



Extinction rate of discovered and undiscovered plants in Singapore

Nadiah P. Kristensen ¹, Wei Wei Seah,² Kwek Yan Chong,¹ Yi Shuen Yeoh,³ Tak Fung,¹ Laura M. Berman ⁴, Hui Zhen Tan,¹ and Ryan A. Chisholm^{1*}

¹Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, Singapore, 117558, Singapore

²Singapore Botanic Gardens, Herbarium Singapore, 1 Cluny Road, Singapore, 259569, Singapore

³National Parks Board, Horticulture and Community Gardening Division, 1 Cluny Road, Singapore, 259569, Singapore

⁴Division of Science, Yale-NUS College, 16 College Avenue West, Singapore, 138527, Singapore

Abstract: Extinction is a key issue in the assessment of global biodiversity. However, many extinction rate measures do not account for species that went extinct before they could be discovered. The highly developed island city-state of Singapore has one of the best-documented tropical floras in the world. This allowed us to estimate the total rate of floristic extinctions in Singapore since 1822 after accounting for sampling effort and crypto extinctions by collating herbaria records. Our database comprised 34,224 specimens from 2076 native species, of which 464 species (22%) were considered nationally extinct. We assumed that undiscovered species had the same annual per-species extinction rates as discovered species and that no undiscovered species remained extant. With classical and Bayesian algorithms, we estimated that 304 (95% confidence interval, 213–414) and 412 (95% credible interval, 313–534) additional species went extinct before they could be discovered, respectively; corresponding total extinction rate estimates were 32% and 35% (range 30–38%). We detected violations of our 2 assumptions that could cause our extinction estimates, particularly the absolute numbers, to be biased downward. Thus, our estimates should be treated as lower bounds. Our results illustrate the possible magnitudes of plant extirpations that can be expected in the tropics as development continues.

Keywords: biodiversity loss, generalized fiducial inference, historical extinctions, inferred extinctions, South-east Asia, species-area relationship, undescribed extinctions, undescribed species

Tasa de Extinción de Plantas Descubiertas y No Descubiertas en Singapur

Resumen: La extinción es un tema importante para la valoración de la biodiversidad global. Sin embargo, muchas medidas de la tasa de extinción no consideran a las especies que se extinguieron antes de que pudieran ser descubiertas. Singapur, la ciudad-estado isleña altamente desarrollada, tiene una de las floras mejor documentadas del mundo. Esto nos permitió estimar la tasa total de las extinciones florísticas en Singapur desde 1822 después de considerar el esfuerzo de muestreo y las criptoextinciones cuando recopilamos los registros de herbarios. Nuestra base de datos incluyó 34,224 especímenes de unas 2,076 especies nativas, de las cuales 464 especies (22%) estaban consideradas como extintas a nivel nacional. Asumimos que las especies no descubiertas tuvieron la misma tasa anual de extinción por especie que las especies descubiertas y que ninguna especie no descubierta permanecía en existencia. Con algoritmos clásicos y bayesianos, respectivamente, estimamos que 304 (95% IC 213–414) y 412 (95% IC 313–534) especies adicionales se extinguieron antes de que fueran descubiertas; las estimaciones correspondientes de la tasa de extinción total fueron 32% y 35% (rango de 30–38%). Detectamos violaciones en nuestras dos suposiciones que podrían causar que nuestras estimaciones de extinción, particularmente los números absolutos, tuvieran un sesgo hacia abajo. Por lo tanto, nuestras estimaciones deberían ser tratadas como límites inferiores. Nuestros resultados ilustran las magnitudes posibles de las extirpaciones de plantas que pueden esperarse en los trópicos conforme el desarrollo continúa.

*Address correspondence to R. A. Chisholm, email ryan.chis@gmail.com

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Palabras Clave: especies no descritas, extinciones históricas, extinciones inferidas, extinciones no descritas, inferencia generalizada de referencia, pérdida de biodiversidad, relación especie-área, sureste de Asia

摘要: 物种灭绝是全球生物多样性评估的一个关键问题。然而,许多灭绝率估计中并没有考虑到那些在被发现之前就已经灭绝的物种。高度发达的岛国新加坡拥有世界上记载最完整的热带植物群,这使得我们能够通过整理草本植物记录来统计采样工作量和隐秘的灭绝事件,以估计新加坡自1822年以来植物灭绝的总速率。本研究的数据库包括来自2076个本地物种的34,224个标本,其中有464个物种(22%)被认为在全国范围内灭绝。我们假设未被发现的物种年均灭绝率与已发现物种相同,且已没有未被发现的现存物种。利用经典算法和贝叶斯算法,我们分别估计出304个(95%置信区间为213-414)和412个(95%可信区间为313-534)新物种在被发现之前就已经灭绝;相应的总灭绝率估计分别为32%和35%(范围为30-38%)。我们还发现存在违反上述两个假设的情况,这可能导致我们对灭绝情况的估计值偏低,特别是对绝对数值的估计。因此,我们对灭绝情况的估计值应被视为下限。本研究表明,随着热带地区的发展,植物灭绝的规模可能会不断扩大。【翻译:胡怡思;审校:聂永刚】

关键词: 生物多样性丧失,广义置信推断,历史灭绝,推断的灭绝,东南亚,物种-面积关系,未描述的灭绝,未描述的物种,处死控制,社会认同的方法,野生动物管理

Introduction

Globally, and especially in the tropics, many species remain undiscovered, whereas known and unknown species continue to go extinct (Costello et al. 2013). This is also true on national and regional scales. Comprehensive analyses for regions with long survey histories and thorough records are invaluable for shedding light on such processes.

The island city-state of Singapore (103°50'E, 01°20'N; originally 520 km²; currently 724 km² due to land reclamation; population 5.64 million) has been used as a case study of tropical biodiversity loss (Corlett 1992; Turner et al. 1994). It is one of few developed countries in the tropics. Since British colonization in 1819, nearly all its original forest cover has been destroyed, although substantial regrowth has occurred. Primary forest currently occupies 0.28% of its landmass. Forested area (primary, old and young secondary, mangrove, and freshwater swamp) totals 22.47% (Yee et al. 2011). Fortunately, the biota of Singapore, especially plants, has been relatively well documented. Collections began soon after 1819, and tens of thousands of specimens are stored in local and international herbaria.

