'Rare' are qualitative estimates of field abundance for each species from Eaton (1974). (e) Plot-level quantitative surveys for Massachusetts trees; details as in Figure 1d. Regression and ANOVA statistics in Table 1

mean and empirical 95% confidence interval for the relative abundance of each species. The raw data and scripts for reproducing all of the statistics and graphics in this paper and in the supplement can be downloaded from https://doi.org/10.5281/zenodo.5177166.

2.4 | Correlating relative abundance in museum records and field collections

Next, we created a scatterplot with the estimated relative abundance of each species in the museum records on the *y*-axis (the response variable), and the estimated relative abundance of the same species in the field surveys on the *x*-axis (the predictor variable). For all data, the linearity of the relationship was considerably improved with a log10–log10 transformation, which also reduced the influence of a small number of very abundant species in each dataset. Because both the *x*- and *y*-variables are strictly bounded between 0.0 and 1.0, we did not need to use a logistic or beta regression, but instead used an ordinary least-squares linear regression to estimate the significance of the linear slope and the proportion of variance explained (r^2). Figure 1 illustrates the raw data, Dirichlet estimates of relative abundance, and fitted slopes for the Florida ant dataset.

For the four 'Walden Pond' datasets from Walden Pond and surrounding areas of Concord, Massachusetts, USA (trees, goldenrods, Ericaceous shrubs, and non-native species) quantitative field data were not available. However, the experienced botanist Richard Eaton provided qualitative assessments of the abundance of each species based on four decades of fieldwork in Concord, Massachusetts from the 1920s to the 1960s (Eaton, 1974). For these datasets, we used a binary classification of Eaton's descriptions and abundance categories into 'common' and 'rare' (see Supporting Information for details). We then used a one-way analysis of variance to test for differences in the average number of museum records per species in the two groups. We also partitioned the variance that could be attributed to the two groups for comparison with the r^2 values from the regression analyses of other datasets with quantitative field data.

TABLE 1 FAMA regression statistics for 17 coupled datasets of field surveys and museum specimen occurrence records

Dataset	Major taxonomic group	S	Nested data structure	Museum records	Field observations	$r^2_{\text{raw counts}}$	$r^2_{\text{rel. abun}^*}$	Slope	Bias	Cut-point	Common species bias	Rare species bias
Florida ants	Invertebrates	192	Partial	13,109	15,281	0.60***	0.74***	0.68	0.32***	0.013	2.9	5.5
New Hampshire bees	Invertebrates	350	No	949	16,535	0.12***	0.20***	0.27	0.73***	0.0024	8.0	39
Massachusetts Butterflies	Invertebrates	10	No	703	4,389	0.59**	0.58**	0.74	0.26 (NS)	0.087	0.79	1.7
North Carolina Butterflies	Invertebrates	942	No	1,393	218,056	0.15***	0.19***	0.18	0.82***	0.0011	4.2	44
Germany Collembola	Invertebrates	427	No	20,903	1,113,802	0.31***	0.29***	0.35	0.65***	0.00044	8.5	266
Saxony Collembola	Invertebrates	129	No	9,394	12,966	0.30***	0.10***	0.31	0.69***	0.0012	1.9	17
Trinidad & Tobago Fishes (abundance)	Vertebrates	40	No	203	15,103	0.05 (NS)	0.18**	0.17	0.83***	0.025	9.5	124
Trinidad & Tobago Fishes (incidence)	Vertebrates	40	No	203	500	0.44***	0.44***	0.51	0.49***	0.022	3.7	9
Ruby Mts. Small Mammals	Vertebrates	25	Yes	745	2,131	0.59***	0.91***	0.69	0.31***	0.085	2.9	2.8
Toiyabe Mts. Small Mammals	Vertebrates	29	Yes	593	1,383	0.23**	0.87***	0.76	0.24***	0.12	5.7	2.3
Connecticut Amphibians (Historical Records)	Vertebrates	11	No	1,375	15,571	0.71**	0.34 (NS)	0.14	0.86***	0.046	1.6	173
Connecticut Amphibians (Total Records)	Vertebrates	11	No	19,647	15,571	0.91***	0.48*	0.46	0.54**	0.02	0.89	13
Walden Pond *Solidago*	Plants	16	No	607	NA	NA	0.27*	NA	NA	NA	NA	NA
Walden Pond Ericaceae	Plants	18	No	541	NA	NA	0.34**	NA	NA	NA	NA	NA
Walden Pond Non-Native Herbs	Plants	82	No	1,630	NA	NA	0.29*	NA	NA	NA	NA	NA
Walden Pond Trees	Plants	32	No	1,001	NA	NA	0.26**	NA	NA	NA	NA	NA
Massachusetts Trees	Plants	66	No	11,015	3,065	0.24***	0.42***	0.27	0.73***	0.02	7.46	3.68

