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A comprehensive assessment of diversity loss in a well-documented tropical insect fauna: Almost half of Singapore's butterfly species extirpated in 160 years

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ABSTRACT

Insects as a group are suffering rapid declines in many parts of the world but are also poorly studied relative to vertebrate taxa. Comprehensive assessments of insect declines must account for both detected and undetected species. We studied extirpations among butterflies, a particularly well-known insect group, in the highly developed and biologically well-surveyed island city-state of Singapore. Building on existing butterfly species lists, we collated museum and naturalist records over the last two centuries and used statistical models to estimate the total extirpation rate since the first major collections in 1854. In addition, we compiled a set of traits for each butterfly species and explored how they relate to species discovery and extirpation. With a database of 413 native species, 132 (32%) of which are recorded as extirpated in Singapore, we used a statistical model to infer that, in addition, 104 unknown species (95% CI 60–162) were likely extirpated before they were ever discovered, suggesting a total extirpation rate of 46% (41–51%). In the trait analyses, we found that butterfly species that were discovered later were weakly associated with rarer larval host plants and smaller wingspans, while species that persisted for longer were weakly associated with higher larval host plant abundance and lower forest-dependence. This exercise is one of the first to offer a holistic estimate of extirpations for a group of insects by accounting for undetected extirpations. It suggests that extirpations among insects, specifically in the tropics, may be higher than naïve estimates based only on known records.

1. Introduction

Insects make up an estimated 90% of the terrestrial world's animal species and are thus essential to the overall state of biodiversity. Insects, more so than vertebrates, may be appropriate indicators of global environmental impacts in the Anthropocene (Briggs, 2017). And yet, the statuses of very few have been evaluated compared to vertebrate species (Régnier et al., 2015). Assessments of insect declines and extinctions remain hampered by two main issues: the lack of baseline information and the lack of rigorous analyses to account for unobserved events. This was reflected in a call for more robust insect data and rigorous analyses from all parts of the world following the highly publicised, and later criticised, review of global insect declines by Sánchez-Bayoa and Wyckhuys (2019) (Cardoso and Leather, 2019; Simmons et al., 2019; Thomas et al., 2019; Wagner, 2019). As such, comprehensive analyses that fulfil these criteria are invaluable because they serve as case studies of insect population trends occurring across the world.

Among insects, butterflies are a well-known group and are known to be valuable indicators of their environment because of their high degree of host-plant specialisation and vulnerability to habitat deterioration (Erhardt and Thomas, 1991; Koh et al., 2004; Jain et al., 2017). Moreover, it has been argued that butterflies are appropriate indicators of change for many insect groups, as preliminary assessments have found similar rates of loss in other groups (Thomas, 2005; Thomas, 2016). Given this, and that butterflies are present in a broad range of habitats, investigating butterfly population declines and losses potentially offers an insightful metric of the decline of habitat quality and

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quantity and of biodiversity as a whole.

The tropical island of Singapore (103°50′E, 1°20′N) has been used as a case study of tropical biodiversity loss (Corlett, 1992; Turner et al., 1994). Singapore's small self-contained area (originally 540 km^2; currently 722 km^2 due to land reclamation), its accessibility as a maritime port (as the main shipping channel between the Indian Ocean and South China Sea) and the enthusiasm of early natural historians have meant that its fauna has been well documented relative to other tropical regions. The city-state has experienced massive forest loss since 1819 and only ≈2.0% of forest remains, most of it secondary (Yee et al., 2011). Many species have been extirpated from Singapore during this process, from large vertebrates such as tigers (Corlett, 1992) to small orchids (Turner et al., 1994; Chong et al., 2009). Most of these species were not endemic to Singapore and continue to persist elsewhere, and thus we refer to them as "extirpations" rather than "extinctions".

The high quality of Singapore butterfly species data (Jain et al., 2018) provides an opportunity to conduct a comprehensive assessment of butterfly declines. A recent study found a 32% extirpation rate of Singapore butterflies since 1926 (Jain et al., 2018). This was based on a locally exhaustive documentation of species extirpations, discoveries and re-discoveries, resulting in a species list comprising 478 species from Singapore (301 resident, nine possibly extirpated, 144 extirpated, five migrants, 19 vagrants) belonging to six families (Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae and Riodinidae) (Jain et al., 2018). This list, though a comprehensive summary of present-day knowledge and existing literature on local species declines, tells only part of the story because it does not account for undetected extirpations—species that were extirpated before they could be discovered (Tedesco et al., 2014; Lees and Pimm, 2014). This is a point that Jain et al. (2018) also conceded, suggesting that there had been a poor-quality historic baseline for butterflies, as evidenced by the high rates of recent (1990–2017) discoveries of species previously not seen in Singapore.

To address the undetected extirpations question, a highly cited study by Brook et al. (2003) made the key assumption that all lowland species found in Peninsular Malaysia originally also inhabited Singapore in 1819, and came up with a strikingly high estimate of 73% extirpations accounting for both detected and undetected species. However, the key assumption of the method of Brook et al. (2003) is not tenable (Chisholm et al., 2016): lowland Peninsular Malaysia has an area over 200 times that of Singapore, and almost certainly has always had many more species. Note that for known extirpations, the numbers of Brook et al. (2003) were also slightly higher than those of Jain et al. (2018), 38% vs. 32%, but this is mainly attributable to the more up-to-date species list used by the latter.