Documenting historical species extinction presents 2 challenges: inferring that a known species is extinct and accounting for species that went extinct before they could be discovered. Depending on data and resources available, there are many ways to infer extinction of known species, including heuristics (e.g., Davison et al. 2008), combined extinction risk metrics and expert judgement (e.g., Szabo et al. 2012), and statistical analyses of detection records (e.g., Solow 2005). Currently, multiple models are combined in a cost-benefit framework to categorize species (Akçakaya et al. 2017). The extinction of undiscovered species has received comparatively less attention.

Although extinction of undiscovered species may have a large effect on extinction rate estimates (Hawksworth

& Cowie 2013), they are difficult to account for. It is simplest to assume that the taxonomic group of interest has the same extinction rate as another better-known group (e.g., extinction rate of birds applied to insects [Dunn 2005]). Another approach is to estimate original species richness based on species composition nearby in relatively undisturbed areas (e.g., Brook et al. 2003; Alcalá et al. 2004). Alternatively, a statistical or phenomenological relationship can be used (Turner et al. 1994; Pitman et al. 2002) (e.g., a power-law relationship [Preston 1962] between species richness and habitat area remaining [e.g., Turner et al. 1994]). Where detailed records exist, a mark-recapture-like method on specimen attributes has been used (Pimm et al. 1994; Duncan et al. 2013). If one assumes extinction and discovery rates are constant over time, a parametric statistical model may be used (Tedesco et al. 2014).

Chisholm et al. (2016) introduced a nonparametric method for estimating undiscovered extinctions based on the assumption that extinction probabilities of undiscovered and discovered species are equal within each year. We used 2 algorithms to obtain interval estimates from this model, explored the model's assumptions, and applied it to records of vascular terrestrial plants in Singapore.

Methods

Data and Discovered Species

Electronic records of plant specimens from Singapore were collated and resolved to create a database of native vascular plants (Supporting Information). Species names were resolved with respect to synonymy and redeterminations. Unresolvable names and records without species-specific names, collection year, or collector name were removed.

Table 1. A hypothetical historical record and example calculations of cumulative probability of extinction P (see text). The two undiscovered cases are two different potential realizations of outcomes that are consistent with the historical record but differ by the number of extant undiscovered species remaining (marked *).

	Year t			Calculations of P
	0	1	2	
Historical record				
discovered extant S_t	100	250	300	
discovered extinct E_t	0	50	100	
discoveries δ_t	200	100	-	
Calculations				
extinction rate μ_t	0.5	0.2	-	$1 - (1 - 0.5)(1 - 0.2) = 0.6$
Assuming $U_2 = 0$				
undiscovered extant U_t	650	125	0*	
undiscovered extinct X_t	0	325	350	$\frac{100+350}{750} = 0.6$
Assuming $U_2 = 100$				
undiscovered extant U_t	900	250	100*	
undiscovered extinct X_t	0	450	500	$\frac{100+500}{1000} = 0.6$

Experts in plant identification for field research and conservation classified species as extant or extinct. Unclassified species that had not been collected within the past 30 years were designated extinct, in keeping with standard practice for plants (e.g., Chong et al. 2009). For other species collected within the past 30 years, we assessed current status in Singapore with the Solow (1993) method, which we chose for its simplicity, and a collection effort correction (McCarthy 1998) (Supporting Information). Seventy species had $p < 0.1$ (null hypothesis that they are extant rejected); however, many of these were known to be common. Therefore, experts were consulted a second time to reassess and classify each of the 70 species (Supporting Information).

The method we used to fit redetection effort, $c(t)$, to the detection records also fitted species' intrinsic redetection probabilities:

$$r_i = \frac{\sum_t I_R(i, t)}{\sum_{t \in T_i} c(t)}, \quad (1)$$

where $I_R(i, t) = 1$ if species i was redetected in year t or $I_R(i, t) = 0$ if not, and T_i is the set of all years that the species was known to be extant and therefore available to be redetected. A species' r_i reflects all factors that influenced its relative propensity to be collected, such as conspicuousness, abundance, and research interest.

Simplified extinction rate example

A naive way to estimate extinction rates is to divide the current number of extinct species by the total number of species. Given the hypothetical historical record in Table 1, this gives $100/(300 + 100) = 0.25$. Chisholm et al.'s (2016) method improves on this by accounting for species discoveries and temporal fluctuations in extinction rate. The extinction probability is 1 minus the cumulative probability of persistence. For the example

in Table 1, this gives $P = 1 - (1 - 0.5)(1 - 0.2) = 0.6$, which is substantially higher than the naive estimate.

Calculating the cumulative persistence probability effectively accounts for species that went extinct before they were discovered, provided they had the same extinction rates as discovered species. Historical numbers of undiscovered, extinct species can then be estimated by working backward. For the example in Table 1, assuming no undiscovered species remain extant, $U_2 = 0$, then in previous years $U_1 = 100/(1 - 0.2) = 125$ and $U_0 = (125 + 200)/(1 - 0.5) = 650$. Then, the total number of species $N_0 = U_0 + S_0 = 750$, and the total number of undiscovered extinctions $X_2 = N_0 - S_2 - E_2 - U_2 = 350$. This recovers the total extinction rate: $(E_2 + X_2)/N_0 = (100 + 350)/750 = 0.6 = P$. Alternatively, if we assume $U_2 = 100$, then $U_0 = 900$, $X_2 = 500$, and again $(100 + 500)/1000 = 0.6 = P$. With this method, the number of undiscovered extinctions has a linear relationship with the number of undiscovered extant species in the current year T : $X_T = (P(S_T + E_T + U_T) - E_T)/(1 - P)$. This example simplifies the problem by using the observed species extinction rates directly. A more complete description would infer confidence intervals on the estimates.