Note: Sampling methods for each study are given in the Supporting Information. S = total number of species recorded (union of field and museum datasets); Museum records = total number of specimens from the museum collection; Field observations = total number of specimens or observations from the field collection. Nested Data Structure indicates whether or not the museum specimens are a nested subset of the field data. The sample size for the regression models is S. $r^2_{\text{raw counts}}$ is the % variation explained in a linear regression model of the counts for each species of museum records (y) versus field occurrences or abundances (x). $r^2_{\text{rel. abun}^*}$ is the % variation explained after the raw counts were converted to relative abundances with the Dirichlet distribution and both axes were $\log_{10}$ transformed (see Figure 1). For the four Walden Pond datasets from Concord, the reported r^2 is the percent variation explained in an analysis of variance model in which the number of specimen records for each species was classified as 'common' or 'rare' in field estimates. For these datasets, the regression analyses could not be used, so most of the other statistical tests were not applicable (NA). 'Slope' is the linear regression slope b, and 'Bias' = 1 − b. The significance test for Bias is against the null hypothesis that the observed slope = 1.0 (no bias). Cut-point is the estimated relative abundance in the field for which the observed regression slope intersects with the theoretical regression line with a slope of 1.0 and an intercept of 0.0 (no bias). The Common Species Bias is the ratio of Relative Abundance in Field Survey/Relative Abundance in Museum Collection for the most common species in the coupled dataset. The Rare Species Bias is the ratio of the Relative Abundance in Museum Collection/Relative Abundance in Field Survey for the most rare species in the coupled dataset. For the statistical tests, NS = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

2.5 | Bias estimation

For comparison, we also tested the observed slope (b) against the expected slope of 1.0, which would be found if the field and museum records provided identical estimates of relative abundance for each species. We used the metric ($1 - b$) a simple measure of bias that ranges between 0 (no bias) and 1 (complete bias). If there is no bias, $b = 1.0$ because the field and museum records, on average, have the same relative abundances. The most extreme bias occurs when $b = 0$ (bias = 1.0). In this case, the museum data would have maximum evenness, where species, on average, are equally represented with a relative abundance of $1/S$. We calculated the intersection of the theoretical and observed slopes as the cut-point for relative abundance. Below the cut-point, the relative frequencies of species in the field are overestimated by museum records. Above the cut-point, the relative frequencies of species in the field are underestimated by museum records.

3 | RESULTS

For 16 of the 17 datasets, the correlation between raw counts of museum records and raw counts of field records was highly significant (Table 1). The exception was Trinidad & Tobago fishes (abundance-based; $r^2 = 0.05$, $p = 0.16$, $n = 40$ species). The correlation between field and museum estimates of relative abundance from the Dirichlet distribution was also highly significant for 16 of the 17 datasets (Figures 2–4). The exception was Connecticut amphibians (historical records; $r^2 = 0.34$, $p = 0.10$, $n = 11$ species). The r^2 values for log–log-transformed proportions ranged from 0.18 (Trinidad & Tobago fishes—abundance-based) to 0.91 (Ruby Range, small mammals). Even for the four historical Walden pond plant datasets, which do not have quantitative abundance estimates (Figure 3b,f), a substantial fraction of variation in the number of museum records per species was explained by the simple field categorization of each species as 'common' or 'rare' ($r^2 = 0.26$–0.34).

