**BIODIVERSITY RESEARCH**

# Correlates of extinction proneness in tropical angiosperms

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## ABSTRACT

Rapid losses and degradation of natural habitats in the tropics are driving catastrophic declines and extinctions of native biotas, including angiosperms. Determining the ecological and life-history correlates of extinction proneness in tropical plant species may help reveal the mechanisms underlying their responses to habitat disturbance, and assist in the pre-emptive identification of species at risk from extinction. We determined the predictors of extinction proneness in 1884 locally extinct ($n = 454$) and extant ($n = 1430$) terrestrial angiosperms (belonging to 43 orders, 133 families, and 689 genera) in the tropical island nation of Singapore (699.4 km$^2$), which has lost 99.6% of its primary lowland evergreen rainforest since 1819. A wide variety of traits such as geographical distribution, pollination system, sexual system, habit, habitat, height, fruit/seed dispersal mechanism, and capacity for vegetative re-sprouting were used in the analysis. Despite controlling for phylogeny (as approximated by family level classification), we found that only a small percentage of the variation in the extinction probability could be explained by these factors. Epiphytic, monoecious, and hermaphroditic species and those restricted to inland forests have higher probabilities of extinction. Species dependent on mammal pollinators also probably have higher extinction probabilities. More comparative studies that use species traits to identify extinction-prone plant species are needed to guide the enormous, but essential task of identifying species most in need of conservation action.

### Keywords

**Conservation, extinction risk, generalized linear mixed-effects models, life history, phylogenetic control, selectivity, species traits, tropical biotas, vulnerability.**

## INTRODUCTION

Although tropical forests contain more than half of global biodiversity, they cover less than 7% of the Earth's land surface (Dirzo & Raven, 2003). Despite their high conservation value, these forests are being destroyed and degraded at unprecedented rates owing to human activities (Laurance, 1999; Achard *et al.*, 2002). Over 40% of the primary forests of tropical Asia and Africa have been cut (Wright, 2005), and unabated deforestation in the tropics will result in catastrophic declines and extinctions of native biotas (Brook *et al.*, 2003; Brook *et al.*, 2006a; Sodhi & Brook, 2006). Recent studies have revealed a ubiquitous pattern of non-random species extinctions across a wide range of organisms (McKinney, 1997; Purvis *et al.*, 2000; Sekercioglu *et al.*, 2002; Koh *et al.*, 2004c; Sodhi *et al.*, 2004; Cardillo *et al.*,

2005). For example, species that possess certain evolved traits (e.g. narrow geographical range) may be more prone to extinction through human activities than others (Brook *et al.*, 2006a). Statistical determination of the traits associated with extinction proneness, especially if based on a *priori* hypotheses, helps reveal the mechanisms underlying a species' response to habitat disturbance, and will assist in the pre-emptive identification of persisting species that face the greatest risk of extinction.

Forest disturbance in the tropics has resulted in the local extinction of many plants (Turner *et al.*, 1994; Turner *et al.*, 1996). However, the mechanisms underlying the responses of plant species to anthropogenic disturbance remain poorly understood. Natural disturbance in a tropical forest creates ephemeral habitats of earlier successional states (e.g. forest gaps) (Connell, 1978; Sheil & Burslem, 2003). Species adapted to such

habitats are characterized by rapid growth, high fecundity, high genetic variability, and dispersal ability, traits that allow them to reproduce quickly and colonize new patches of highly variable and impermanent habitats, but they often have poorer competitive ability in later seral stages (Odum, 1969; Horn, 1974; Connell & Slatyer, 1977; Denslow, 1987). On the other hand, species adapted for the comparatively stable old-growth forest environment may be characterized by traits associated with slow growth, long lifespan, and high gametic investment (and consequent low fecundity), traits that facilitate acquisition of limited resources (e.g. light and nutrients) to survive in a highly competitive environment. Additionally, these forest species may possess life-history strategies (e.g. epiphytic habit) that allow them to exploit unique microhabitats in the multilayered environment of a tropical rainforest. When anthropogenic forest disturbance transforms a forest or maintains it in earlier successional states (e.g. open habitats), different ecological and life-history traits may predispose some species to extinction while allowing others to thrive or at least persist.

With this conceptual framework, we compared ecological and life-history traits between extirpated (locally extinct) and extant angiosperm species in the highly urbanized tropical island nation state of Singapore (103°50′ E, 01°20′ N; 699.4 km$^2$). Such a large database recording true species extirpations is an unusual opportunity to study the potential drivers of extinction *per se* than extinction risk (e.g. IUCN Red List category) alone, providing an important insight into the ultimate drivers of extinction. In Singapore, historical losses of lowland evergreen rainforest cover (99.6%) and terrestrial vascular plant species (25.3%) over almost two centuries have been well documented (Brook *et al.*, 2003). We ask the following questions: (1) Are angiosperm species with narrower geographical distributions more prone to extinction than those more widely distributed? (2) Do angiosperm species restricted to forests have high extinction proneness? (3) Does reliance on animal-assisted pollination or seed dispersal elevate their extinction risk? (4) Do intrinsic life history attributes, such as sexual system, habit, maximum height, and the capacity for vegetative resprouting, affect extinction risk in angiosperms?