SEUX model

The SEUX model (Chisholm et al. 2016), which we name for its four variables, tracks the number of species in each year t in 1 of 4 states: discovered and extant, S_t ; discovered and extinct, E_t ; undiscovered and extant, U_t ; and undiscovered and extinct, X_t . The time series $\mathbf{S} = (S_0, \dots, S_T)$ and $\mathbf{E} = (E_0, \dots, E_T)$ are known from data (e.g., herbaria records), but $\mathbf{U} = (U_0, \dots, U_T)$ and $\mathbf{X} = (X_0, \dots, X_T)$ are unknown. The ultimate goal is to infer the total number of undiscovered extinctions, X_T .

Within each year, species can transition from extant to extinct ($S \rightarrow E$ or $U \rightarrow X$) or undiscovered to

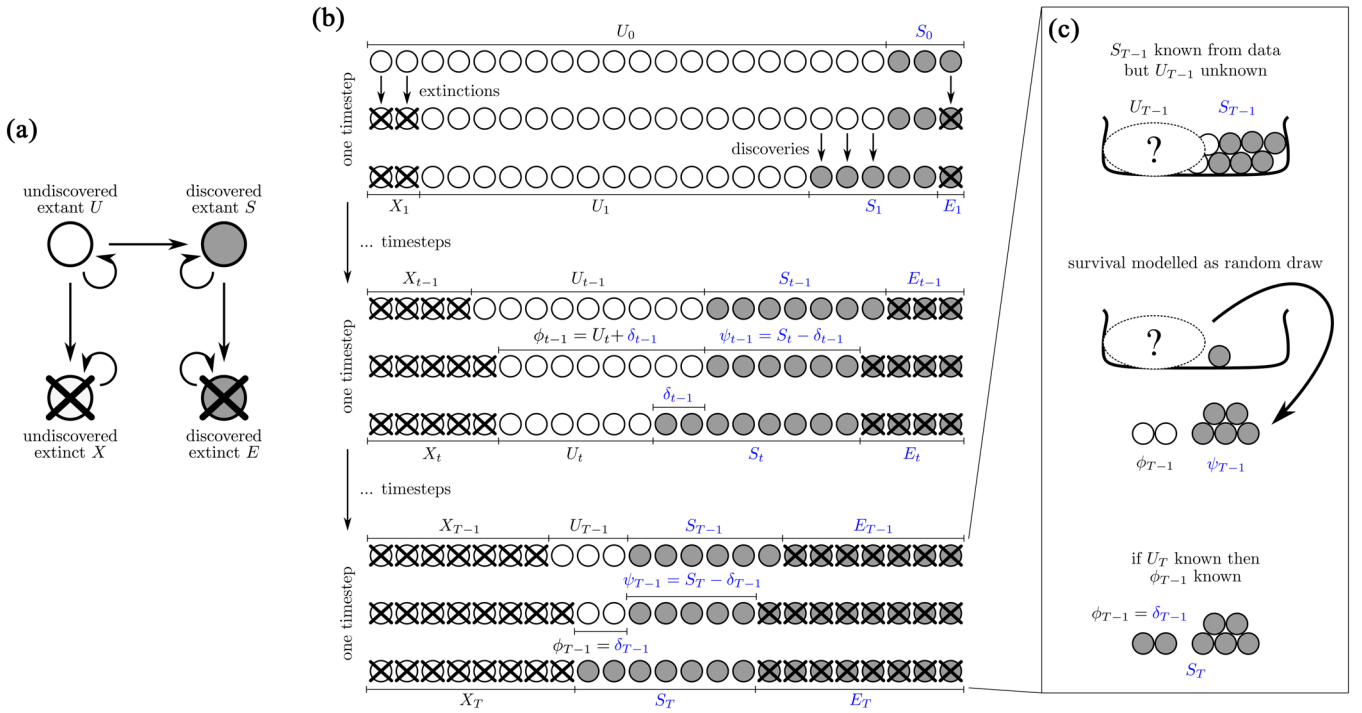


Figure 1. The SEUX model showing (a) possible states and transitions and a hypothetical scenario with (b) a whole time series with variables and (c) the operation of the hypergeometric model within a time step. Within each time step, it is assumed that survival or extinction occurs before discovery, and survival is modeled as a random draw in an urn model. The scenario shown has no undiscovered extant species remaining at the end of the observation period, $U_T = 0$. If U_T is known, then ϕ_{T-1} can be calculated as shown in (b).

discovered ($U \rightarrow S$). We assumed a species discovered in a particular year would not go extinct in that same year (i.e., transition U to E not permitted), which is equivalent to assuming that the process of survival and extinction precedes discovery within each year (Fig. 1).

The initial conditions were S_0 observed, $E_0 = 0$, U_0 unknown, and $X_0 = 0$. Over the observation period $t = 1, \dots, T$, the variables were updated as follows:

$$S_t = \Psi_{t-1} + \Delta_{t-1}, \quad (2)$$

$$E_t = E_{t-1} + S_{t-1} - \Psi_{t-1} \quad (3)$$

$$U_t = \Phi_{t-1} - \Delta_{t-1}, \quad (4)$$

$$X_t = X_{t-1} + U_{t-1} - \Phi_{t-1}, \quad (5)$$

where Ψ_{t-1} is the number of surviving discovered species (observed), Φ_{t-1} is the number of surviving undiscovered species (unobserved), and Δ_{t-1} is the number of species discovered (observed) in the previous year.

The key assumption is that extinction probabilities in each year, μ_t , are the same for discovered and undiscovered species. We also assumed a discovery probability, ν_t for each year t . Therefore, the random

variables above are binomially distributed:

$$\Psi_{t-1} \sim \text{Bi}(S_{t-1}, 1 - \mu_{t-1}), \quad (6)$$

$$\Phi_{t-1} \sim \text{Bi}(U_{t-1}, 1 - \mu_{t-1}), \quad (7)$$

$$\Delta_{t-1} \sim \text{Bi}(\phi_{t-1}, \nu_{t-1}), \quad (8)$$

where μ and ν are vectors of unknown parameters.

