



Two centuries of biodiversity discovery and loss in Singapore

Ryan A. Chisholm^{a,1} , Nadiah P. Kristensen^a, Frank E. Rheindt^a , Kwek Yan Chong^b , John S. Ascher^a, Kelvin K. P. Lim^c, Peter K. L. Ng^c , Darren C. J. Yeo^{a,c} , Rudolf Meier^{a,d} , Heok Hui Tan^c , Xingli Giam^e , Yi Shuen Yeoh^b, Wei Wei Seah^b, Laura M. Berman^a , Hui Zhen Tan^a , Keren R. Sadanandan^{a,f} , Meryl Theng^{a,g}, Wan F. A. Jusoh^{a,h} , Anuj Jain^{i,j} , Blanca Huertas^k , David J. X. Tan^{al} , Alicia C. R. Ng^a, Aloysius Teo^a, Zeng Yiwen^{a,m}, Tricia J. Y. Cho^a , and Y. C. Keita Sin^a

Edited by Barry W. Brook, University of Tasmania, Hobart, TAS 7005, Australia; received May 30, 2023; accepted October 22, 2023 by Editorial Board Member Alan Hastings

There is an urgent need for reliable data on the impacts of deforestation on tropical biodiversity. The city-state of Singapore has one of the most detailed biodiversity records in the tropics, dating back to the turn of the 19th century. In 1819, Singapore was almost entirely covered in primary forest, but this has since been largely cleared. We compiled more than 200 y of records for 10 major taxonomic groups in Singapore (>50,000 individual records; >3,000 species), and we estimated extinction rates using recently developed and novel statistical models that account for “dark extinctions,” i.e., extinctions of undiscovered species. The estimated overall extinction rate was 37% (95% CI [31 to 42%]). Extrapolating our Singapore observations to a future business-as-usual deforestation scenario for Southeast Asia suggests that 18% (95% CI [16 to 22%]) of species will be lost regionally by 2100. Our extinction estimates for Singapore and Southeast Asia are a factor of two lower than previous estimates that also attempted to account for dark extinctions. However, we caution that particular groups such as large mammals, forest-dependent birds, orchids, and butterflies are disproportionately vulnerable.

deforestation | tropical extinctions | biodiversity loss | dark extinctions | Singapore

The impacts of tropical deforestation on the global carbon budget are well quantified (1), but much greater uncertainty surrounds impacts on biodiversity. Accurate assessments of biodiversity loss require reliable baseline data and follow-up surveys. Both are sorely lacking in most of the tropics. Singapore, an island city-state in Southeast Asia, is unique among tropical countries for its comprehensive record of biodiversity collection over two centuries. When modern Singapore (Fig. 1) was founded in 1819, the predominant vegetation was lowland dipterocarp forest (443 km² of a total land area of 540 km²; Fig. 1*B*), with smaller areas of mangrove forest and freshwater swamp forest (2–5). Since then, almost all the primary dipterocarp forest has been cleared; less than 1% remains (2, 6). An additional 21.0% of the landscape is secondary forest, although much of this is considered relatively species-poor young forest; only 4.3% of total area is considered better-quality old secondary forest (2, 3, 7) (Fig. 1*B*). Over 90% of the mangrove and freshwater swamp forest area has also been lost (3).

We aimed to estimate biodiversity loss in Singapore over the last two centuries. We compiled biodiversity records for native resident species in Singapore dating back to the turn of the 19th century for 10 major taxonomic groups: nonvolant terrestrial mammals (henceforth “mammals”), birds, reptiles, amphibians, primary freshwater fishes (“fishes”), butterflies, bees, phasmids, freshwater decapod crustaceans (“decapod crustaceans”), and vascular plants (“plants”) (*SI Appendix, Detailed Materials and Methods*). Our final database comprised 50,678 records from museums, herbaria, published literature, checklists, inventories, and online databases (Table 1). We refer to loss of species from Singapore as extinctions, although these are almost all local extinctions because the species concerned persist in neighboring countries.

Any holistic accounting of extinctions must account for dark extinctions, i.e., species that went extinct before they could be recorded (8, 9). Early estimates of extinctions in Singapore focused only on known extinctions (2, 10, 11). A 2003 study attempted account for dark extinctions by assuming that in 1819 all species in similar habitats in Peninsular Malaysia (all habitats except mountains, lakes, large rivers and savannahs) were also present in Singapore (12). However, this violates ecology’s fundamental species–area law: the area of Singapore is less than 1% that of the relevant habitats in lowland Peninsular Malaysia (Fig. 1*A*) and would thus be expected to originally have had only 20 to 50% as many species, assuming typical power-law scaling exponents of 0.15 to 0.35 documented in nature (13). This means that the reported extinction estimates for Singapore [73% across nine taxonomic groups (12)] were almost certainly too high. To produce more accurate

Significance

Accurate estimates of tropical extinction rates are needed to evaluate human impacts on biodiversity and inform conservation planning. Singapore has lost most of its tropical primary forest since 1819 and yet has an exceptionally detailed biodiversity record. We compiled the largest database of Singapore biodiversity records to date (>50,000 individual records; >3,000 species; 10 major taxonomic groups) and estimated extinctions using statistical methods that account for “dark extinctions”—extinctions of undiscovered species. The estimated overall extinction rate was 37%, a factor of two lower than previous estimates for Singapore, although extinctions were concentrated among larger, charismatic species. Extrapolations suggest that by 2100 Southeast Asia will resemble a “tropical Europe,” with roughly 80% of the original species surviving in human-dominated landscapes.

The authors declare no competing interest.

This article is a PNAS Direct Submission. B.W.B. is a guest editor invited by the Editorial Board.

Copyright © 2023 the Author(s). Published by PNAS. This article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

Although PNAS asks authors to adhere to United Nations naming conventions for maps (<https://www.un.org/geospatial/mapsgeo>), our policy is to publish maps as provided by the authors.

¹To whom correspondence may be addressed. Email: ryan.chis@gmail.com.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2309034120/-/DCSupplemental>.

Published December 11, 2023.