The need to quantify undetected extinctions and extirpations in general is essential for forming a comprehensive assessment of humanity's effects on biodiversity (Chisholm et al., 2016). Accurate estimates and projections of extinction rates are also necessary for estimating the global taxonomic effort required to discover biodiversity that remains unknown before too many more undetected extinctions occur (Costello et al., 2013). Recently, new statistical methods have been devised for estimating undetected extinctions/extirpations (Tedesco et al., 2014; Chisholm et al., 2016; Kristensen et al., in revision). Using Singapore as a case study again, these methods have estimated that 31–36% of birds (Chisholm et al., 2016) and 32–35% of plants (Kristensen et al., in revision) have been extirpated in the last two centuries.

In this study, we applied a non-parametric extinction model (Chisholm et al., 2016; Kristensen et al., in revision), to produce estimates of undetected extirpations, and extirpations as a whole, in Singapore's butterfly fauna. An updated data set of earliest and latest butterfly species records was used. We also compiled a set of traits for each butterfly species and tested the hypotheses that more-conspicuous species would have been detected earlier and that more forest-dependent species would have been extirpated earlier.

2. Methods

2.1. Compilation of butterfly records

Using the dataset from Jain et al. (2018) as a baseline, we refined the list of butterfly species in Singapore and their respective record dates by collating individual records from specimens in museum collections, available literature and contemporary sighting records (refer to Supplementary information for full list of records and sources). Key texts used include works from Corbet and Pendlebury (1956, 1978), and national checklists by Khew and Neo (1997) and Khew (2015). Records of specimens were also acquired from available online databases, some of which are hosted on the Global Biodiversity Information Facility (GBIF) and the Naturalis Biodiversity Center in Leiden.

In addition, we physically searched through the butterfly collections (Main and Types Collections) at the Natural History Museum London (NHMUK). Over the period January–May 2018, we tracked down the oldest recorded specimens for each known butterfly species from Singapore. The specimens were then digitally imaged and uploaded online to the Biodiversity of Singapore digital reference collection (https://singapore.biodiversity.online/taxon/A-Arth-Hexa-Lepi). The NHMUK has about 5 million butterfly collections and these specimens are often sorted based on taxonomy and biogeography—they are rarely sorted according to the collector, country or time frame. Therefore searching for the physical specimen record was a time-consuming process. Each species from the Singapore butterfly list was cross-checked against the NHMUK internal database system to locate cabinet series, after which 800–1000 drawers were individually checked for potential Singapore specimens. Upon locating specimens, each specimen was examined to validate its record. In cases where there were typification errors or dubious specimen records, original species descriptions were referred to before the specimen was accepted. Our highest priority was to find specimens with the type locality in Singapore. As for non-type specimens known from Singapore, the priority was to find those collected during the colonial period (1800–1900; e.g., within Alfred Russel Wallace's collection).

For modern records, we used Jain et al. (2018) as the main reference (which comprised records from local bulletins and issues of the journals Raffles Bulletin of Zoology, Nature in Singapore, and Singapore Biodiversity Records). We supplemented our dataset with verified sightings on an iNaturalist project, Butterflies of Singapore (hosted on GBIF; https://www.inaturalist.org/projects/butterflies-of-singapore). Only records that were uploaded by known experts (e.g., Gan Cheong Weei, Simon Chan) or by the Nature Society Butterfly Group administrator (whose records were verified by A. Jain previously), were included (n = 5430). Additionally, we manually trawled through all the posts (by experts or identified by experts) on the Butterflies of Singapore and Malaysia Facebook group (a private group) and extracted every single butterfly sighting for Singapore, which yielded 151 records, all from the year 2017. Other records came from the NSS website and ButterflyCircle blog that are run by experts (http://butterflycircle.blogspot.com/). A crucial difference between our list and that of Brook et al. (2003) is that we did not assume that species recorded in Peninsular Malaysia were historically present in Singapore.

We excluded migrant and vagrant species (i.e., species without breeding records, documented only from sporadic sightings of up to three individuals and more than three individuals respectively; e.g., *Vanessa cardui* and *Appias lyncida vasava* respectively), and species with doubtful records (i.e., no confirmed first record or no confirmed last record). Species that had more than one subspecies were merged into one species as we were only interested in investigating species-level extirpations. For each species, we also compiled a list of record dates. The first record date of each species was obtained from the first specimen or sighting recorded. Otherwise, the first publication citing its presence in Singapore was used as a proxy. The last record date for all extant species was taken as the present year (2017, the year when the

Table 1
Ecological and morphological traits of Singapore's native butterfly species analysed in this study.

Trait	Definition	References
Number of host plant genera	Known number of larval host plant genera, excluding species with predaceous larvae.	Briggs, 2017; Robinson et al., 2001
Larval host plant abundance	Averaged inferred abundance of larval host plants for known host genera and families in Singapore. Host plant abundance classified as common (if common, naturalized, cultivated, weed of uncertain origin), intermediate (if vulnerable), rare (if endangered), or extirpated.	Chong et al., 2009; Briggs, 2017
Wingspan	Mean forewing length averaged between sexes (mm).	Briggs, 2017; Corbet and Pendlebury, 1992
Habitat specialisation	A binary metric of habitat preference: 1 = forest dependent, for species never recorded outside a primary lowland forest; 0 = non-forest dependent, for species encountered in other habitats (e.g., secondary forest).	Corbet and Pendlebury, 1992
Adult conspicuousness	Proportion of colours other than black, brown, or grey on the underside (for Lycaenidae and Hesperiidae) or upper side (for all other families) of both pairs of wings visually estimated as low (< 30%), moderate (30–70%), or high (> 70%). The more visible sex is scored.	Briggs, 2017; Corbet and Pendlebury, 1992

bulk of our collation work was performed). The last record date for extirpated species was taken as that of the most recent specimen or sighting. In cases where a date was recorded as “prior to XXXX”, where XXXX is a year, the year XXXX was used. Where a date was recorded as a range of years, “XXXX–YYYY”, the mean of the range was used. In 44 cases, the first and last dates of a species were both recorded as the same range of years (e.g. first and last record are both recorded as “prior to 1956”): we deleted such species due to high uncertainty.