Let $N_t = \Phi_{t-1} + \Psi_{t-1} = U_t + S_t$ be the total number of species that survive to a given year. Because Ψ_{t-1} and Φ_{t-1} are independent and share parameter $1 - \mu_{t-1}$, N_t is binomially distributed and $P(\mathbf{n} | \mu, n_0 = U_0 + S_0) = \prod_{t=1}^T P(n_t | n_{t-1}, \mu_{t-1})$. The number of discovered (or undiscovered) survivors at each time step is hypergeometric with sample size n_t . So Eqs. 6 and 7 can be replaced with

$$N_t \sim \text{Bi}(n_{t-1}, 1 - \mu_{t-1}) \quad (9)$$

$$n_t - \Phi_{t-1} = \Psi_{t-1} \sim \text{Hyp}(n_{t-1}, S_{t-1}, n_t). \quad (10)$$

Thus, the joint probability of the data conditional on \mathbf{n} and ν is

$$P_{\mathbf{n}, \nu}(\mathbf{S}, \psi) = \prod_{t=1}^T T_{n_{t-1}, n_t}^P(\psi_{t-1} | S_{t-1}) P_{\nu_{t-1}, n_t}(S_t | \psi_{t-1}), \quad (11)$$

where

$$P_{n_{t-1}, n_t}(\psi_{t-1} | S_{t-1}) = \frac{\binom{S_{t-1}}{\psi_{t-1}} \binom{n_{t-1} - S_{t-1}}{n_t - \psi_{t-1}}}{\binom{n_{t-1}}{n_t}}, \quad (12)$$

$$P_{v_{t-1}, n_t}(S_t | \psi_{t-1}) = \binom{n_t - \psi_{t-1}}{S_t - \psi_{t-1}} v_{t-1}^{S_t - \psi_{t-1}} (1 - v_{t-1})^{n_t - S_t}. \quad (13)$$

Equation 12 is the probability of obtaining a number of discovered extant species surviving from year $t - 1$ to year t (ψ_{t-1}) given the number of discovered extant species in year $t - 1$ (S_{t-1}). Equation 13 is the probability of obtaining the number of discovered species in year t after accounting for discoveries during the last year and ϕ_{t-1} .

Algorithms to Infer Undiscovered Extinctions

To estimate the total number of undiscovered extinct species, X_T , Chisholm et al. (2016) assumed that the number of undiscovered species extant in the present day, U_T , was known. Below, we devised algorithms to obtain classical confidence intervals for X_T , which likewise treat U_T as known, and Bayesian credible intervals, which incorporate a U_T prior. Both methods yield interval estimates for U_0 from which intervals for X_T are calculated. We introduced the parameter ω to explore the model's sensitivity to the assumption that extinction probabilities in each year are the same for discovered and undiscovered species.

Classical Confidence Intervals

Classical confidence intervals for U can be estimated using the quantiles of a large sample from its confidence distribution (Xie & Singh 2013). We sampled a candidate confidence distribution with a step-by-step algorithm, which started with the U_T assumption and worked backward in time, sequentially sampling each U_{t-1} conditional on components in later years (c.f. example in Table 1). The algorithm was derived using the generalized fiducial approach (Hannig et al. 2016). The statistical model implied a data-generating algorithm, which we inverted to obtain a fiducial distribution for U .

The likelihood in Eq. 11 translates directly into a data-generating algorithm. Let us define the cumulative distributions

$$B_{n_t, n_{t+1}}(\psi_t, S_t) = 1 - P_{n_t, n_{t+1}}(\Psi_t \leq \psi_t | S_t) \quad (14)$$

and

$$C_{v_t, n_{t+1}}(S_{t+1}, \psi_t) = 1 - P_{v_t, n_{t+1}}(S_{t+1}' \leq S_{t+1} | \psi_t), \quad (15)$$

which correspond to Eqs. 12 and 13, respectively. Then, given parameters \mathbf{n} , \mathbf{v} , a sample \mathbf{S} , ψ can be

obtained with the following algorithm:

```

Initialise  $S_0$ 
For  $t = 0 \dots T - 1$ 
     $\alpha_1 \leftarrow \text{rand01}()$ 
     $\psi_t \leftarrow B_{n_t, n_{t+1}}^{-1}(\alpha_1, S_t)$ 
     $\alpha_2 \leftarrow \text{rand01}()$ 
     $S_{t+1} \leftarrow C_{v_t, n_{t+1}}^{-1}(\alpha_2, \psi_t)$ 
    
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(16)

The inverse functions correspond to sampling from discrete distributions (Lemieux 2009).

The data-generating algorithm can be inverted to sample \mathbf{n} given \mathbf{S} and ψ observed:

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initialize  $N_T = U_T + S_T$ 
For  $t = T - 1 \dots 0$ 
     $\alpha \leftarrow \text{rand01}()$ 
     $n_t \leftarrow B_{\psi_t, S_t}^{-1}(\alpha, n_{t+1})$ 
    
```

(17)

The sample U can be calculated from \mathbf{n} ($U_t = n_t - S_t$) or by rearranging the inverse function to sample U directly. We took the latter approach. We replaced $B_{n_t, n_{t+1}}(\psi_t, S_t)$ with the equivalent formulation

$$H_{U_t, U_{t+1}}(\psi_t, S_t) = 1 - P_{U_t, U_{t+1}}(\Psi_t \leq \psi_t | S_t), \quad (18)$$

where

$$P_{U_{t-1}, U_t}(\psi_{t-1} | S_{t-1}) = \frac{\binom{S_{t-1}}{\psi_{t-1}} \binom{U_{t-1}}{U_t + S_t - \psi_{t-1}}}{\binom{S_{t-1} + U_{t-1}}{S_t + U_t}}. \quad (19)$$

Then, we obtained a sample U with the following algorithm:

```

initialize  $U_T$ 
For  $t = T - 1 \dots 0$ 
     $\alpha \leftarrow \text{rand01}()$ 
     $U_t \leftarrow H_{\psi_t, S_t}^{-1}(\alpha, U_{t+1})$ 
    
```

(20)

We used a mid- P correction to account for data discreteness (Supporting Information). Via repeated sampling of U as described above, a probability function $b_{\mathbf{S}, \psi}(U)$ is implicitly defined, which is a generalized fiducial distribution for U .