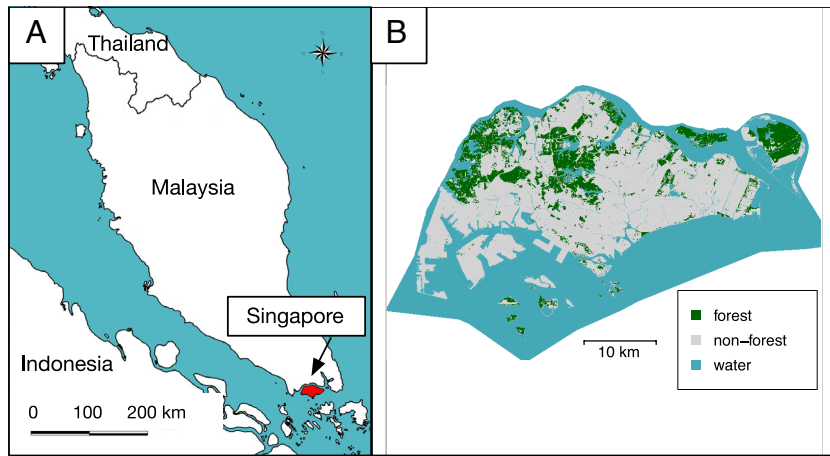


Fig. 1. Singapore is an island city-state at the southern tip of the Malay Peninsula and has been largely deforested. (A) The narrow Johor Strait separates Singapore (shown in red) from Peninsular Malaysia and mainland Southeast Asia. (B) In 1819, when modern Singapore was founded, the country was predominantly covered by lowland dipterocarp forest, but over the last two centuries the majority of the original forest cover has been lost (3). Only 4.3% of good-quality forest cover remains, in small patches of primary forest and larger areas of old secondary forest (green). [The Singapore figure was generated from a high-resolution map of Singapore's terrestrial ecosystems (5), with forest defined as freshwater swamp forest, mangrove forest, or vegetation with limited human management and a tree canopy.]

estimates, we employed both recently developed and novel statistical methods that infer dark extinctions from detection patterns in known species (14, 15) (*Materials and Methods; SI Appendix, Detailed Materials and Methods*).

Results and Discussion

Our overall cumulative estimated extinction rate in Singapore was 37% (95% CI [31%, 42%]) (Fig. 2A and *SI Appendix, Detailed Results*). Extinctions in Singapore began in the mid-19th century (Fig. 2B) when large swathes of secondary and primary forest were cleared for a first wave of logging and agriculture, in particular for gambier and pepper plantations (2, 6). These early extinctions were concentrated among plants and terrestrial invertebrates. The concentration among plants is likely due to the restricted spatial distributions of many species. The concomitant early insect declines are at least partly attributable to the extinction of host plants (16, 17). A subsequent wave of extinctions in the early 20th

Table 1. Numbers of species and records included in our database for each taxonomic group

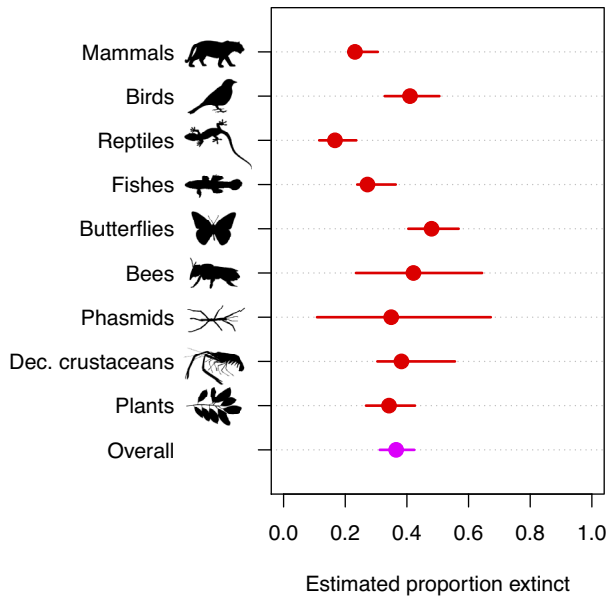
Taxonomic group	No. of species	No. of records
Mammals	32	64
Birds	154	3,847
Reptiles	121	2,925
Amphibians	25	1,132
Fishes	46	676
Butterflies	413	7,108
Bees	129	239
Phasmids	46	258
Decapod crustaceans	23	205
Plants	2,076	34,224
Total	3,065	50,678

The database includes all species recorded in Singapore except nonnative, marine, migrant, vagrant, visitor (nonbreeding), and doubtful species (see *SI Appendix, Detailed Materials and Methods* for details). For mammals and bees, only first and last records were compiled for each species. For several species of bee, there was only one record. For birds, only unique year-species records were compiled because of the large number of records per species.

century heavily impacted vertebrate species (Fig. 2B) and coincided with the loss of large areas of secondary forest to cultivation, especially of rubber (2, 6). Hunting may have contributed to extinctions of some large species, in particular mammals, but for birds, the historical evidence suggests that hunting was confined to disturbed areas and edge habitats: almost all the bird species historically targeted by hunters are still extant today (*SI Appendix, The History of Hunting in Singapore*). Similarly, there is no evidence that honey or damar harvesting contributed to bee extinctions (*SI Appendix, The History of Hunting in Singapore*). In the middle to late 20th century, coinciding with Singapore's rapid urbanization after World War II (2), birds and butterflies were especially hard hit (Fig. 2B). Ongoing clearance of remnant primary forest patches in the 20th century likely contributed disproportionately to ongoing plant extinctions: today Singapore's tiny remnant patches of primary forest are floristically richer than its secondary forests (2). The number of extinct species in most groups has since levelled off, with few extinctions recorded so far in the 21st century, although there is some continuing attrition among forest-dependent birds (Fig. 2B).