However, for all datasets except Massachusetts butterflies, the slope of the relationship between field and museum relative abundance was significantly less than the predicted slope of 1.0 (Table 1). These shallow slopes indicate systematic bias in estimates of relative abundance. Compared to field surveys, museum collections consistently overestimated the relative abundance of rare species and underestimated the relative abundance of common species. The cut-point between over- and under-estimation ranged from a relative abundance of 0.00044 (Germany springtails) to 0.12 (Toiyabe Range small mammals). Below the cut-point, relative abundance of the more rare species was overestimated in museum collections. Above the cut-point, the relative abundance of the more common species was underestimated in museum collections.

For the rarest species in each of the 13 quantitative studies, museum collections consistently overestimated relative abundance compared to field collections. The smallest bias (ratio of museum relative abundance/field relative abundance) was 1.7 (Massachusetts butterflies), but 3 of the 13 datasets had rare species biases greater than 100-fold: Germany springtails (266), Connecticut amphibians (173; historical records) and Trinidad & Tobago fishes (124; abundance-based). For example, with the Germany springtails dataset, the rarest species are over-represented in museum collections by 266 times their abundance in the field. Across all studies, the median over-estimation of the rarest species in museum collections was 7.1-fold (mean = 76.7).

For 11 of the 13 studies, the most common species had a higher relative abundance in field collections than in museum collections, and ranged from a ratio (field relative abundance/museum relative abundance) of 1.6 (Connecticut amphibians—historical records) to 9.5 (Trinidad & Tobago fishes—abundance-based). For the remaining 2 of the 13 studies (Massachusetts butterflies, Connecticut amphibians—total records), relative abundance of the most abundant species was greater in museum records than in field collections. Among all studies, the median field/museum relative abundance ratio of the most common species was 3.67 (mean = 4.2).

4 | DISCUSSION

Two major patterns emerged from these analyses. First, the relative abundances of species measured in coupled field surveys and museum collections were consistently correlated (Table 1): species that are well represented in museum collections are abundant in the field, and species that are sparsely represented in museum collections are rare in the field. These results suggest qualitative patterns of relative commonness and rarity can be judiciously estimated from museum specimens for many taxa and sampling methods (Figures 2–4), even when no independent field data are available for quantitative calibration.

Second, quantitative estimates of relative abundance from museum specimens were nevertheless predictably biased. Compared to standardized field surveys, the relative abundance of rare species in museum collections was consistently overestimated by 1-fold to over 100-fold, and the relative abundance of common species was underestimated by 1-fold to 10-fold. These distortions mean that museum data should not be used to fit parametric species abundance distributions such as the log-normal or the log-series (McGill et al., 2007). Museum data may also not be useful for the estimation of the number of 'missing' or undetected species (Chao et al., 2014) because this estimate is very sensitive to the absolute number of individuals of rare species (but see Jones et al., 2019).

Although there was a consistent signal of association between field and museum estimates of relative abundance, there was also a substantial amount of unexplained variation within each study, and differences between studies in the strength of the correlations and their slopes (Table 1). What factors might contribute to such differences? It is instructive to consider some of the individual datasets which provide insight into particular mechanisms that are important.