2.2. Undetected extirpations analyses

For the main analyses, a nonparametric undetected extinctions model was used (Chisholm et al., 2016), which we call ‘SEUX’ after its four variables. The key assumption of SEUX is that detected and undetected species have the same extirpation probability within each year. The deterministic version of the underlying model (Chisholm et al., 2016; Kristensen et al., in revision) can be written as follows:

$$S_{t+1} = (1 - \mu_t)S_t + \nu_t(1 - \mu_t)U_t$$

$$E_{t+1} = E_t + \mu_t S_t$$

$$U_{t+1} = (1 - \nu_t)(1 - \mu_t)U_t$$

$$X_{t+1} = X_t + \mu_t U_t$$

where S_t, E_t, U_t and X_t are the numbers of detected extant, detected extirpated, undetected extant, and undetected extirpated species, respectively, in year t; and μ_t and ν_t are the extirpation rate and detection rate, respectively, in year t. The equations differ slightly from those in Chisholm et al. (2016) in that the extirpation process is assumed here to occur before the detection process in any given year, as in Kristensen et al., in revision. We fitted to our data a stochastic version of the above model (Kristensen et al., in revision), which treats the number of extirpated and detected species in each year as binomial random variables. The stochastic model gives similar results to the deterministic model but yields more-accurate confidence intervals on the estimates.

The SEUX method takes as input the first and last record dates of a group of species. The data are then converted into a time series of the number of detected extant species S_t and the number of detected extirpated species E_t in each year t up to the present year $t = T$. The method then produces estimates of the proportion of all species that are extirpated and the absolute number of undetected extirpated species at each time step ($\widehat{p}_t$ and $\widehat{X}_t$, respectively). A time series of the estimated number of undetected extant species $\widehat{U}_t$ is also produced, assuming that $\widehat{U}_T = 0$, i.e., there are no undetected extant species in the present day. If the latter assumption does not hold, then the estimate of $\widehat{p}_t$ is still robust, but the estimates of $\widehat{X}_t$ and $\widehat{U}_t$ are not (Chisholm et al., 2016). We conjectured that the assumption of perfect knowledge in the present day would be a reasonable approximation for butterflies in Singapore because they, like the previously assessed birds (Chisholm et al., 2016), are a well-studied taxonomic group.

We started the model in the year 1854, coinciding with the first extensive collections made by Alfred Russell Wallace. Although we could have started the model in 1833, when the very first butterfly was recorded (*Euploea crameri bremeri*), doing so leads to large uncertainty in the number of undetected extirpations because, out of the four species collected before 1854, one was never seen again (a small sample size effect; Kristensen et al., in revision). Thus we deliberately restricted our attention to extirpations that occurred from 1854 onwards.

We initially ran the analysis with all butterfly families. We then reran it excluding the Lycaenidae family: the cryptic nature of many lycaenids means that they are the group most likely to violate the model's assumption of perfect detection in the present day (George M. van der Poorten pers. comm.).

In order to test the key SEUX assumption, that extirpation rates (μ_t) do not vary systematically between detected and undetected species, we also explored temporal trends in butterfly extirpation. For species detected in each half century (1800–1849, 1850–1899, 1900–1949, 1950–1999, and 2000–2017), we calculated the probability of extirpation in that half century and every subsequent half century. If the SEUX assumption holds, then a species' probability of extirpation in a given time period should be independent of the time period in which it was discovered. Note that the coarse-graining of the data into half century intervals was only done for this latter part of the analysis testing the key SEUX assumption, in order to have sufficient statistical power to test for differences between groups of species detected at different times. In the main model fitting exercise, we used the full resolution annual data.

2.3. Compilation of butterfly traits and analyses

We compiled five species traits for each butterfly species. We chose traits that were a priori plausibly associated with detectability or vulnerability to extirpation: wingspan, adult conspicuousness, number of larval host plant genera, host plant abundance, and habitat specialisation (Table 1). We followed a previous method of classification (Koh et al., 2004) for the first four traits, and we improved an earlier measure of adult conspicuousness. Earlier studies measured conspicuousness using the wing colorations on the upper side for all species (Koh et al., 2004; Jain et al., 2017). Instead, we used resting behaviour to determine the side (upper or lower) from which to measure conspicuousness. Resting behaviour was assessed at the family level: Lycaenidae and Hesperiidae typically rest with their wings closed (underside visible); other families rest with their wings open (upper side visible; Khew, 2015). To classify habitat specialisation, though higher resolution information was available for extant species (Jain et al., 2017), we used an older reference for the entire Malay Peninsula (Corbet and Pendlebury, 1992) because we needed data for both extant and extirpated species.

To examine the relationship between species traits and the times they were first recorded and last recorded, two multiple linear regressions were performed: one with first record as the dependent variable and one with last record as the dependent variable. In both regressions