In general, generalized fiducial inference can be used to obtain a parameter distribution, following which the quality of the procedure is evaluated, for example, with simulations (Hannig 2013). Our algorithm (20) performed well in simulations, producing U_0 confidence intervals with coverage that matched or exceeded the nominal value for a wide range of μ and \mathbf{v} scenarios (Supporting Information). To formally prove the algorithm

is correct, we would need to prove that $H_{U_t, U_{t+1}}(\psi_t, S_t)$ combined with the discreteness correction satisfies all technical requirements of a confidence distribution. Then, our algorithm would be equivalent to the step-by-step approach of Veronese and Melilli (2018).

To quantify the effect of the assumption that undiscovered and discovered species have equal survival probabilities, we introduced their odds ratio as a parameter

$$\omega = \frac{\left(\frac{1-\mu_{u,t}}{\mu_{u,t}}\right)}{\left(\frac{1-\mu_{s,t}}{\mu_{s,t}}\right)}, \quad (21)$$

where $\mu_{s,t}$ and $\mu_{u,t}$ are the extinction probabilities for discovered and undiscovered species, respectively, and ω is assumed constant in time. Then Eq. 19 is replaced with Fisher's noncentral hypergeometric distribution:

$$P_{U_{t-1}, U_t}(\psi_{t-1} S_{t-1}) = \frac{\binom{S_{t-1}}{\psi_{t-1}} \binom{U_{t-1}}{U_t + S_t - \psi_{t-1}} \omega^{U_t + S_t - \psi_{t-1}}}{\sum_{y=y_{\min}}^{y_{\max}} \binom{U_{t-1}}{y} \binom{S_{t-1}}{U_t + S_t - y} \omega^y},$$

$$y_{\min} = \max(0, S_t + U_t - S_{t-1}), \text{ and}$$

$$y_{\max} = \min(S_t + U_t, U_{t-1}). \quad (22)$$

Setting $\omega = 1$ in Eq. 22 retrieves Eq. 19, $\omega < 1$ means the extinction probabilities of undiscovered species are higher than discovered species, and $\omega > 1$ means they are lower. We explored the effect of ω on the results of the classical inference.

Bayesian Credible Intervals

We conducted our analysis in a Bayesian framework and used Markov chain Monte Carlo (MCMC) sampling with a Metropolis-within-Gibbs sampler (Gelman et al. 2004). The conditional dependency between the unobserved variables has a linear structure; therefore, a Gibbs sequence is obtained by sampling sequentially from

$$\Phi_t^{(j)} \sim P_{S, \psi}(\phi_t | \phi_{t+1}^{(j-1)}, \phi_{t-1}^{(j)})$$

$$\propto P_{S, \psi}(\phi_{t+1}^{(j-1)} | \phi_t) P_{S, \psi}(\phi_t | U_t^{(j)}), \quad (23)$$

where j is the sample number, the relationship $\phi_{t-1} = U_t + S_t - \psi_{t-1}$ links unknown parameters, and probabilities on the right side are calculated by rewriting Eq. 12 as a function of ϕ_t and U_t (details in Supporting Information). A sampling distribution must also be defined at the end points of the chain. We imposed a uniform prior on U_0 and, to match the default setting for the classical intervals above, we assumed $U_T = 0$. Alternatively, an informative prior for U_T can be sampled instead.

Two independent chains were monitored for convergence with trace plots and the Gelman-Rubin convergence diagnostic ($\hat{R} < 1.1$ for all U_t [Gelman & Shirley

2011]); a burn-in of 15,000 iterations was consequently discarded. To ensure samples were sufficiently large, we verified that: the combined sample size exceeded the minimum multivariate effective sample size for 95th percentile bounds with a tolerance of $\varepsilon = 0.1$ for every U_t ; the multivariate MCMC SE on the mean and 95th percentile bound estimates was small relative to the SD in the posterior (Vats et al. 2017); and the posterior distributions produced by the two chains were visually similar.

Time Step Size and Time Range of Data

To match most herbaria records, a natural time step length for the SEUX model is 1 year; however, this choice is arbitrary and influences model predictions. For example, one could arbitrarily decrease the time step length and thus increase the number of time steps in which no discovered extinctions occur. Because the model allows undiscovered extinctions to occur in time steps with no discovered extinctions, this would arbitrarily increase total extinction rate. To avoid this, we required that every time step have at least 1 discovered extinction. Years with no discovered extinctions were combined with later years within a time step, so time step lengths varied. This procedure may also provide a rough method for accounting for unevenness of collection effort over time.

The starting date chosen for the time series also influences the model results due to the small sample size effect. The decision involves a trade-off between inferring extinctions farther back in time versus reliability of those estimates. The model itself can be used to explore the effects of that decision. We chose a start date of 1822 because it coincides with the first extensive collection of plants in Singapore (Burkill 1927) and by that time 183 species had been collected.

Results

Data and Discovered Species

We collated 34,224 records of plants in Singapore. Periods of intensive collection were 1822, the 1890s, and the 1990s and 2000s. Collection rates were low during WWII and the early 1980s. The cumulative number of species discovered has not yet plateaued (Fig. 2).

The fitted redetection effort reflected collector activity and WWII (Fig. 3a). Effort generally increased through the last century, except for recent years, for which collections are yet to be entered into databases. The distribution of species' intrinsic redetection probabilities was bimodal (Fig. 3b). The relationship of average intrinsic redetection probability to year of discovery was U-shaped, gradually declining over the last 2 centuries but rapidly increasing again after 1980 (Supporting Information).