Previously, Turner *et al.* (1994) provided a preliminary qualitative analysis of extinctions among different life forms and habitat associations of vascular plants in Singapore. Our analysis improves upon this study in three ways: (1) it is quantitative (probabilistic), (2) it is based on a more comprehensive set of species traits, and (3) it controls for phylogenetic effects (using family level classification as a surrogate) that might otherwise confound relationships owing to shared evolutionary history. Our study demonstrates the need to use trait-based comparative studies for identifying extinction-prone plant species. Such analyses serve as important tools to facilitate the enormous but essential task of assessing the conservation status of tropical angiosperms.

## METHODS

We restricted our analyses to the 1884 species (1430 extant; 454 extinct) of eudicots, monocots, and magnoliids native to Singapore, excluding aquatic species (Table 1). We adopted the classification system of the Angiosperm Phylogeny Group (2003) for taxonomic ranks of family and above. We collected data on geographical distribution, pollination system, sexual system, habit, habitat, height, fruit/seed dispersal mechanism, and capacity for vegetative re-sprouting for each species (Table 1) based on published floras, revisions, herbarium specimens, and our personal observations (e.g. van Steenis, 1948–1954, 1955–1958, 1960–1972, 1971–1976, 1974–1978, 1979–1983; Whitmore, 1972, 1973; Ng, 1978, 1989; van Steenis & de Wilde, 1984–1989; Kalkman *et al.*, 1992–1994, 1995–1996, 1997; Soepadmo & Wong, 1995; Turner, 1995; Soepadmo *et al.*, 1996; Kirkup *et al.*, 2000; Soepadmo & Saw, 2000; Nooteboom, 2001, 2002, 2005; Soepadmo *et al.*, 2002). These traits were selected on the basis of previous studies (e.g. McIntyre *et al.*, 1995; Duncan & Young, 2000) that suggest that they may be associated with extinction proneness.

Each species was placed in one of three geographical distribution categories (Malesian; Asiatic and/or Australian and/or Pacific and/or African; and pantropical). We coded the pollination system as nominal factors using primary pollinating agent categories (insect, mammal, bird, and wind). We classified each species according to its sexual system (monoecious, dioecious, or displaying heteromorphic incompatibility, i.e. di- or tri-styly; and hermaphrodite or polygamous). Each species was placed into one of three categories on the basis of its habit (obligate epiphyte; tree or treelet; and shrub/herb/climber), and each was grouped according to its habitat (disturbed habitats [e.g. plantations]; inland mature forest comprising dryland or freshwater swamp forests; and coastal ecosystems such as mangrove, tidal zones, and sandy/rocky shores). Each species was also classified into one of six categories based on height (mechanically dependent on other plants; ≤ 1.0 m; > 1.0–2.0 m; > 2.0–10.0 m; > 10.0–20.0 m; and > 20.0 m). Species were classified into three categories according to the fruit/seed dispersal mechanism (biotic, i.e. animal-dispersed; abiotic, i.e. wind- or water-dispersed; and explosive/no obvious adaptation), and into two categories based on their capacity for vegetative resprouting (present or absent). All the extinctions examined here are local/population extinctions. Extinct species were defined as those that have not been sighted or collected in the wild for 30 years or more (Ng & Wee, 1994; Tan, 1995) despite active searching by botanists in both protected and unprotected areas.

## Statistical analysis

To determine the influence of each ecological trait on the extinction probability of angiosperm species, we fitted generalized linear mixed-effect models (GLMM) to the data using the lmer function implemented in the ʀ Package (R Development Core Team, 2004). For each GLMM, we coded species extinction probability (i.e. extirpated vs. extant) as a binomial response variable and each ecological trait as a linear predictor (fixed effects – see below), assigning each model a binomial error distribution and a logit link function. All ecological traits were coded as

Table 1 Taxonomic and species summary for the three classes (eudicot, monocot, and magnoliid), orders, families, and genera of extant and extirpated Singaporean angiosperms analysed in this study. Also shown is the species summary for each level of the extinction correlates examined.