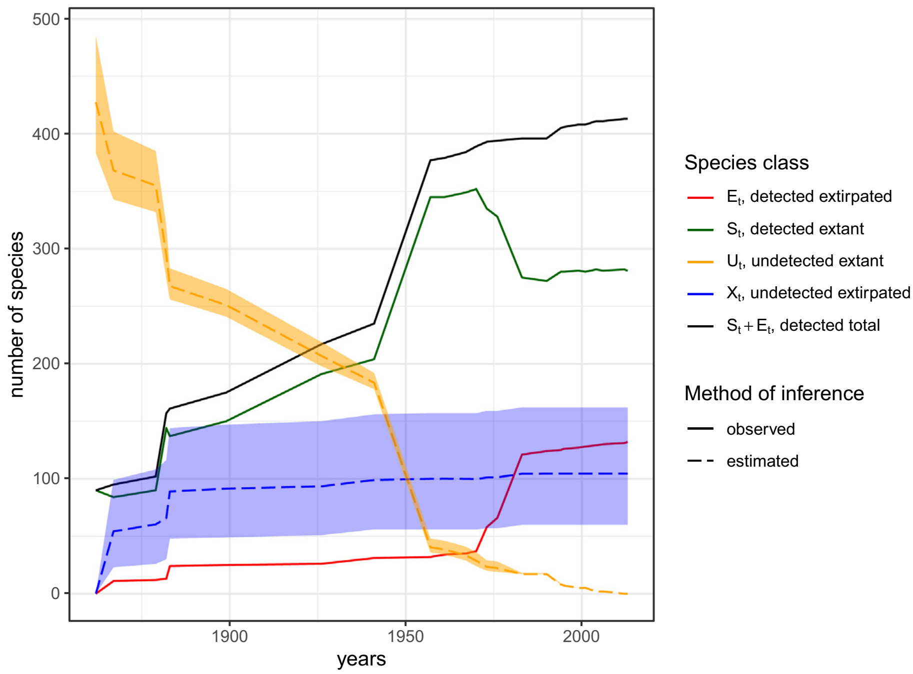

Fig. 1. Time series of all detected resident native butterfly species in Singapore (solid lines) and inferred undetected extirpations (blue dashed line) with 95% CI (shaded region). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the five traits were the independent variables. Note that only detected species could be used in the trait analyses because the identities of the undetected species are, by definition, unknown. Prior to doing the regressions, we looked at correlations among traits to assess for possible multicollinearity. We also assessed multicollinearity after the regressions were fitted using variance inflation factors.

All analyses were performed using R version 3.5.1 (R Development Core Team, 2018).

3. Results

After the first butterfly records in Singapore in the mid-19th century following British colonisation in 1819, there was a gradual increase in species detections up until the mid-1900s when the biggest increase in detections took place (black time series, Fig. 1). This was followed by a spate of detected extirpations (dip in green time series S_t corresponding to an increase in the red time series E_t, Fig. 1) in the 1970s. Several new discoveries were made from the 1990s up to 2011.

Of the 413 native butterfly species known (excluding species with no confirmed records) to have occurred in Singapore since 1854, 132 were considered extirpated or potentially extirpated from Singapore. This list consisted of additional species not present in Jain et al. (2018), confirmed by historical records obtained from the NHMUK collections, including six new additions in various families: *Halpe homolea*, *Scobura phiditia*, *Neptis magadha charon*, *Faunis gracilis*, *Graphium arycles arycles*. These species were all singletons (sighted in a single year) discovered between 1854 and 1899, and we did not find them recorded again. An additional singleton species, *Graphium ramaceus pendleburyi*, was excluded from our analysis because its single record was in 1844, i.e., before our 1854 start date.

In our initial application of the SEUX model to the entire post-1854 data set (n = 413), we estimated the number of undetected extirpations as 104, with a 95% confidence interval of [60, 162], implying 236 total extirpations (Fig. 1), and an overall extirpation rate of 46% (95% CI [41%, 51%]). When we repeated the analysis excluding the taxonomically complex family Lycaenidae (see the Methods section), the total number of known species was 240, the number of known extirpated species was 63, and the estimated number of undetected extirpated species was 69 [32, 122] (Fig. S1 in Supplementary Information; Table 1), which implies 132 [95, 185] total extirpations, and an estimated overall extirpation rate of 43% (95% CI: [35%, 51%]). Reassuringly, these numbers are similar to those for the analysis of the full data set, indicating that the main results are robust even though lycaenids may violate the model assumption of perfect present-day detection.

A comparison with past studies (Table 2) shows that while our dataset of butterflies recorded in Singapore included 32 more species than that of Brook et al. (2003), it included 21 fewer species than that of Jain et al. (2018), which is attributable to our conservative criteria for species inclusion in our analysis (i.e., we discarded species for which we could not get confirmed records). The most notable difference was in the number of undetected extirpations. Our estimates of the number of undetected extirpated species were less than a quarter of those of Brook et al. (2003), and our 95% confidence intervals did not include the

Table 2
Our results in comparison with other studies documenting butterfly species in Singapore.

Dataset	No. of resident native species $\{S_t + E_t\}$	No. extirpated $\{E_t\}$	No. undetected extirpations [95% CI] $\{X_t\}$	Prop. extinct (excl. undetected extirpations) ($p_t = \frac{E_t}{S_t + E_t}$)	Prop. extinct (incl. undetected extirpations) ($p_t = \frac{E_t + X_t}{S_t + E_t + X_t}$)
This study (full dataset)	413	132	105 [60, 163]	0.32	0.46 [0.41, 0.51]
This study (excluding Lycaenids)	240	63	69 [32, 122]	0.26	0.43[0.35, 0.51]
Jain et al., 2018	434	153	–	0.34	–
Brook et al. (2003)	381	145	482	0.38	0.73