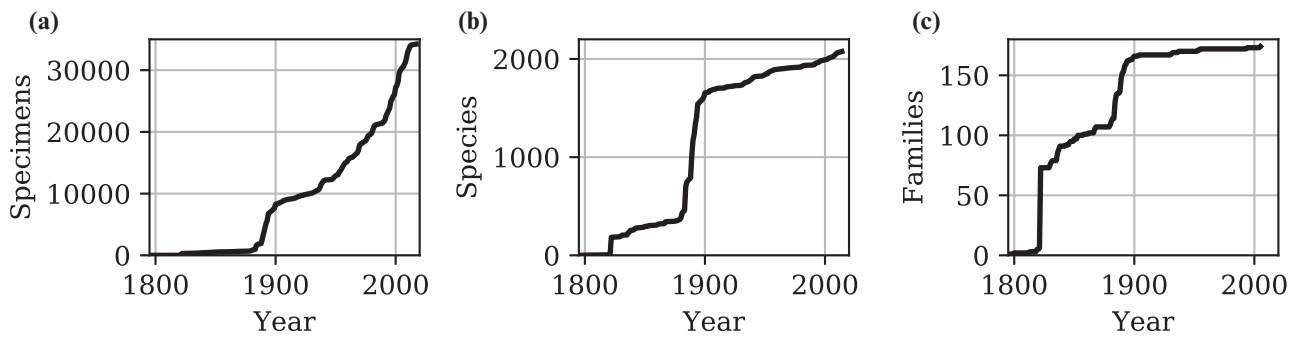


Figure 2. The cumulative number of (a) specimens, (b) species, and (c) families in the combined collections database of plant species of Singapore. The complete database of species detection records is in Supporting Information.

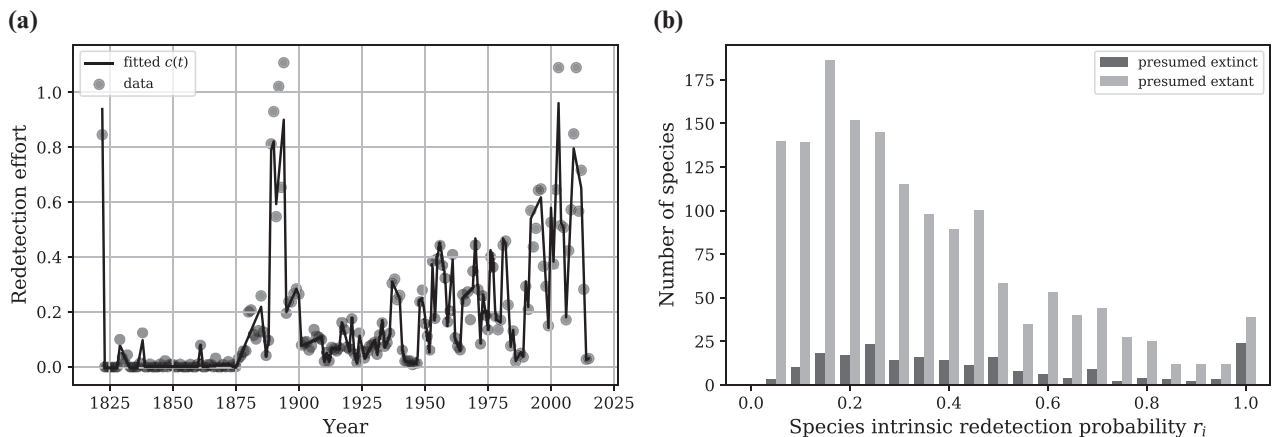


Figure 3. The (a) fitted spline of redetection effort over time for Singapore plants, $c(t)$, and (b) the distribution of inferred species' intrinsic redetection probabilities (r_i) (equation in Supporting Information), each of which gives the number of redetections of a species divided by the total redetection effort over its known lifetime. For this figure, species are presumed extant if they are designated as common in Chong et al. (2009), if they are judged to be extant by experts, or if they were last collected after 1985. Otherwise, they are presumed extinct. The list of species and their corresponding redetection probabilities are in Supporting Information.

Of the 2076 plant species included in the detection records, 464 were inferred extinct (Fig. 4a), for an estimated discovered extinction rate of 22% (Table 1).

Extinction of Undiscovered Species and Total Extinction Rate

Assuming that discovered and undiscovered species have equal extinction probabilities within a time step, and assuming that no undiscovered extant species remain in the present, then the 2 algorithms estimated that 304 (95% confidence interval, 213–414) and 412 (95% credible interval, 313–534) undiscovered extinctions have occurred since 1822 (Fig. 4a), with the Bayesian method giving the higher estimate. The total extinction rate from both methods was higher than the naïve estimate but lower than that of a previous study of Singapore plants (Brook et al. 2003) (Table 2).

As expected, the estimated total extinction rate increased as the survival probability of undiscovered

species was experimentally decreased via the parameter ω (Fig. 4b). An odds ratio of $\omega = 0.17$ was required to match Brook et al.'s (2003) high estimate (Supporting Information). The total extinction rate estimate was not sensitive to random species deletions from the record or variation in the current number of undiscovered extant species (Supporting Information). However, the estimated absolute number of undiscovered extinct species increased as U_T increased (Fig. 4c & Supporting Information).

Discussion

Extinction Rates in Singapore and Implications for Southeast Asia

We collated a rich botanical data set from 2 centuries of plant collections and showed how the data can be used to estimate total extinction rates. Accounting