| Taxonomy/Status | Number | Correlate | Level | Number of species | Extant | Extirpated |
|---|---|---|---|---|---|---|
| Eudicot | 1316 | *Fruit/seed dispersal* | Animal-assisted | 1210 | 1000 | 210 |
| Monocot | 447 | | wind/water-assisted | 508 | 285 | 223 |
| Magnolid | 121 | | None | 163 | 143 | 20 |
| No. of orders | 43 | *Distribution* | Malesian | 944 | 704 | 240 |
| No. of families | 133 | | Asia/Austr/Pac/Afr | 911 | 700 | 211 |
| No. of genera | 689 | | Pantropical | 29 | 26 | 3 |
| Extirpated | 454 | *Habit* | Epiphyte | 235 | 74 | 161 |
| Extant | 1430 | | tree/treelet | 800 | 689 | 111 |
| | | | Other | 849 | 667 | 182 |
| | | *Habitat* | Coastal | 193 | 143 | 50 |
| | | | Forest | 1292 | 938 | 354 |
| | | | Margins/edges | 399 | 349 | 50 |
| | | *Height* | Mechanically dependent | 628 | 379 | 249 |
| | | | ≤ 1 m | 138 | 103 | 36 |
| | | | > 1 to ≤ 2 m | 69 | 52 | 18 |
| | | | > 2 to ≤ 10 m | 226 | 187 | 39 |
| | | | > 10 to ≤ 20 m | 237 | 207 | 30 |
| | | | > 20 m | 558 | 488 | 70 |
| | | *Pollination system* | Insect | 1762 | 1333 | 429 |
| | | | Mammal | 32 | 23 | 9 |
| | | | Bird | 26 | 16 | 10 |
| | | | Wind | 53 | 50 | 3 |
| | | *Sexual system* | Monoecious | 194 | 163 | 31 |
| | | | Dioecious | 382 | 334 | 48 |
| | | | Hermaphrodite or polygamous | 1306 | 932 | 374 |
| | | *Veg resprouting* | Present | 613 | 987 | 229 |
| | | | Absent | 1180 | 384 | 193 |

categorical factors. Species are phylogenetic units with shared evolutionary histories and are not therefore statistically independent units (Felsenstein, 1985). It was necessary to decompose the variance across species by coding the random-effects error structure of the GLMM as a hierarchical taxonomic (class/order/family) effect (Blackburn & Duncan, 2001). We had insufficient replication within genera to include the genus in the nested random effect. Our method is more appropriate than the independent-contrasts approach (Purvis *et al.*, 2000) in situations where a complete phylogeny of the study taxon is unavailable, when categorical variables are included in the analysis, and when model selection, rather than hypothesis testing, is the statistical paradigm being used. The amount of variance in the extinction probability response variable captured by each model considered (see below) was assessed as the percentage deviance explained (%DE) (Brook *et al.*, 2006b). We also examined the relationships using generalized linear models (GLM) in addition to GLMMs to examine the influence of ignoring the phylogenetic control of the hierarchical taxonomic random effect (function glm in the R package). The 'null' model used to calculate the percentage DE was a fitted linear model with no fixed effects (i.e. a universal [intercept] risk estimate for all species), but included the taxonomic random effect for the GLMMs.

We checked for collinearity among ecological traits using the 'perturb' package in R (Hendrickx *et al.*, 2004). For a specified 100 iterations, 'perturb' either adds a small random perturbation value (mean of 0 and standard deviation of 1) to continuous variables or randomly reclassifies categorical variables (with 95% probability of reclassifying to the same category). Function 'perturb' then re-estimates the model to assess the effect of the perturbations on parameter estimates. Collinearity is deemed a serious problem if perturbation of one variable causes the parameter estimates of others to become unstable and fall outside their 95% confidence interval. We found no evidence for collinearity among the ecological traits, so we retained all of them for subsequent analyses.

Our model-building strategy used existing knowledge from other studies, ecological theory, and logic to construct a plausible set of a *priori* hypotheses to examine the predictors of extinction risk in tropical vascular plants. Based on information from woody species in Costa Rican wet forests (Chazdon *et al.*, 2003), we also included several models incorporating the interaction between *sexual system* and *habit* as well as the interactions between *sexual system* and *fruit/seed dispersal mechanism*, between *habit* and *fruit/seed dispersal mechanism*, and between *habit* and *fruit/seed dispersal mechanism*. We originally intended to

**Table 2** A set of generalized linear mixed-effects models used to examine the correlation between a species' ecological and life-history attributes and its extinction proneness. Model combinations, derived *a priori*, represent particular analytical 'themes' grouping related traits and testing for particular interaction effects. Terms include DP = *fruit/seed dispersal mechanism*, DT = *distribution*, HB = *habit*, HBT = *habitat*, HT = *height*, PL = *pollination system*, SS = *sexual system*, and VG = *vegetative resprouting*. Allometry refers to size/longevity.