4.1 | Effects of collector bias

The 'rarity-seeking' syndrome should be most extreme for large-bodied organisms (especially birds and mammals), which are expensive and time-consuming to capture and prepare, and require substantial space and resources in museums (see Section 4.5 below). But in many other taxa, investigators will also preferentially collect and deposit specimens of rare versus common species. The effect can be isolated most clearly in the small mammal datasets assembled by Rebecca Rowe from the Toiyabe and Ruby mountain ranges in Nevada USA. These are historical collections from mammalogists that were made near the turn of the century. The 'field' collections in this case represent data from their field notebooks, in which the investigators counted and recorded the identity of every individual trapped, even those they did not preserve as voucher specimens. The 'museum' collections represent the subsample of those captures that were prepared and deposited in the Museum of Natural History, University of Kansas (Ruby Mountains), and the Museum of Vertebrate Zoology, University of California at Berkeley (Toiyabe Range). Thus, the bias in these coupled datasets reflects only the decisions of the individual investigators about which species and specimens to prepare and deposit. This bias (Ruby Range = 0.31; Toiyabe Range = 0.24) is actually among the lowest in these datasets (minimum bias = 0.0, which occurs when museum and field collections yield identical estimates of relative abundance). However, it reflects the strength of the collector rarity effect from only a single group of investigators. This bias will be greatly magnified in accumulated museum collections as each individual investigator deposits rare species (which will likely differ between collections) and avoids common species (which are likely the same in all collections).

In contrast, the Connecticut amphibian dataset (historical records) has a high bias of 0.86, and is based on the comparisons of Mark Urban's long-term field collections with historical records of museum specimens in the Yale-Myers Research Forest deposited by a variety of different collectors (a maximum bias of 1.0 would indicate that all species in the museum collection have equal abundances). Other datasets exhibiting high bias include the abundance data of Trinidad & Tobago fishes (bias = 0.83), and citizen science collections of North Carolina butterflies (bias = 0.82).

4.2 | Abundance versus occupancy sampling

Another factor that can influence the relationship between museum and field records is the sampling method. Of course, individual sampling methods for particular taxa all incorporate biases that favour some species over others. However, a more general distinction in field sampling is between individual-based assessment and sample-based assessment (Gotelli & Colwell, 2001). In individual-based assessment, an investigator collects and identifies a number of randomly chosen individuals to estimate their relative abundances. Our use of the Dirichlet distribution specifically treats the individual records in field (and museum) collections this way. In sample-based assessment, the presence of each species in individual sampling units (pitfall traps, seines, plots) is recorded. The underlying abundances are not used, and instead the incidence of each species is tabulated as the number of sampling units within which it is present (Gotelli & Chao, 2013).

For the Trinidad & Tobago fishes study, we were able to treat the field data as individual- or sample- based. This was possible because the collector, Dr. Dawn Phillip (Phillip, 1998), used standardized survey methods to collect, count, and identify all the individuals at 78 different sampling sites (see Supporting Information for details). We used the pooled abundance records for an analysis of individual-based assessment, and we used the species incidences at the 78 sites for an analysis of sample-based assessment.

The sample-based assessment data fit the museum records much better than did the individual-based assessment data, with less bias (slope bias = 0.49 vs. 0.83) and more precision (r^2 = 0.44 vs. 0.18). The greatest distortions were found for the most common species. For example, the most abundant species in the field collection was *Poecilia reticulata*, which was represented by 4,165 individuals at 56 sites, but only represented by 6 museum specimen records. In contrast, the most abundant species in the museum collection was *Roeboides dientonito* (*R.s dayi*), represented by 14 records. In the field, 655 specimens of *R. dientonito* were collected at 25 sites. Because the sample-based assessment considers only the incidence of a species across a set of samples, it is less subject to distortions from very high local abundances of common species and measurement error from counting individuals.

4.3 | Spatial extent of sampling

Ideally, the spatial extent of the samples should be the same for the museum and field collections. However, these conditions are rarely met, particularly when the field samples are taken from a single location within a larger area encompassed by the museum records. On the one hand, smaller spatial extents will lead to less habitat heterogeneity, and smaller temporal extents will lead to less variability in abiotic conditions. On the other hand, smaller spatial and temporal extents will inevitably reduce the abundance and species numbers available for comparison. All else being equal, space- or time-averaged samples should better capture general trends because they are less vulnerable to inter-annual fluctuations in abundance and site- or collector-specific idiosyncracies (Rowe, 2007; Shaffer et al., 1998). However, it is hard to predict for any particular dataset what net effect, if any, spatial scale will have on comparisons of museum and field collections.