Most of the taxonomic groups in our database are today well studied in Singapore, and there is a high degree of confidence in which species recorded in the past are currently extant or extinct. But there are exceptions. Recent rediscoveries of several snake species in Singapore after apparent absences of up to 172 y (18) highlight the patchiness of this group's historical record. Among butterflies, since 1990 at least 116 butterfly species have been rediscovered or newly discovered, representing a third of known extant species (19). Among Singapore plants, uncertainty is particularly high, as evidenced by regular rediscoveries of plant species that were presumed extinct (20). To address this issue, a species' extinction status can be defined as a probability, rather than a binary status, but existing methods for inferring this probability from a sequence of detection dates for a species (21) can produce inaccurate results, especially in data-poor situations (15). We developed statistical methods that instead use the detection histories of all n species in a taxonomic group to jointly infer the probabilities that each species is extinct ($p_{\text{extinct},i}$ for species i). Species with $p_{\text{extinct},i} > 0$ are also assigned an estimated time of extinction conditional on being extinct. We applied these methods to our three richest datasets: birds, butterflies, and plants. For

A



B

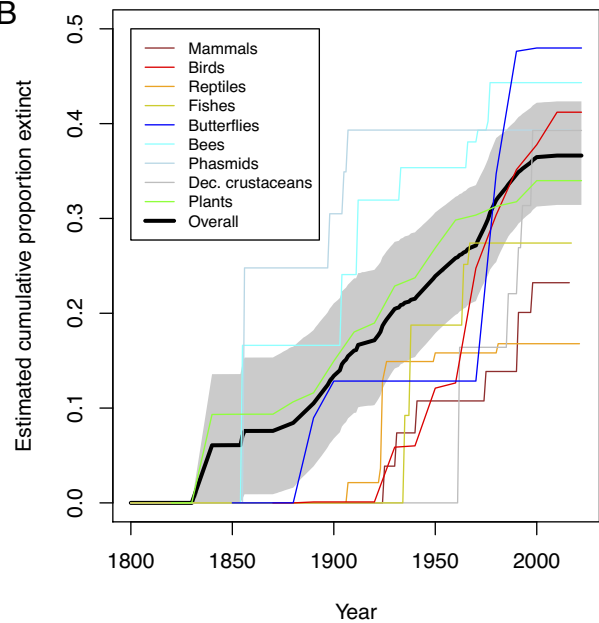


Fig. 2. Singapore has lost a substantial fraction of its species over the last two centuries. (A) The overall estimated proportion of extinct species is 37% (95% CI [31%, 42%]), based on nine major taxonomic groups (magenta point at bottom with 95% CI indicated with lines). Extinction rates have varied across taxonomic groups (red points and lines). Amphibians are excluded from the graph and from the overall estimate because there were no confirmed extinctions, precluding estimation of dark extinctions (*SI Appendix, Detailed Materials and Methods*). (B) Extinctions began in the mid-19th century and continued at a substantial rate until the late 20th century. The thick black curve shows the estimated overall extinction rate by combining the results for the nine taxa (colored curves), with the shaded region showing a 95% CI (separate CIs for each taxonomic group are omitted here for clarity; see *SI Appendix, Detailed Results and Figs. S1 and S3*). Early waves of extinction in the 19th century impacted plants and terrestrial invertebrates. A subsequent wave in the first half of the 20th century impacted vertebrates. Several taxa were also subject to large numbers of extinctions in the second half of the 20th century.

birds and butterflies, most of the inferred probabilities were close to zero or one, indicating high certainty in their current statuses (*SI Appendix, Detailed Results and Fig. S5 B and C*). For plants, of the 2,076 species with verifiable records in Singapore, 305 had intermediate probabilities of being extinct: $0 < p_{\text{extinct},i} < 0.9$ (Fig. 3A). By identifying such species, our methods can help direct survey effort to where uncertainty is greatest. As a case in point, the plant species *Homalomena griffithii* [now *H. nathanielii* (22)] was assigned $p_{\text{extinct},i} = 0.52$ by our model (Fig. 3B) and was subsequently rediscovered in Singapore [i.e., after our plant dataset was collated (23)]. Given the high biodiversity of the tropics and uncertain status of many species, our methods should prove broadly useful around the world for targeting survey efforts towards species whose extinction status is in doubt.

Our estimated extinction rates were generally lower than previous estimates for Singapore. The 2003 study estimated that the overall extinction rate in Singapore, accounting for dark extinctions, was double our estimate (as high as 73%) (12), but, as discussed earlier, this was based on flawed assumptions. Our estimate for Singapore bird extinctions (41%) was somewhat higher than that of a previous study also accounting for dark extinctions (33%) (14) because we used an updated dataset that excluded disturbance- and savannah-adapted species that are almost certainly recent immigrants (*SI Appendix, Detailed Materials and Methods*). These species have taken advantage of the radically transformed environment in Singapore, in which extensive tracts of open habitat exist that were almost entirely absent pre-1819. Our estimated plant extinction rate (34%) was commensurate with that from a recent study on the same dataset that integrated a simpler model for accounting for dark extinctions with expert opinion (32 to 35%) (15), and substantially higher than one obtains without accounting for dark extinctions based on a recent flora checklist for Singapore (25%) (24).

Extinctions in Singapore have been higher for particular taxonomic groups and for particular subsets of species within each group (Fig. 2A). The highest estimated extinction rates were for butterflies (48%), bees (42%), and birds (41%). For bees, extinctions were concentrated among stingless bees, which may be more vulnerable because they are eusocial and thus have low effective population sizes (25); although stingless bees can suffer negative effects of honey overharvesting and meliponiculture (26), we found no evidence of such impacts in Singapore (*SI Appendix, The History of Hunting in Singapore*). For birds, extinction rates were much higher for species dependent on primary or old-growth secondary forest (estimated extinction rate 89%). Among birds able to persist in grassland and parkland, there were no recorded extinctions, although the oriental pied hornbill (*Anthracoceros albirostris*) was temporarily absent from the 1960s to the 1990s, after which it reestablished a population with active conservation assistance (27). For mammals, there is a notable absence of large-bodied species in Singapore. In 1819, Singapore already lacked elephants, tapirs, gibbons, rhinoceroses, wild cattle, and other taxa widespread across the region at the time. Their absence has been attributed to pre-historical extinction filters over the approximately 10,000 y since Singapore was isolated from mainland Southeast Asia by rising sea levels (2). Even among the mammal species extant in 1819, extinctions have been concentrated among larger species. The last tiger (*Panthera tigris*) was shot in Singapore in the 1930s (28), and the other previously extant large cat species, the leopard (*Panthera pardus*), is also now extinct. In total, three out of five (60%) mammal species larger than 10 kg have gone extinct in the last 200 y, compared to only 4 out of 27 species (15%) below 10 kg. Among Singapore plants, our results corroborate previous findings that extinctions have been highest among orchids (15, 29): We assessed 68% of known orchid species in Singapore as extinct. Singapore's