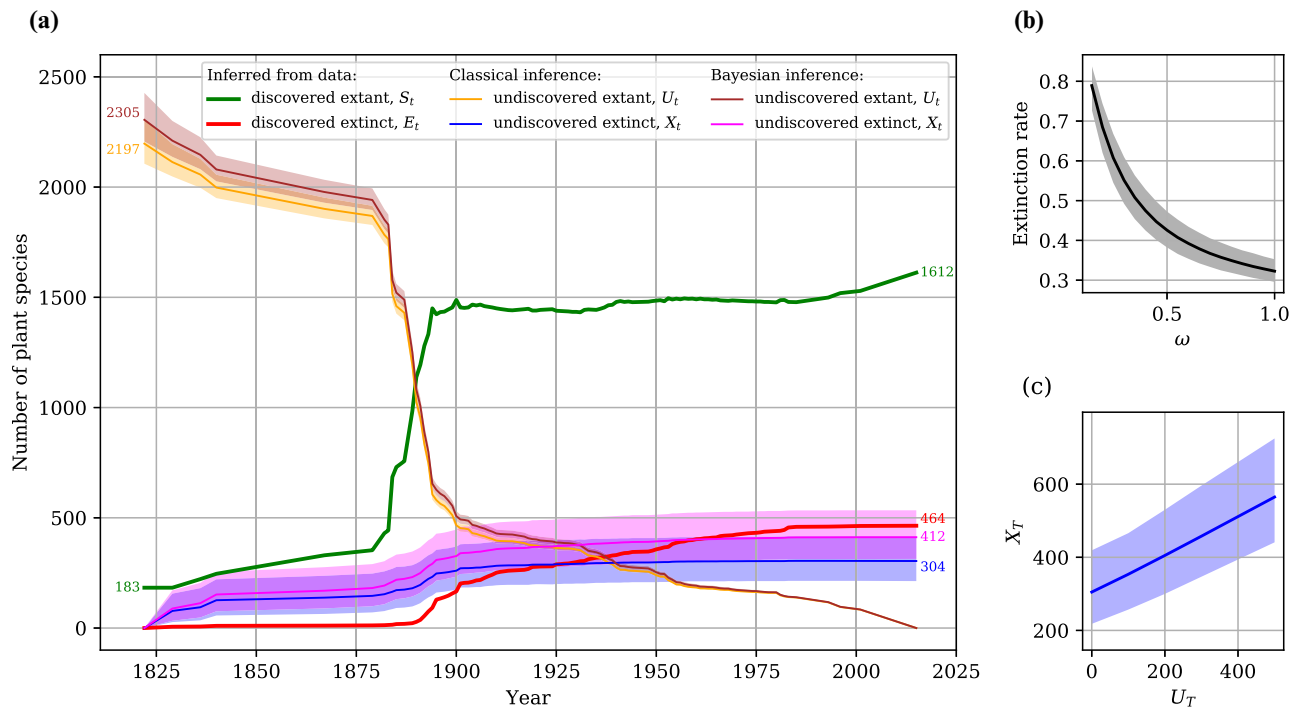


Figure 4. The (a) SEUX model estimates for Singapore plants given the default parameter values $\omega = 1$, $U_T = 0$, and (b and c) responses of the estimates to variation in those parameters (solid lines, mean values; shading, 95% confidence or credible intervals from classical or Bayesian inference). Code is available in Supporting Information.

Table 2. Estimates (95% CI) of extinction rates for plants in Singapore from this study and previous studies.

Description and source	Total	Extinct	Extinct (%)
Discovered species only			
Turner et al. 1994; Brook et al. 2003	2277	594	26
Chong et al. 2009	2145	639	30
This study	2076	464	22
Total: discovered + undiscovered			
Brook et al. 2003	6549	4866	74
This study: classical	2380 (2289, 2490)	768 (677, 878)	32 (30, 35)
This study: Bayesian	2488 (2389, 2610)	876 (777, 998)	35 (33, 38)

solely for discovered plant extinctions gave an estimated extirpation rate of 22% over 200 years. Accounting for undiscovered plant extinctions as well led to higher total extinction rate estimates of 32–35% (total range 30–38%) (Table 2). The uncertainty range was moderate, which reflected the difficulty of inferring undiscovered extinctions even under our model's simplifying assumptions. Nevertheless, these numbers are similar to the estimates for Singapore birds (Chisholm et al. 2016). Extrapolating our numbers to Southeast Asia under projected deforestation rates (Brook et al. 2003; Chisholm et al. 2016), we estimated that 17–18% of plant species will be extirpated regionally by 2100 (for comparison, 28–33% of plant species are currently classified as threatened [Joppa et al. 2010]).

Although our extinction estimates are high, they are much lower than Brook et al.'s (2003) estimate

of 74% Singapore plant extinctions in the present day and 46% regional plant extinctions by 2100. The discrepancy between our estimate and Brook et al.'s (2003) is attributable to their extreme assumption that the original species assemblage in Singapore was similar to that of comparable ecosystems throughout Peninsular Malaysia—an area over 100 times the size (Jain et al. 2018). This assumption violates one of ecology's few laws: the species-area relationship (Lawton 1999; Lomolino & Weiser 2001). If region A has an area that is 1% of region B, then an empirical rule of thumb (a power-law species-area relationship with an exponent $z = 0.2$ to 0.3) is that region A will have 60–75% fewer species than region B. Brook et al.'s (2003) method attributes this portion of difference in species richness to extinctions rather than a regular manifestation of the species-area relationship. Their method may have further overestimated

Singapore's historic species richness because Singapore (an island) is partially isolated from the mainland species pool and Peninsular Malaysia spans over 5° of latitude, whereas Singapore spans only a fraction of a degree.

Are our estimated plant extinction rates in Singapore consistent with ecological theory? Based on the species-area relationship, if the forested area is reduced to 2.83% of its original extent (current extent of primary, old secondary, mangrove, and freshwater swamp [Yee et al. 2011]), one would expect roughly 51–66% of the species to have gone extinct. Why have these high rates of extinction not been observed? Turner et al. (1994) performed a similar calculation for Singapore plants and suggested that higher theoretical rates were not observed because extinction debt has not yet been paid. Although we agree extinction debt remains, this does not explain the discrepancy because the species-area relationship itself ignores extinction debt. We suggest 2 more likely explanations. First, traditional species-area relationships implicitly assume that remaining habitat is contiguous (Pereira et al. 2012; Chisholm et al. 2018), whereas Singapore's remnant forest is highly fragmented and thus captures some beta diversity. When fragmentation is accounted for, theoretical estimates of tree species extinctions in Singapore accord well with reality (Chisholm et al. 2018). A second explanation is that almost one-fifth of Singapore contains young secondary growth (Yee et al. 2011), which harbors a substantial proportion of the original species.

Further plant extinctions can be expected in Singapore. The extinction curve has not plateaued (Fig. 4a), and there is likely an outstanding extinction debt to be paid in future (Vellend et al. 2006; Hahs et al. 2009), which may be exacerbated by isolation of remnant habitat from immigrants (Drayton & Primack 1996) and impediments to recruitment to secondary forest (Goldsmith et al. 2011). To mitigate future extinctions, a priority is to preserve existing forest remnants, including secondary forests. Increasing connectivity between existing patches will facilitate dispersal and increase effective population sizes. Our plants database may assist species-specific targeted conservation efforts by identifying species that are probably extant but infrequently sighted indicating rarity and vulnerability to extinction.