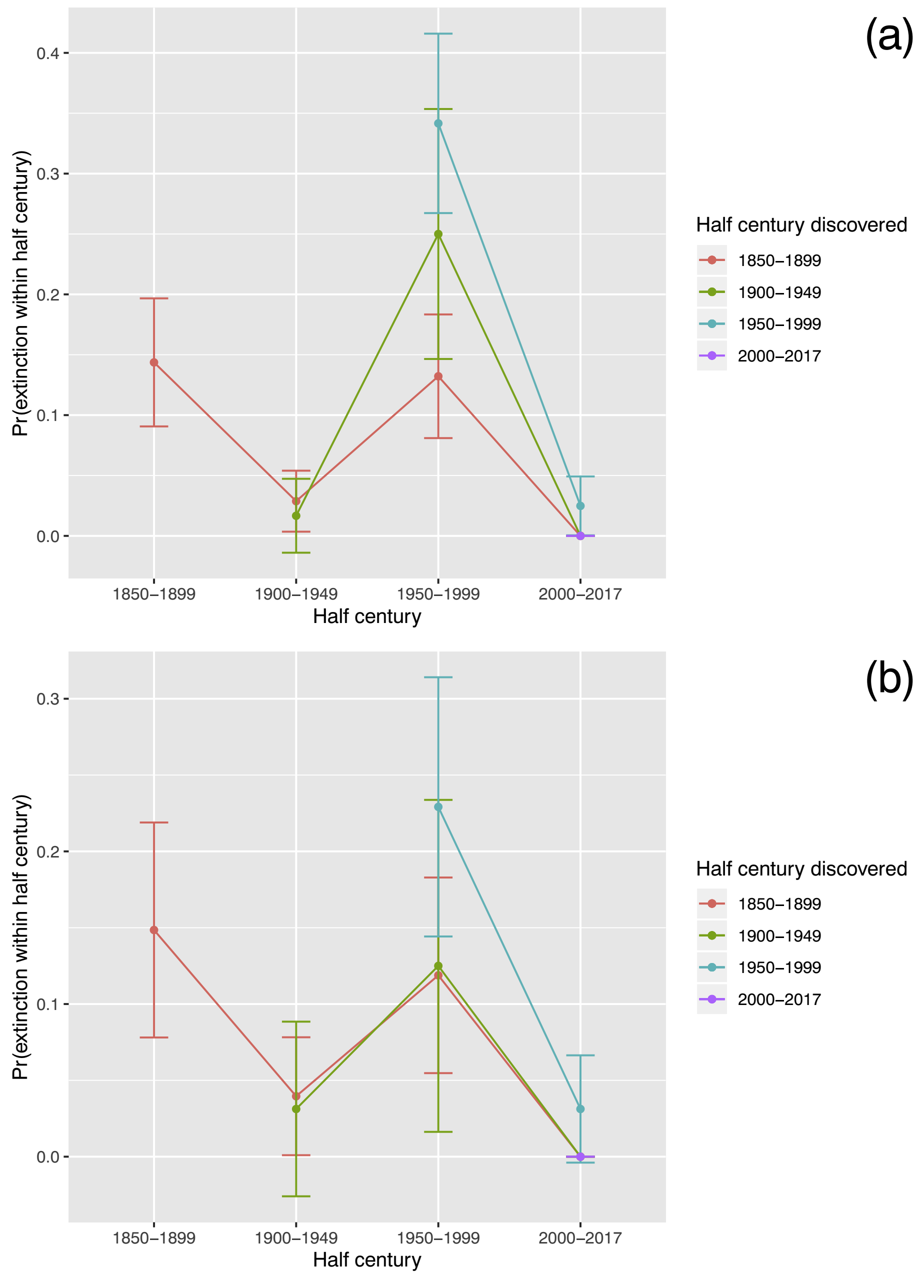

Fig. 2. Probability of extirpation over time for detected butterfly species, stratified by date discovered (colours): (a) the full dataset including Lycaenidae; b) the dataset excluding Lycaenidae. Data are aggregated by half century. Whiskers show 95% confidence intervals. Differences in the time series within each graph indicate correlations between extirpation and discovery dates across species, e.g., panel (a) shows that species discovered between 1950 and 1999 were more likely to be extirpated in that half century than other extant but earlier discovered species.

Brook et al. (2003) estimates (Table 2).

Probability of extirpation was positively related to discovery date across species, i.e., species that were discovered later appeared to be more prone to extirpation (i.e., the half century in which a species was discovered) (Fig. 2). In the full dataset, the probability of extirpation in species discovered between 1950 and 1999 was significantly higher than those discovered between 1850 and 1899 (Fig. 2a). This suggests violation of the model assumption that extirpation rates do not vary systematically between detected and undetected species. This problem was largely mitigated in the dataset excluding Lycaenidae, where the association between discovery and extirpation dates was weaker and not statistically significant (Fig. 2b).

Some of our trait variables were statistically significantly correlated. Number of host plant genera is negatively related to both larval host plant abundance (Spearman's $\rho = -0.350$, $p = 1.09 \times 10^{-7}$) and habitat specialisation ($\rho = -0.362$, $p = 5.80 \times 10^{-8}$), while the two latter variables were positively correlated ($\rho = 0.340$, $p = 3.01 \times 10^{-8}$). Also, habitat specialists tended to be less conspicuous ($\rho = -0.136$, $p = 0.00830$). However, these correlations were not strong enough to warrant exclusion of variables from the multivariate analyses. This was subsequently confirmed by the variance inflation factors calculated from the multivariate fits, which were all < 1.4.

The multivariate analyses revealed some statistically robust effects of traits on discovery and extirpation dates, but explained only a small fraction of the variance in dates across species. The relationship between species traits and first/last record dates could only be explored for the 206 species for which all traits were available. The multiple linear regression for discovery dates indicated that species discovered earlier were associated with larger wingspans: a 1 mm increase in

Table 3
Relationship between traits of resident native butterfly species and their first record dates in Singapore (n = 206, R^2 = 0.08).