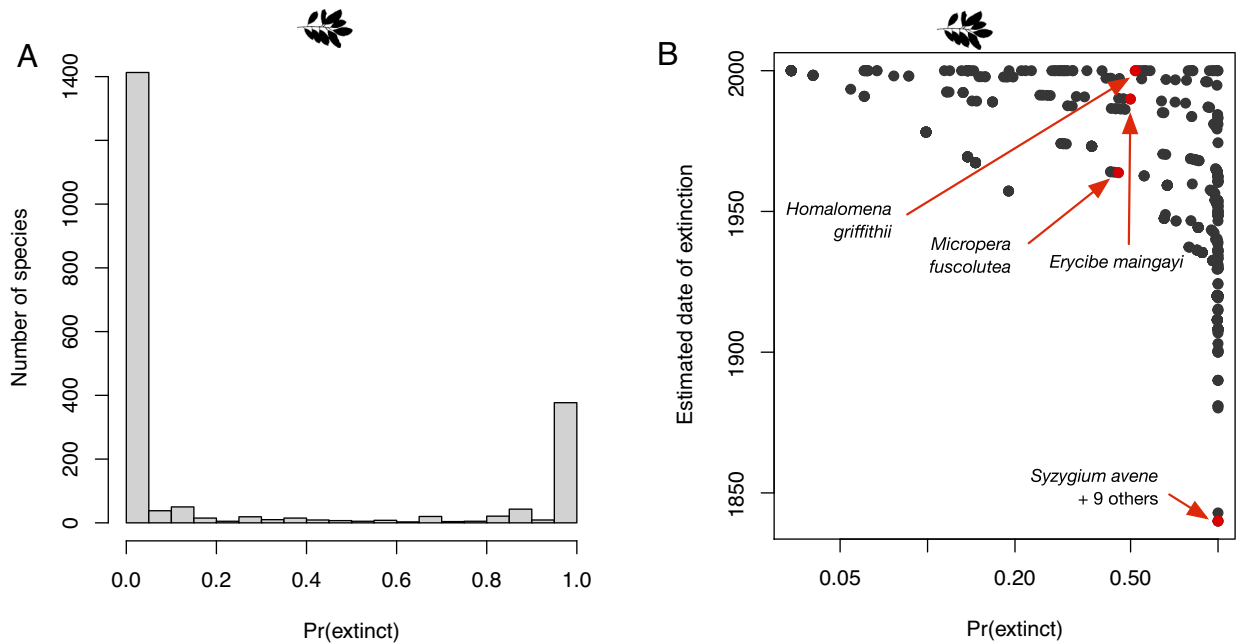


Fig. 3. Our methods allow joint estimation of probabilities of being extinct, along with estimated dates of extinction, for all species in an ensemble, illustrated here for Singapore plants. (A) Of Singapore's 2,076 plant species with verifiable records, 1,385 are known or inferred to be extant ($p_{\text{extinct},i} = 0$), 386 are inferred to be almost certainly extinct ($p_{\text{extinct},i} \geq 0.9$), and the remaining 305 are subject to some uncertainty ($0 < p_{\text{extinct},i} \leq 0.9$). (B) The estimated dates of extinction, conditional on a species being extinct, are negatively correlated with $p_{\text{extinct},i}$ (i.e., species more likely to be extinct are estimated to have gone extinct earlier). The earliest extinction date of 1840 is assigned to 10 species, including *Syzygium avene*, which was seen only in 1822 and 1836. Estimated dates of extinction also depend on species' estimated detectability based on sighting records. The three species *H. griffithii*, *Micropera fuscolutea*, and *Erycibe maingayi* have similar estimated probabilities of being extinct ($p_{\text{extinct},i} \approx 0.5$) but different estimated detectabilities and thus varying estimated dates of extinction.

present-day flora and fauna are thus, in important ways, more depauperate than the summary numbers (Fig. 2A) alone suggest. Extinctions have disproportionately affected charismatic species, such as large mammals, birds, butterflies (30) and orchids. The disappearance of charismatic species can be a double blow for conservation biology, because such species serve to motivate public support for conservation action (31).

One caveat to our results is that Singapore may have unpaid extinction debt: The populations of some remaining species are confined to small forest remnants and may not be viable (2, 32–34). Despite this, overall extinctions have slowed or ceased in most taxonomic groups (Fig. 2B). It is even possible that total current species richness is below equilibrium (2), because the remaining areas of secondary forest (Fig. 1B) are well protected and will mature in coming decades, and the threat of poaching is much lower than in surrounding countries (35, 36). Indeed, some species have already recovered or have recolonized Singapore naturally from nearby Malaysia (37); others may be able to reestablish with human assistance. The reestablishment of the oriental pied hornbill in Singapore was facilitated by direct conservation actions including artificial nest boxes (27). The lesser mouse-deer (*Tragulus kanchil*) had an estimated population of 50 individuals in the 1990s, but has since recovered to around 200 individuals (38). Similarly, the Raffles' banded langur (*Presbytis femoralis*) had plummeted to a population of 15 to 20 individuals in Singapore in the 1990s and was predicted to go extinct (39), but has since recovered to more than 60 individuals and is potentially expanding its range (40). A necessary condition for natural recolonization of locally extinct species is the ability of individuals to disperse from Malaysia across the Johor Strait, which is 600 m across at the narrowest point (2). The feasibility of such dispersal is evidenced by crossings in recent decades of mammal species not known to have originally occurred in Singapore: the dusky langur (*Trachypithecus obscurus*), the Asian elephant (*Elephas maximus*), and the Malayan tapir (*Tapirus indicus*) (41–43). The next few decades

will reveal whether Singapore has passed through its deforestation bottleneck and associated nadir of species diversity.