For the springtail data, we were able to compare two field and museum datasets at different spatial scales, one for Germany (n = 427 species) and one for a subset of the data from the state of Saxony, Germany (n = 129 species), both sampled over the same time period. The slope of the relationship between museum and field specimens was comparable (Germany slope = 0.35, Saxony slope = 0.31), but the precision was higher for the larger-scale Germany data (r^2 = 0.29)

than for the smaller-scale Saxony data ($r^2 = 0.10$). Additional comparisons of this sort will be necessary to determine whether there are consistent effects of spatial and temporal scale on the relationship between museum and field records.

4.4 | Species declines and the temporal extent of sampling

Just as the spatial extent of museum and field collections should be similar, both datasets should ideally cover the same time period of collecting. However, it is often the case that museum collections will contain much older material than is available for comparison with recent field sampling. In these cases, there is the possibility of a mismatch because species that were formerly common have declined in abundance in recent decades. For example, in the New Hampshire bees dataset, previous analyses of museum records have documented local extinction of wild bees (e.g. *Bombus affinis*, Jacobson et al., 2018) as well as dramatic species declines (e.g. *Halictus rubicundus* and *Lasioglossum imitatum*, Mathiasson & Rehan, 2019). In these cases, the prevalence of such species in older museum collections cannot be easily attributed to a rarity effect or other collecting biases (see Section 4.5 in the Discussion). Thus, the correlation between museum and field records may be tighter than the empirical data suggest (Figures 2–4), which further supports the use of museum collections as an invaluable resource for species status assessments and long-term biodiversity conservation (Suarez & Tsutsui, 2004).

The cut-point analysis of the regression models also can provide some insights into temporal trends of species. For the species-rich assemblages (≥40 species), the largest cut-point frequency observed was 0.022 (Table 1; Trinidad & Tobago fishes [incidence]). Thus, the relative abundance of species in museum collections that comprise less than ~3% of the records are usually overestimated. Resurvey studies that do not find these species should be cautious about inferring extinction because these species were probably historically more rare than museum collections suggest.

4.5 | Caveats

We successfully applied FAMA to several plant and animal datasets (Figures 2–4), including four vertebrate datasets for small mammals, freshwater fishes, and forest amphibians. However, birds and large-bodied mammals were deliberately excluded from our analyses because we could not find comparable datasets, and because museum collections of those groups may not be well correlated with field abundances for the following reasons:

1. *Capturability*. Birds, mammals, reptiles, amphibians and fishes that can be easily netted, seined, trapped, or poisoned are often over-represented in museum collections (Krumholz, 1948; McDiarmid et al., 2012; Remsen and Good, 1996), whereas wary or secretive species that can only be obtained with highly specialized or labour-intensive collecting techniques are typically under-represented.
2. *Size*. Acquisition patterns of vertebrate specimens in museum collections are partially driven by cost considerations. Specimen preparation and storage costs are proportional to specimen size. Because most museum specimens are catalogued for posterity, storage costs are perpetual. This governs the number and size of specimens that are accessioned and catalogued. For example, even the world's most capacious mammal collection (National Museum of Natural History, Smithsonian Institution, USA) has limits on the number of baleen whales that can be stored.
3. *Field identification*. Vertebrate species that can be readily identified in the field are more likely to be cherry-picked or culled prior to preparation and cataloguing in museum collections.
4. *Sex bias*. Males of sexually dimorphic species are catalogued more frequently in collections than females (Cooper et al., 2019). This reflects a tendency of collectors to choose larger, brighter specimens with exaggerated secondary sexual characteristics.
5. *Rarity*. Specimens of rare and uncommon species are more likely to be disproportionately preserved in museum collections than common species (Kruckeberg & Rabinowitz, 1985).
6. *Regulatory licenses*. Virtually all scientific collecting of birds, mammals, reptiles, amphibians, and fishes conducted in North America for the past 30 years has been licensed by state and federal agencies that place strict limits on the number of specimens of each species that can be collected regardless of local species abundance. For example, restrictions on bird collecting in the United States date to the passage of the Migratory Bird Treaty Act of 1918 (https://www.fws.gov/laws/lawsdigest/migtrea.html). Species-specific limits are often negotiated in advance of field collecting with permitting agencies, which exercise the ultimate control on the number of specimens deposited in museums (Finley, 1988; McKnight, 1980). To a lesser extent, these issues can potentially affect comparison of field and museum collections for any taxon, but the constraints are especially severe for birds and large mammals.