Trait	Effect size	SE	*p*-Value
Intercept	1937.104	8.370	< 0.001*
Number of host plant genera	−0.387	0.615	0.531
Larval host plant abundance (intermediate)	16.509	7.761	0.035*
Larval host plant abundance (rare)	−3.964	8.664	0.648
Larval host plant abundance (extirpated)	12.581	28.641	0.672
Wingspan	−0.538	0.239	0.026*
Habitat specialisation	−7.780	6.431	0.228
Adult conspicuousness (intermediate)	−11.861	6.925	0.088
Adult conspicuousness (high)	−11.366	7.336	0.123

* p-Value ≤ 0.05

Table 4
Relationship between traits of resident native butterfly species and their last record dates in Singapore (n = 206, R^2 = 0.23).

Trait	Effect size	SE	*p*-Value
Intercept	2017.429	2.919	< 0.001*
Number of host plant genera	−0.038	0.215	0.858
Larval host plant abundance (intermediate)	−12.560	2.706	< 0.001*
Larval host plant abundance (rare)	−6.267	3.021	0.039*
Larval host plant abundance (extirpated)	−43.734	10.335	< 0.001*
Wingspan	0.077	0.083	0.357
Habitat specialisation	−5.307	2.242	0.019*
Adult conspicuousness (intermediate)	−4.997	2.414	0.040*
Adult conspicuousness (high)	−2.668	2.558	0.298

* p-Value ≤ 0.05

wingspan was associated on average with detection 0.54 years earlier (Table 3; R^2 = 0.08). The multiple linear regression for last record dates indicated that species with lower larval host plant abundance, higher habitat specialisation (forest dependence), and greater conspicuousness were less likely to have been seen recently (Table 4; R^2 = 0.23). Most of these effects were weak and amounted to just five or so years difference in the average last record date. However, the effects of host plant abundances were reasonably strong. The two butterfly species (*Ideopsis gaura perakana*, *Elymnias esaca esaca*) with extirpated host plants were last recorded in 1970 and are thus assumed to be extirpated; this is 44 years earlier than the average last record date for species with common host plants. Butterfly species with host plants of rare and intermediate abundance had last record dates an average of 6 and 13 years, respectively, earlier than species with common host plants (Table 4). See Supplementary Information S3 for graphical representations of trait values versus dates of first and last record.

4. Discussion

The highly urbanised island of Singapore has often been used as an example of what biodiversity in other nations in Southeast Asia, and around the tropics, could look like if habitat destruction continues at current rates. The high fidelity of Singapore's butterfly data in particular provides a window on to the potential magnitude of tropical insect extinctions after deforestation. Previously, Brook et al. (2003) estimated that 38–73% of butterfly species have been extirpated from Singapore. The lower bound was based on observed extirpations and the upper on the assumption that all lowland species found in Peninsular Malaysia (excluding savanna species, because Singapore lacks this habitat) also inhabited Singapore in 1819. The upper bound assumption is untenable considering that Singapore is a small fraction of the size of Peninsular Malaysia (0.4%), and spans just a small fraction of a degree in latitude (Peninsula Malaysia spans 5°). Our model's more defensible assumptions give a more realistic assessment of Singapore's butterfly fauna, and thus a more reliable case study of tropical insect extirpations.

The decades following Singapore's colonisation witnessed very high extirpation rates among butterflies known at the time: 14.9% of the species discovered before 1900 also were extirpated before 1900. These high early observed extirpation rates, during a period where many species remained to be discovered, suggest that a high number of species were never detected before they were extirpated—this is the essential underlying logic of the SEUX model (Chisholm et al., 2016). This early spate of extirpations is likely attributable to the earliest period of species discovery (44.3% of all species discovered were between 1854 and 1899) coinciding with a period of rapid primary forest loss (Fig. 3; > 95% loss between 1820 and 1899; Corlett, 1992). We consider our high estimates of undetected extirpations to be biologically plausible, because this rapid forest loss would have wiped out many butterfly species, particularly primary forest specialists. The half century 1950–1999 also saw high rates of butterfly extirpations, which we attribute to the rapid urbanisation of Singapore in the same period (Fig. 3). This was a time where large swathes of agricultural land were converted into other land uses such as public housing and industrial estates (Jain et al., 2018). However, these later extirpations have less influence on the estimated rate of undetected extirpations in the SEUX model, because most species were known by this period. Overall, our findings confirm the prediction of Jain et al. (2018) that, because the historic baseline for butterfly data was poor, undetected extirpations for butterflies should be higher than for birds. For birds, accounting for undetected extirpations increased the estimated extirpation rate in Singapore from 1819 to 2015 only slightly, from 30% to 33% (Chisholm et al., 2016).

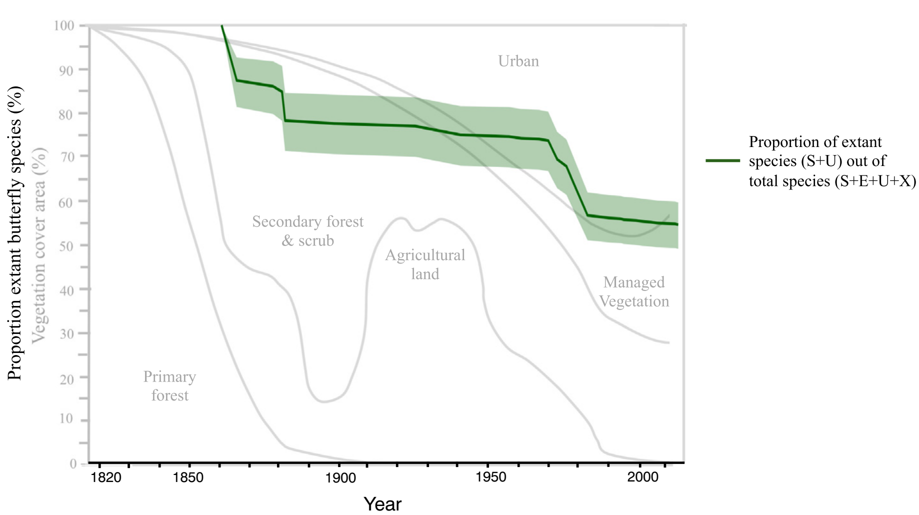

Fig. 3. Vegetation cover change and proportion of extant (detected and undetected) resident native butterfly species in Singapore with 95% CI (shaded region). The vegetation cover graph was adapted from Jain et al. (2018), who drew from several sources (Corlett (1992) for 1819–1990; Yee et al. (2011) and NParks (2019) for 2017). Agricultural land included tree crops such as rubber; managed vegetation included parks, gardens, and turf.