Singapore allows for an unusually detailed reconstruction of tropical extinctions, but it has idiosyncrasies that should be borne in mind when drawing general conclusions about tropical biodiversity loss. For example, the lack of confirmed amphibian extinctions in Singapore (*SI Appendix, Detailed Materials and Methods*) may just be due to poor baseline data in which, by chance, the few species destined for extinction were missed (amphibians were our second-least speciose group; Table 1). Alternatively, amphibians may have already passed through an extinction filter over the millennia during which Singapore was isolated from Malaysia by the salt water barrier of the Johor Strait, although it is unclear why this prehistorical filter would not also have led to lower historical extinction rates among our other freshwater taxa (fishes and decapod crustaceans; Fig. 2A). Whichever explanation is correct, we would not expect the low observed amphibian extinction rates in Singapore to be replicated elsewhere in the tropics.

Following the approach of past studies on Singapore extinctions (7, 12), we extrapolated our results to predict regional extinction rates in Southeast Asia by 2100. We used the species–area method and deforestation projections of Ref. 7, which we calibrated with our observed species–area exponents resulting from deforestation in Singapore. We estimated that 18% (95% CI [16 to 22%]) of species would go extinct regionally by 2100 under a business-as-usual scenario (*SI Appendix, Detailed Results and Fig. S8*). For the two taxa considered by the authors of ref. 7, birds and mammals, their estimated extinction rates were roughly double ours, which is attributable entirely to their use of higher species–area exponents, obtained from data on land-bridge islands. We consider our extinction estimates to be more realistic because our exponents are based on Singapore's actual historical experience of deforestation and species loss. Our Southeast Asian extinction estimates for 2100 were towards the lower bound of the 13 to

42% projected by ref. 12 (*SI Appendix, Detailed Results and Fig. S8*). Again we consider our estimates more realistic, because the upper bound of ref. 12 was propagated from the flawed assumption, discussed earlier, that all Peninsular Malaysia species in similar habitats were originally present in Singapore (12).

Our projections to Southeast Asia assume that forest loss and degradation will continue to be the major drivers of biodiversity over the next century (44), as they have been in Singapore over the past two centuries. Other projections of future biodiversity loss in Southeast Asia have made the same implicit assumption (7, 12). However, if humanity is unable to mitigate greenhouse gas emissions, forest loss may become eclipsed by climate change as a driver of biodiversity loss, in which case alternative modelling approaches will be needed (45). We also note that wildlife trapping and hunting are widespread problems in Southeast Asia but historically played an apparently minor role in driving extinctions in Singapore (*SI Appendix, The History of Hunting in Singapore*) and are nearly absent there today (35, 36). Indeed, the Sunda pangolin (*Manis javanica*) and the straw-headed bulbul (*Pycnonotus zeylanicus*) are two Southeast Asian species that are globally critically endangered due to poaching but have strongholds in Singapore (46, 47). It remains to be seen whether poaching rates will drop across other Southeast Asian countries as they develop—if not, species targeted by poachers will be lost at higher rates than extrapolations from Singapore would suggest.

Overall, Singapore's experience points to a future "tropical Europe" in Southeast Asia (48), where over 80% of species persist in a largely transformed landscape, but many large mammals, forest-dependent birds, butterflies, orchids, and other charismatic species are extinct. We recommend shifting the emphasis of conservation messaging away from very high extinction projections (12, 49) and towards a more classical approach based on landscape-scale conservation and umbrella species, whereby reserves and connectivity corridors established for charismatic species provide large-scale landscape protection (50). This in turn will benefit other species and be synergistic with other conservation goals, such as protection of carbon stocks to mitigate climate change (51). In Singapore and other cities, the focal charismatic species should include mainly small to medium-sized species, such as langurs, pangolins, hornbills, and butterflies, which can feasibly persist in highly urbanized landscapes with conservation assistance. At larger scales across Southeast Asia, the focal species can encompass tigers, orangutans, elephants, rhinoceroses, and other endangered large mammals.

Materials and Methods

Our goal was to estimate extinction rates for each taxonomic group in Singapore over the last two centuries. By "extinction" we mean local disappearance, i.e., extirpation, from Singapore. Almost all of these are local extinctions because almost all of Singapore's extinct species persist in neighboring countries. We compiled biodiversity records from Singapore, dating back to the oldest natural history material known from the country, a specimen of the plant *Podocarpus polystachyus* collected in 1796 by Christopher Smith. We compiled data for 10 major taxonomic groups (*SI Appendix, Detailed Materials and Methods*). We excluded nonnative species, marine species, migrant species, vagrant species, visitor (nonbreeding) species and doubtful species.

Two groups, both associated with actual or potential movement of individuals across the Johor Strait from Malaysia, posed particular challenges to classification. The first group comprises a few large species, for which there is uncertainty as to whether populations in Singapore were self-sustaining pre-1819 or reliant on immigrants (e.g., elephants and tigers). We treated these on a case-by-case basis (*SI Appendix, Detailed Materials and Methods*). The second group comprises species that temporarily went extinct in Singapore after 1819 and then at some point recolonized from Malaysia across the Johor Strait. Recolonization is limited by the fact that most of remnant Singapore's forests are towards the center of the main island

(Fig. 1), and thus the very species that have been hardest hit by extinctions are least able to recolonize. Habitat destruction in Malaysia has also reduced the prospect of recolonization of forest-dependent species. Nevertheless, there are examples of successful recolonizers (e.g., the pied hornbill, *Anthracoceros albirostris*), and we classified such species as extant except in a few cases where evidence clearly indicates that the modern population is derived from escaped captive individuals [e.g., the white-rumped shama *Copsychus malabaricus* (52); *SI Appendix, Detailed Materials and Methods*]. We emphasize that these two problematic groups comprise only a small fraction of Singapore's recorded species and thus the uncertainty surrounding their status has little impact on our final extinction estimates.