5 | CONCLUSIONS

In spite of these complexities, the overall results suggest the FAMA relationship is generally robust: species that are common in museum collections are relatively abundant in the field, and species that are sparsely represented in museum collections are relatively rare in the field. This relationship can be used to estimate relative abundance for many taxa, although birds and large mammals may remain an important exception. The use of museum records to estimate relative abundance can be greatly improved if a comparable field calibration dataset can be used as we have done here (Figure 1). Inferences will also be strengthened if the museum records are carefully curated to restrict the spatial and temporal domain, eliminate pseudo-replication and possibly

control for the collection method if that information is available. In general, close collaborations between ecologists and museum specialists are likely to yield the most reliable results (Gotelli, 2004), whereas naive analyses of museum records, citizen science data, or other online biodiversity datasets can generate potentially serious distortions. With careful pre-screening of the data, it should be possible to use museum records to compare the relative abundance of the same species at different places or different times.

Although our analyses do provide a powerful proof-of-concept, they do not lend themselves to any simple rules for sample size or spatial and temporal domains. Importantly, they do not provide a carte blanche for all kinds of analyses of museum records. Indeed, our analyses are restricted to the estimation of species relative abundance, which is a community-level pattern. For example, Booher et al. (in prep) successfully used the Florida ant data to document important shifts in the relative abundance and rank of 126 native species and 51 introduced species across 60 years. In contrast, our methods and results cannot be used to justify the more common use of museum specimens to estimate processes at the population level, such as changes in phenology or trends in population density, which have sometimes proven controversial (e.g. Ascher et al., 2020; Fric et al., 2020, 2021; Larsen & Shirey, 2021; Soroye et al., 2020).

Our results are timely for several reasons. First, digitized specimen records are widely becoming available from museums (Heberling et al., 2021; Johnson et al., 2011), greatly increasing the opportunities for FAMA analysis. Second, extensive field surveys, often based in part or entirely on citizen science data, are becoming more widely available (Johnston et al., 2018; Silvertown, 2009). Examples from our own analyses include the citizen science datasets for New Hampshire bees, Germany and Saxony springtails, and North Carolina butterflies. Some of these groups are sparsely represented in museum collections, but our FAMA analyses suggest that relative abundances can still be extracted from these records for analyses of communities from the past and for comparisons with contemporary collections. At the same time that citizen science data are becoming more popular, we lamentably note that financial resources and institutional and societal support for natural history collections continue to decline (Johnson et al., 2011; Tewksbury et al., 2014). As plant and animal abundance is increasingly altered by human activities and climate change, FAMA analyses of museum records may provide the only baseline for quantitative estimates of species relative abundances in past decades.

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CONFLICT OF INTEREST

None of the authors has a conflict of interest associated with this publication.

AUTHORS' CONTRIBUTIONS

N.J.G. and D.B.B. conceived of the study during an analysis of the Florida ants dataset; N.J.G. developed the methods and analysed the data; Dataset curation and contributions: ants (D.B.B., C.S.M., A.V.S.), bees (S.M.R.), Massachusetts butterflies (R.B.P.), North Carolina butterflies (G.N.), collembola (U.B., C.F., D.J.R. and W.U.), fishes (F.A.M.J., A.E.M.), small mammals (R.J.R.), amphibians (N.R., D.K.S. and M.C.U.) and plants (R.B.P., M.R.). The first draft of the manuscript was written by N.J.G., R.B.P. and G.R.G. All authors contributed equally to editing and revisions of the text.

DATA AVAILABILITY STATEMENT

R scripts and data files for reproducing all of the statistics and graphics in this paper are available at https://doi.org/10.5281/zenodo.5177166 (Gotelli et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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