The observed 46% extirpation rate of butterflies in Singapore over 160 years exceeds likely background extirpation levels, i.e., levels that would be expected in the absence of human disturbance. The observed rate translates to an annual extirpation rate of 0.38%. For comparison, we estimate the background extirpation rate for butterflies on a tropical island the size of Singapore to be on the order of 0.10% per year. This rough estimate is based on data from Diamond (1971) suggesting that the background extirpation rate of birds on a tropical island similar in size to Singapore (Karkar Island off the coast of Papua New Guinea) is roughly half that of similar-sized temperate islands (the Channel Islands in California), and data from Diamond (1969) and Miller (1984) suggesting that background extirpation rates for birds and butterflies on temperate islands (again the Channel Islands in California) are roughly similar. Thus, we can tentatively conclude that the butterfly extirpation rate in Singapore over the last 160 years has been about four times the background level. Importantly, these extirpations have not been offset by new immigrations: the butterfly diversity of Singapore has declined over time.

Is the observed high extirpation rate consistent with ecological theory? The power-law species–area relationship (SAR) is commonly used to estimate species loss with habitat loss. If we use the standard exponent of z in the range 0.2–0.3 in the formula $S = cA^z$, where S is species richness, A is area, and c is a constant, we estimate that 98% habitat loss would lead to a species loss of $1 - (1 - 0.98)^z$, i.e., 54–69%. This is higher than our estimate of 46% from the empirical data. We attribute this mainly to two assumptions of the power law SAR (Chisholm et al., 2016): (i) no species persist in cleared habitats; and (ii) the remaining habitat is contiguous. For Singapore butterflies, the first of these is violated because some species live in parks and gardens (Khew, 2015), more consistent with the countryside biodiversity model that accounts for their persistence in non-natural habitat (Pereira and Daily, 2006). The second power-law SAR assumption is violated because the remaining habitat in Singapore is spread in patches over a broad area so it can capture more beta diversity than a power-law SAR model would assume (Chisholm et al., 2016; Thompson et al., 2019).

As we look to the future, it is likely that the number of butterfly extirpations in Singapore will increase as extinction debt is paid. Some extant species may be present in unsustainably low numbers and disappear in coming decades. Others may be victims of coextinction. Large extinction debts of plants (Vellend et al., 2006) can have cascading impacts on butterflies at both the larval and nectarivorous adult stage because butterflies are dependent on their larval host plants and nectar plants for survival. For example, *Troides helena* and *Pachliopta aristolochiae* butterflies were nearly extirpated as a result of the decline of their native host plant *Aristolocia jackii* in Singapore (Jain unpublished data). Extinction debt may be particularly high for butterflies dependent on slow-growing trees, which have long generation times and correspondingly long extinction debt repayment periods. On a technical point, we note that the power-law SAR method discussed above does not account for extinction debt (Thompson et al., 2019), and so even though ongoing payment of extinction debt may eventually bring the data more in line with the power law's predictions, the underlying mechanisms will be different.

Our analysis of the dataset without the problematic Lycaenidae family, which includes several hard-to-detect species, largely affirmed the robustness of the main analysis but pointed to a continuing need for more work on this group. Among the Lycaenidae, there is a general lack of confidence in accurate determination of species statuses (extirpated vs. extant) because of their highly specific habitat requirements and cryptic morphology (details in the Methods section). Small degrees of environmental change can have large effects on the incidence of some lycaenid species, to the point that certain species can be observed only at a specific time of day along under specific environmental conditions (New, 1993; George M. van der Poorten pers. comm.). In addition, this was complicated by the difficulty of species identification. Many cryptic species can be identified only with examination of minute details in wing markings and genitalia (Corbet and Pendlebury, 1956; D'Abrera, 1986). We encountered an example of this during our study: *Arhopala epimuta epiala* (Lycaenidae) was misidentified as *Arhopala agesilaus gesa* in Doggett's collection (confirmed by George M. van der Poorten), the latter a species never recorded in Singapore. It is also speculated by butterfly naturalists that there are cryptic lycaenid species yet to be discovered in Singapore (Khew, 2015). The relatively high chance of misidentification and the likelihood that there are still species to be discovered means that our estimates of the absolute numbers of extirpated and extant species should be taken tentatively, because these depend on the SEUX model's assumption that there are zero undetected extant species in the present day. However, the fractional estimates of overall extirpations should be robust, because they do not rely on this assumption and also because similar results emerged from our analysis without the complex Lycaenidae family (Table 2).

The trend of smaller butterfly species associated with rarer larval host plants being discovered later was weakly consistent with our hypotheses. Collector interest may be skewed towards butterfly species that are larger and more conspicuous. In our data set, an earlier mean first record date was recorded for species in the families Nymphalidae, Papilionidae, Pieridae and Riodinidae, which are generally larger and/or more conspicuous than species from Lycaenidae and Hesperiidae (Fig. S5; New, 1993, de Jong et al., 1996). The relative lack of attention to lycaenids appears to have been the case since early collectors (New, 1993), and persists in taxonomy and in modern hobbyist activity due to the high level of expertise required for this group (Khew, 2015; pers. obs.). In addition, the difficulty of identifying small, cryptic lycaenid species is likely to have contributed to later first record dates among that group.