Comprehensive estimates of extinction rates must account for dark extinctions, the extinction of species before they could be discovered (8). Dark extinctions will be lower for Singapore than most other tropical areas because of the detailed baseline data, but nevertheless may be a nonnegligible fraction of total extinctions. In recent years, robust statistical techniques have been developed for estimating dark extinctions (8, 9, 14), and these have been applied to birds, plants, and butterflies in Singapore (14, 15, 17). These techniques account for dark extinctions by assuming that the same average per-species extinction rate applies to discovered and undiscovered species (8, 9, 14). This is similar to how extinction rates on geological timescales are estimated from the fossil record using the extinctions-per-million-species-years (E/MSY) approach (53).

One published technique for accounting for dark extinctions uses the susceptible-extinct-unknown extant-unknown extinct (SEUX) model, a compartmental model named for its four compartments: known extant (*S*), known extinct (*E*), unknown extant (*U*), and unknown extinct (*X*) species (14). The SEUX model is mathematically related to mark-recapture methods used for estimating single species' population sizes in ecology (8). The SEUX model requires as input only the first and last record dates of each known species (14). We applied this basic method to mammals, reptiles, fishes, bees, phasmids, and decapod crustaceans (*SI Appendix, Detailed Materials and Methods*). We did not apply the SEUX model to amphibians, where there were zero confirmed extinctions and thus the model would trivially estimate zero dark extinctions (*SI Appendix, Detailed Materials and Methods*).

For our three richest datasets—plants, birds, and butterflies—we developed a more sophisticated model, which we call the matrix-of-detections-gives-extinction-estimates (MODGEE) model (*SI Appendix, Detailed Materials and Methods*). The main advantage of the MODGEE model over the SEUX model is that it takes as input the full species-by-time detection matrix, rather than just the first and last detection dates for each species and therefore does not discard potentially rich information about intermediate records. The MODGEE model has the added benefit of producing an estimated probability that each species is extinct and an estimated date of extinction for each species conditional on it being extinct.

The MODGEE model defines detection and extinction parameters for *n* species over *T* time periods as follows. The parameters m_t determine the probability species going extinct μ_t in each time period *t*, via the formula $\mu_t = 1 - e^{-m_t}$. The parameters h_t represent the detection effort in time period *t* and the parameters d_i represent the detectability of species *i*. The detection effort and detectability parameters combine to produce a probability of detection of species *i* in time period *t* (given that the species is extant) equal to $\delta_{i,t} = 1 - e^{-d_i h_t}$. The likelihood of parameter vectors \mathbf{m} , and \mathbf{h} , and parameter d_i given a binary vector \mathbf{x}_i of length *T*, representing detections ($x_{i,t} = 1$), and nondetections ($x_{i,t} = 0$) for species *i*, is as follows:

$$L(\mathbf{m}, \mathbf{h}, d_i | \mathbf{x}_i) = \prod_{t=1}^T (x_{i,t} (1 - e^{-d_i h_t}) + (1 - x_{i,t}) e^{-d_i h_t}) e^{-m_t} + \sum_{t=1}^T (1 - e^{-m_t}) \times \left(\prod_{\tau=1}^{t-1} (x_{i,\tau} (1 - e^{-d_i h_\tau}) + (1 - x_{i,\tau}) e^{-d_i h_\tau}) e^{-m_\tau} \right) \times \left(\prod_{\tau=t}^T (1 - x_{i,\tau}) \right).$$

The likelihood for an ensemble of *n* species is the product of likelihoods over *i* from 1 to *n*. The values of the $2T + n$ parameters can then be estimated from a binary detection matrix of dimensions $n \times T$ via likelihood maximization.

In practice, the full likelihood maximization is numerically challenging for reasons explained in *SI Appendix, Detailed Materials and Methods*. Therefore, we developed a two-step maximum likelihood procedure, with detection parameters (**d** and **h**) being estimated in the first step and extinction parameters (**m**) being estimated in the second step (*SI Appendix, Detailed Materials and Methods*). Provided that the detection matrix is not too sparse, the fitting procedure performs well (*SI Appendix, Detailed Results and Fig. S4*). CIs on parameter estimates can be generated by bootstrapping the original data or by simulating the model with fitted parameter values and then refitting the model (*SI Appendix, Detailed Materials and Methods and Figs. S3 and S4*).

The main quantity of interest in our analyses (e.g., Fig. 2A) is the cumulative extinction rate at time *T*, which can be calculated from the parameterised model via the following formula:

$$\xi_T = 1 - \prod_{t=1}^T (1 - \mu_t) = 1 - \prod_{t=1}^T e^{-m_t}$$

Other quantities of interest that can be calculated from the fitted model include the probability $p_{\text{extinct},i}$ that species *i* is extinct at the final timestep *T*, and the expected time of extinction conditional on being extinct.

Data, Materials, and Software Availability. All study data are included in the article and/or [supporting information](#); the data along with R code for reproducing the results are also provided in an online repository: <https://github.com/nadihpk/MDGEE-dark-extinctions-estimator> (54).

ACKNOWLEDGMENTS. We thank Judith Marshall and Francis Seow-Cheon for discussions about phasmids, Leong Tzi Ming, Sankar Ananthanarayanan, Shivaram Rasu, and David Gower for discussions about amphibians, and Kenneth Er and

David Middleton for discussions about plants. We thank two anonymous reviewers for helpful comments. We thank Ben Price for granting access to insect collections in the Natural History Museum, London, and Amoret Spooner for granting access to insect collections in the Oxford University Museum of Natural History. We gratefully acknowledge the various museums and herbaria, for making their data freely available online, and the participants in Global Biodiversity Information Facility. We acknowledge funding from James S. McDonnell Foundation grant 220020470, and Singapore Ministry of Education Academic Research Fund Tier 1 grant R-154-000-A12-114 and Tier 2 grant R-154-000-A62-112.