SEUX Model Assumptions and Recommendations

The SEUX model, like other extinction rate estimation techniques (e.g., E/MSY [Pimm et al. 2014; Tedesco et al. 2014]), assumes that the average extinction rates of discovered and undiscovered species are the same. However, if undiscovered species actually have higher extinction probabilities, then the method underestimates the total extinction rate. We introduced the ω parameter in the SEUX model to quantify this effect and further

assess the plausibility of the Brook et al. (2003) estimate. Estimated extinction rates are larger for lower ω . The Brook et al.'s (2003) estimate requires $\omega = 0.17$, indicating that undiscovered species were approximately 5 times as likely to go extinct as discovered species. Although $\omega = 0.17$ is probably unrealistically low, the true odds ratio may differ somewhat from $\omega = 1$.

There are several factors that could lead to $\omega < 1$ (i.e., undiscovered species having higher extinction probabilities than discovered species). However, our understanding of these relationships is largely qualitative. All else being equal, species with low abundance are harder to detect and more extinction prone (e.g., McCarthy et al. 2014). The link between low abundance and extinction risk is a general phenomenon (McKinney 1997) and has been observed specifically for habitat fragmentation (table 2 in Henle et al. 2004) and plants (Matthies et al. 2004; Sutton & Morgan 2009). Similarly, small species (Sutton & Morgan 2009; Marini et al. 2012) and species with restricted geographical ranges (e.g., Scheffers et al. 2012) are harder to detect and more vulnerable to habitat loss. Undiscovered species may also be more extinction prone because they cannot benefit from species-targeted conservation. However, collectors often have a bias toward novel specimens and rare finds (Guralnick & Van Cleve 2005; Pyke & Ehrlich 2010), which we expect to ameliorate $\omega < 1$ to an unknown degree. Obtaining reasonable quantitative estimates for ω is an area for future work.

A particular vulnerability of SEUX is that rare species, which tend to be simultaneously hard to detect and extinction prone, may be preferentially lost soon after habitat destruction begins, leading to underestimation of early undiscovered extinctions. To overcome this, collections need to include a large, early, and representative sample. We judge the size and timing of early plant collections in Singapore to be largely adequate because within 3 years of the arrival of British colonialists, 183 species from 73 families had already been collected. Nevertheless, we found some evidence for low early coverage of extinction-bound species. We observed that early-discovered Singapore species had higher intrinsic redetection probability and lower extinction probability (Supporting Information), which suggests that early collectors sampled easier-to-detect species that were less extinction prone. This implies ω decreases the farther back in time one goes.

We expect low coverage of early extinction-bound species to be the main challenge for future workers. Early collectors generally focus on capturing a wide spectrum of biodiversity, whereas recent collectors tend to focus on species of conservation concern (Boakes et al. 2010). Recently discovered species are generally more likely to be threatened (Giam et al. 2012) and have a narrower range (Treurnicht et al. 2017). However, these general patterns are influenced by the taxonomic

group and collectors' biases (Guralnick & Van Cleve 2005; Boakes et al. 2010; Pyke & Ehrlich 2010). For example, early Singapore collections included some species-rich families with high extinction rates (notably orchids [Supporting Information]). Future workers interested in characterizing museum-collection biases may find our new method for inferring redetection effort useful. It addresses some of the shortcomings of previous methods (Duffy et al. 2009) and produced estimates of Singapore plants' intrinsic redetection probabilities as a byproduct (Supporting Information).

To estimate the absolute number of undiscovered extinctions (as opposed to the percentage), SEUX additionally requires information about how many extant species remain undiscovered (U_T); however, U_T is—by definition—unknown. If a prior can be obtained for U_T (e.g., expert opinion), that can be easily incorporated into our Bayesian approach to obtain credible intervals for X_T . Our classical approach, however, requires a U_T value (incorporating a U_T confidence distribution is theoretically possible but it is unclear how it would be obtained). In some circumstances, $U_T = 0$ is a reasonable assumption (e.g., Singapore birds [Chisholm et al. 2016]); otherwise, another method (reviewed in Chao & Chiu [2016]) can be used to estimate U_T . Either way, the X_T estimate must be interpreted as predicated on the U_T value (Fig. 4c). For Singapore plants, we followed Chisholm et al. (2016) and assumed $U_T = 0$. However, given the lack of plateau in Fig. 2b, that new records and rediscoveries continue to be made throughout nature reserves (e.g., Chong et al. 2018; Ho et al. 2018; Khoo et al. 2018), and that existing species have been reassessed recently as new species (e.g., Niissalo et al. 2014), this is almost certainly false. Therefore, the absolute number of undiscovered extinctions we found should be interpreted as a lower bound, additional to the effect of overestimating ω discussed above.

The temporal pattern of extinctions produced by SEUX can be informative, provided it is interpreted with care. We assumed species went extinct the year after last detection, which ensures a conservatively higher estimate of total extinctions, but also means that the extinction pattern is influenced by the pattern of species discovery. Many of the extinctions appearing in the uptick in the late 1800s (Fig. 4a) are more likely to have occurred in the first two decades of the 1900s, when plantations decimated the secondary forests that had replaced the original primary forest after initial deforestation (Corlett 1992).

Future workers may be interested in more sophisticated methods for inferring discovered extinctions. Structured elicitation methods can be used for expert determinations (Keith et al. 2017). We used one of the simpler statistical methods (reviews in Solow [2005], Rivadeneira et al. [2009], and Boakes et al. [2015]); however, if additional data are available (e.g., on species-

specific threats and survey quality), then these can be incorporated (Akçakaya et al. 2017). Nevertheless, we found that even our simple method was useful to supplement heuristics and narrow the list of species that required closer scrutiny from experts.

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Data and Code Accessibility

The Singapore plant collections provide an unusually rich database. We hope future researchers will find this data set and code (Supporting Information) useful as a testing ground for their work.

Supporting Information

Data and code accessibility (Appendix S1), inferring redetection effort (Appendix S2), inferring discovered extinctions (Appendix S3), details of classical inference (Appendix S4), details of Bayesian inference (Appendix S5), additional results for Fisher's extended SEUX (Appendix S6), and additional results for sensitivity of the SEUX model (Appendix S7) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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