Butterfly species that had lower host plant abundances and that were habitat specialists tended to be extirpated earlier. Since larval host plant abundance is strongly associated with butterfly abundance (Schultz and Dlugosch, 1999; Dennis et al., 2004; Curtis et al., 2015; Jain et al., 2017) and co-extinctions are likely to occur between species and their host plants (Stork and Lyal, 1993; Koh et al., 2004), it is plausible that rarer butterflies get discovered later and tend to be extirpated earlier. Unlike our study, Koh et al. (2004) found larval host plant specificity (number of host plant genera) to be an important correlate in butterfly extirpation probability. This may be because high host plant specificity does not always correlate with low host plant abundance (i.e., a species may be specific to one larval host plant but that host plant may be common), although species that have a narrower dietary breadth are generally more sensitive to changes in host plant abundance (Dapporto and Dennis, 2013; Curtis et al., 2015). It is also important to note that common butterfly species will have more observations, which increases the chance that more host plant genera are described in the literature, thus increasing the likelihood of confounding the variables associated with host plants. Our result that habitat specialists are extirpated earlier is consistent with the earlier study (Koh et al., 2004). One trait we did not look at, and that could account for a fraction of the unexplained variance in extirpation dates across species, is dispersal ability, which has been negatively associated with butterfly extirpation risk elsewhere in the tropics (Basset et al., 2015).

Our estimated total extirpation rate of 46% for butterflies is higher than corresponding estimates for birds and plants in Singapore (31–36, 32–25% respectively). The high sensitivity of butterflies relative to other taxa has also been documented in Britain, where the fraction of species exhibiting range declines is 71% for butterflies versus 54% for birds and 28% for plants (Thomas et al., 2004). Butterfly declines may be indicative of insect declines more broadly (Thomas, 2005). Again in Britain, the fraction of species exhibiting range declines among moths (66%; Conrad et al., 2006) is similar to that among butterflies (71%). The extirpation rate of bumblebees (7.6%) and dragonflies (6.9%) in Britain is similar to that of butterflies (6.6%; Thomas, 2005). The potential of butterflies to serve as an indicator group for insects is of particular importance in the context of the paucity of data for insects in general.

The significantly higher total extirpation rate of 46% (41–51%) compared to known extirpations (32%) signals the importance of accounting for undetected species when assessing insect extirpations. Applying the SEUX method on datasets from well-studied cities or areas such as New York City, London, Los Angeles, and Southern Europe is a worthwhile direction for future research. Additionally, future studies that have species records with precise location data can consider using an occupancy modelling approach (e.g. presence or absence within 10 km × 10 km grids; Thomas, 2005; Conrad et al., 2006) in the SEUX framework to provide better estimates of last detection dates and to capture detected and undetected range losses at finer grains. If it is generally true that total insect extirpation rates are substantially greater than observed rates, this would be a hugely important finding given the integral roles insects play in ecosystems, and their high diversity. Insects act as pollinators, decomposers and prey for animals higher up the food chain, and thus their declines will have cascading effects on plants and animals in the ecosystem (Lister and Garcia, 2018).

4.1. Limitations

Though butterflies are a relatively well-studied taxonomic group in Singapore on which several ecology and conservation studies have been published (Koh et al., 2004; Jain et al., 2016; Jain et al., 2017; Jain et al., 2018), we encountered several challenges in obtaining a complete and accurate dataset of first and last records for native resident butterfly species. Firstly, we could not obtain true first locality records (i.e., specimens in collections) for a substantial number of species (n = 124) that were listed in our main reference as occurring in Singapore (Corbet and Pendlebury, 1956). Though we did go to significant efforts to obtain early records, even further effort in searching in collections may improve the quality of the data in this regard. However, that necessitates accessing additional collections in multiple global locations in person, each of which require significant resources to gather. We also note that the bias in collecting and record keeping of butterfly species against smaller and less conspicuous species could have influenced the quality of our dataset. In addition, errors could have arisen in data labels of museum specimens referenced (e.g., locality names changed and inaccuracy in record keeping). In future exercises, inferring redetection effort from a collection of all records, instead of just first and last, could prove useful in understanding biases and errors (Kristensen et al., in revision).

5. Conclusions

Amidst the current surge of academic and public interest in insect declines and the realisation that there is a lack of baseline data, we have presented an assessment of species extirpations in one of the world's best-documented tropical insect faunas. The substantially higher estimate of overall extirpations compared to known extirpations signals the importance of accounting for undetected species in insects. This exercise corroborates the findings of existing studies that suggest insects may be more susceptible to diversity loss than other taxa, highlighting the need to identify and protect declining species. Lastly, this study illustrates that even among butterflies, some species-rich taxa (Lycaenidae) remain understudied. This points to the general need to redouble survey and taxonomic efforts on cryptic and elusive insect groups, where current conservation status of known species is uncertain and more unknown species await discovery.

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CRediT authorship contribution statement

Meryl Theng: Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Wan F.A. Jusoh:** Investigation, Data curation. **Anuj Jain:** Resources, Supervision. **Blanca Huertas:** Investigation, Resources. **David J.X. Tan:** Investigation. **Hui Zhen Tan:** Investigation. **Nadiah P. Kristensen:** Methodology, Software. **Rudolf Meier:** Supervision. **Ryan A. Chisholm:** Conceptualization, Methodology, Software, Validation, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

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