Author affiliations: ^aDepartment of Biological Sciences, Faculty of Science, National University of Singapore, Singapore 117558, Singapore; ^bSingapore Botanic Gardens, National Parks Board, Singapore 259569, Singapore; ^cLee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, Singapore 117377, Singapore; ^dCenter for Integrative Biodiversity Discovery, Leibniz Institute for Evolution and Biodiversity Science, Museum für Naturkunde, Berlin 10115, Germany; ^eDepartment of Ecology and Evolutionary Biology, The University of Tennessee, Knoxville, TN 37996; ^fEvolution of Sensory Systems Research Group, Max Planck Institute for Biological Intelligence, Seewiesen 82319, Germany; ^gDepartment of Ecology and Evolutionary Biology, School of Biological Sciences, University of Adelaide, Adelaide, SA 5005, Australia; ^hSchool of Science, Monash University Malaysia, Subang Jaya 47500, Malaysia; ⁱNature Society (Singapore), Singapore 389466, Singapore; ^jbioSEA Pte Ltd., Singapore 679521, Singapore; ^kDepartment of Life Sciences, Natural History Museum, London SW7 5BD, United Kingdom; ^lDepartment of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131; and ^mCentre for Nature-based Climate Solutions, Department of Biological Sciences, Faculty of Science, National University of Singapore, Singapore 117546, Singapore

Author contributions: R.A.C. designed research; R.A.C., N.P.K., F.E.R., K.Y.C., J.S.A., K.K.P.L., P.K.L.N., D.C.J.Y., R.M., H.H.T., X.G., Y.S.Y., W.W.S., L.M.B., H.Z.T., K.R.S., M.T., W.F.A.J., A.J., B.H., D.J.X.T., A.C.R.N., A.T., Z.Y., T.J.Y.C., and Y.C.K.S. performed research; R.A.C. and N.P.K. analyzed data; N.P.K., F.E.R., K.Y.C., J.S.A., K.K.P.L., P.K.L.N., D.C.J.Y., R.M., H.H.T., X.G., Y.S.Y., L.M.B., H.Z.T., K.R.S., M.T., W.F.A.J., A.J., B.H., D.J.X.T., A.C.R.N., A.T., Z.Y., T.J.Y.C., and Y.C.K.S. edited the paper; and R.A.C. wrote the paper.

- E. T. A. Mitchard, The tropical forest carbon cycle and climate change. *Nature* **559**, 527–534 (2018).
- R. T. Corlett, The ecological transformation of Singapore, 1819–1990. *J. Biogeogr.* **19**, 411–420 (1992).
- A. T. K. Yee, R. T. Corlett, S. C. Liew, H. T. W. Tan, The vegetation of Singapore—an updated map. *Gardens' Bulletin Singapore* **63**, 205–212 (2011).
- P. K. L. Ng, R. T. Corlett, H. T. W. Tan, *Singapore Biodiversity: An Encyclopedia of the Natural Environment and Sustainable Development* (Didier Millet, Singapore, 2011).
- L. Y.-F. Gaw, A. T. K. Yee, D. R. Richards, A high-resolution map of Singapore's terrestrial ecosystems. *Data* **4**, 116 (2019).
- T. O'Dempsey, "Singapore's Changing Landscape since c. 1800" in *Nature Contained: Environmental Histories of Singapore*, T. Barnard, Ed. (National University of Singapore Press, Singapore, 2014), pp. 17–48.
- D. S. Wilcove, X. Giam, D. P. Edwards, B. Fisher, L. P. Koh, Navjot's nightmare revisited: Logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.* **28**, 531–540 (2013).
- M. M. Boehm, Q. C. Cronk, Dark extinction: The problem of unknown historical extinctions. *Biol. Lett.* **17**, 20210007 (2021).
- P. A. Tedesco *et al.*, Estimating how many undescribed species have gone extinct. *Conserv. Biol.* **28**, 1360–1370 (2014).
- I. M. Turner *et al.*, A study of plant species extinction in Singapore: Lessons for the conservation of tropical biodiversity. *Conserv. Biol.* **8**, 705–712 (1994).
- G. W. H. Davison, P. K. L. Ng, H. C. Ho, The Singapore Red Data Book: Threatened Plants and Animals of Singapore (Nature Society, Singapore, ed. 2, 2008).
- B. W. Brook, N. S. Sodhi, P. K. L. Ng, Catastrophic extinctions follow deforestation in Singapore. *Nature* **424**, 420–423 (2003).
- D. Storch, P. Keil, W. Jetz, Universal species-area and endemics-area relationships at continental scales. *Nature* **488**, 78–81 (2012).
- R. A. Chisholm, X. Giam, K. R. Sadanandan, T. Fung, F. E. Rheindt, A robust non-parametric method for quantifying undetected extinctions. *Conserv. Biol.* **30**, 610–617 (2016).
- N. P. Kristensen *et al.*, Extinction rate of discovered and undiscovered plants in Singapore. *Conserv. Biol.* **34**, 1229–1240 (2020).
- L. P. Koh *et al.*, Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634 (2004).
- M. Theng *et al.*, A comprehensive assessment of diversity loss in a well-documented tropical insect fauna: Almost half of Singapore's butterfly species extirpated in 160 years. *Biol. Conserv.* **242**, 108401 (2020).
- I. S. Law, X. Neo, D. N. Chan, R. Shivaram, Rediscovery of the Selangor mud snake, *Raclinia indica*, in Singapore. *Singapore Biodivers. Rec.*, 165–167 (2020).
- A. Jain, S. K. Khew, C. W. Gan, E. L. Webb, Butterfly extirpations, discoveries and rediscoveries in Singapore over 28 years. *Raffles Bull. Zool.* **66**, 217–257 (2018).
- K. Y. Chong *et al.*, Herbarium records do not predict rediscovery of presumed nationally extinct species. *Biodivers. Conserv.* **21**, 2589–2599 (2012).
- A. R. Solow, Inferring extinction from sighting data. *Ecology* **74**, 962–964 (1993).
- W. S. Yeng, P. C. Boyce, Taxonomic and Nomenclatural Notes On Malaysian Araceae I – Resolving *Homalomena ovata*, and a new name in *Homalomena* for *Chamaecladon ovatum*. *Aroidiana* **45**, 543–552 (2022).
- B. C. Ho *et al.*, The plant diversity in Bukit Timah Nature Reserve, Singapore. *Gardens' Bull. Singapore* **71**, 41–134 (2019).
- S. Lindsay *et al.*, Flora of Singapore: Checklist and bibliography. *Gardens' Bull. Singapore* **74**, 3–860 (2022).
- J. Romiguier *et al.*, Population genomics of eusocial insects: The costs of a vertebrate-like effective population size. *J. Evol. Biol.* **27**, 593–603 (2014).
- A. F. Carvalho, Illegalities in the online trade of stingless bees in Brazil. *Insect Conserv. Divers.* **15**, 673–681 (2022).
- M. Cremades *et al.*, Re-introduction of the Priental Pied Hornbill in Singapore with emphasis on artificial nests. *Raffles Bull. Zool.* **24**, 5–10 (2011).
- C. K. W. Tan, T. O'Dempsey, D. W. Macdonald, M. Linkie, Managing present day large-carnivores in 'island habitats': Lessons in memoriam learned from human-tiger interactions in Singapore. *Biodivers. Conserv.* **24**, 3109–3124 (2015).
- K. Y. Chong, H. T. W. Tan, R. T. Corlett, "A checklist of the total vascular plant flora of Singapore: Native, naturalised and cultivated species" (Raffles Museum of Biodiversity Research, National University of Singapore, Singapore, 2009), p. 273.
- M. S. Guiney, K. S. Oberhauser, Insects as flagship conservation species. *Terrestrial Arthropod Rev.* **1**, 111–123 (2008).
- F. Courchamp *et al.*, The paradoxical extinction of the most charismatic animals. *PLoS Biol.* **16**, e2003997 (2018).
- M. A. Niissalo, J. Leong-Škorničková, G. S. Khew, E. L. Webb, Very small relict populations suggest high extinction debt of gingers in primary forest fragments of a tropical city. *Am. J. Bot.* **104**, 182–189 (2017).
- A. Jain, F. K. S. Lim, E. L. Webb, Species-habitat relationships and ecological correlates of butterfly abundance in a transformed tropical landscape. *Biotropica* **49**, 355–364 (2017).
- E. Cros *et al.*, Fine-scale barriers to connectivity across a fragmented South-East Asian landscape in six songbird species. *Evol. Appl.* **13**, 1026–1036 (2020).
- W. X. Chio *et al.*, Regional and local extirpation of a formerly common Sundaic passerine, the Straw-headed Bulbul *Pycnonotus zeylanicus*. *Forktail* **35**, 3–11 (2019).
- H. C. Nash *et al.*, "The Sunda pangolin in Singapore: A multi-stakeholder approach to research and conservation" in *Pangolins*, D. W. S. Challender, H. C. Nash, D. W. C. Waterman, Eds. (Academic Press, 2020), pp. 411–425.
- T. Lamperty *et al.*, Rewilding in Southeast Asia: Singapore as a case study. *Conserv. Sci. Practice* **5**, e12899 (2023).
- M. D. Y. Khoo *et al.*, Persistence of a locally endangered mouse-deer amidst the re-emergence of two larger ungulates in small urban rainforest fragments. *Global Ecol. Conserv.* **30**, e01807 (2021).
- C. Pitra, C. Hütche, C. Niemitz, Population viability assessment of the banded leaf monkey in Singapore. *Primate Rep.* **42**, 47–47 (1995).
- M. D. Y. Khoo, M. C. K. Soh, B.P.Y.-H. Lee, Biodiversity record: Raffles' banded langur at Dairy Farm Nature Park. *Nat. Singapore* **14**, e2021059 (2021).
- K. K. P. Lim, M. A. H. Chua, N.T.-L. Lim, Freshwater fishes, terrestrial herpetofauna and mammals of Pulau Tekong, Singapore. *Nat. Singapore* **9**, 165–198 (2016).
- F. Cheong, Malayan tapir at Changi North. *Singapore Biodiversity Records*, 94–95 (2016).
- A. Ang, S. Jabbar, M. Khoo, Dusky langurs *Trachypithecus obscurus* (Reid, 1837) (Primates: Cercopithecidae) in Singapore: Potential origin and conflicts with native primate species. *J. Threatened Taxa* **12**, 15967–15974 (2020).
- A. C. Hughes, Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* **8**, e01624 (2017).

45. T. P. Dawson, S. T. Jackson, J. I. House, I. C. Prentice, G. M. Mace, Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**, 53–58 (2011).
46. W. X. Chiok, E. Y. Ng, Q. Tang, J. G. H. Lee, F. E. Rheindt, A distance sampling survey of the Critically Endangered Straw-headed Bulbul *Pycnonotus zeylanicus* in Singapore. *Bird Conserv. Int.*, **31**, 468–480 (2020).
47. P. B. Lee *et al.*, Sunda pangolin (*Manis javanica*) National Conservation Strategy and Action Plan: scaling up pangolin conservation in Singapore. (Singapore Pangolin Working Group, Singapore, 2018).
48. R. T. Corlett, Becoming Europe: Southeast Asia in the Anthropocene. *Elem. Sci. Anth.* **1**, 000016 (2013).
49. N. S. Sodhi, L. P. Koh, B. W. Brook, P. K. L. Ng, Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* **19**, 654–660 (2004).
50. J.-M. Roberge, P. Angelstam, Usefulness of the umbrella species concept as a conservation tool. *Cons. Biol.* **18**, 76–85 (2004).
51. L. P. Koh, Y. Zeng, T. V. Sarira, K. Siman, Carbon prospecting in tropical forests for climate change mitigation. *Nat. Commun.* **12**, 1271 (2021).
52. E. Y. X. Ng *et al.*, Conservation genomics identifies impact of trade in a threatened songbird. *Biol. Conserv.* **214**, 101–108 (2017).
53. S. L. Pimm, G. J. Russell, J. L. Gittleman, T. M. Brooks, The future of biodiversity. *Science* **269**, 347–350 (1995).
54. N. Kristensen, R. Chisholm, MODGEE-dark-extinctions-estimator. Github. <https://github.com/nadiahpk/MODGEE-dark-extinctions-estimator>. Accessed 13 November 2023.