| Model no. | Model | Analytical theme |
|---|---|---|
| 1 | ~HT + SS + HB + VG | Allometry + demography |
| 2 | ~HT + SS + HB | Allometry + demography |
| 3 | ~HT + SS + HB + SS*HB | Allometry + demography + interaction |
| 4 | ~HT + DT + PL + DP | Allometry + extrinsic properties |
| 5 | ~HT + PL + DP + HB | Allometry + combination |
| 6 | ~HT + PL + DP + HB + DP*HB | Allometry + combination + interaction |
| 7 | ~HT + DT + HBT | Allometry + distribution/habitat |
| 8 | ~HT + HBT | Allometry + habitat |
| 9 | ~HT + SS + DP | Allometry + sexual system + dispersal |
| 10 | ~HT + SS + DPS + SS*DP | Allometry + sexual system + dispersal + interaction |
| 11 | ~HT + SS + PL | Allometry + sexual system + pollination |
| 12 | ~HT + DT + SS + HB + HBT + VG + PL + DP | Saturated (all single terms) |
| 13 | ~HT + DT + SS + HB + HBT + VG + PL + DP + SS*HB | Saturated + interaction 1 |
| 14 | ~HT + DT + SS + HB + HBT + VG + PL + DP + DP*HB | Saturated + interaction 2 |
| 15 | ~HT + DT + SS + HB + HBT + VG + PL + DP + SS*DP | Saturated + interaction 3 |
| 16 | ~HT + DT + SS + HB + HBT + VG + PL + DP + SS*HB + DP*HB + SS*DP | Saturated + all interactions |
| 17 | ~HT | Allometry |
| 18 | ~1 | Null |
| 19–33 | Above models without HT | – |
| 34–37 | Above models without DP | – |
| 38–42 | Above models without DT | – |
| 43–46 | Above models without SS | – |
| 47–50 | Above models without HB | – |
| 51–55 | Above models without HBT | – |
| 56–60 | Above models without VG | – |
| 61–68 | Above models without PL | – |

consider an interaction between *sexual system* and *pollination* (Chazdon *et al.*, 2003). However, given that there were many levels within each of these factors, certain factorial combinations had no data, and the models fail to converge with this interaction term. Therefore, our data offered insufficient replication to include this factorial interaction in the model set.

The first group of models in the set also included the *height* term as a possible allometric scaling factor (size/longevity). Maximum plant height has been previously identified as an important determinant of extinction risk in temperate systems (Thompson, 1994; Walker & Preston, 2006). Next, we included several variants of the models already described by systematically removing particular terms to determine their contribution to the model fits. The full model set (*n* = 68 models) is shown in Table 2.

We used an estimate of Kullback–Leibler (K-L) information loss to assign relative strengths of evidence to the different competing models (Burnham & Anderson, 2002), Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC$_c$), and the dimension-consistent Bayesian Information Criterion (BIC) (Burnham & Anderson, 2002). These indices of model parsimony identify relative evidence of model(s) from a set of candidate models (Burnham & Anderson, 2004). The relative likelihoods of candidate models were calculated using

AIC$_c$ and BIC weights (Burnham & Anderson, 2002), with the weight (*w*AIC$_c$ and *w*BIC) of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. However, the K-L prior used to justify AIC$_c$ weighting can favour more complex models when sample sizes are large (Burnham & Anderson, 2004; Link & Barker, 2006) (as was the case for our data set), so we considered BIC weighting to determine the contribution of the most important major correlates of extinction, and AIC$_c$ weighting to identify the most parsimonious models for maximizing prediction accuracy (Burnham & Anderson, 2004; Link & Barker, 2006). The sample size for each model was reduced in most cases due to some missing data in some of the hypothesized correlates (updated sample sizes given in Results).

The final stage in the analysis was to examine the potential influence of extensive habitat removal in Singapore as the major determinant of extinction. This hypothesis predicts that actual removal, rather than particular combinations of life-history traits, is the major determinant of the observed extinction patterns. We tested this hypothesis directly by excluding all extirpated species where the original forest site of collection no longer exists on the island (i.e. habitat fragment removed). This left us with 163 extirpated species in the new data set (105 species

without existing sites, and 186 species where these data were unavailable, were removed), to which we applied the aforementioned GLMMs. We also conducted the similar analysis using 105 extirpated species without existing sites to cross-match the model ranking.

## RESULTS

The dimension-consistent BIC applied to the models considered ranked the two-term model, incorporating *sexual system* and *habit* as the highest ($w$BIC = 0.81); however, this model accounted for only 3.67% of the deviance in extinction probability. This demonstrates that although there was evidence for an effect of *sexual system* and *habit* on extinction probability, it was weak. Therefore, epiphytes are predicted to suffer a greater extinction probability than trees (Fig. 1a), and dioecious species have lower extinction rates than monoecious or hermaphroditic/polygamous species (Fig. 1a).

As predicted, the model ranking according to $w$AIC$_c$ favoured more complex models, with the addition of the terms *pollination system*, *seed/fruit dispersal mechanism*, *habitat*, and *vegetative resprouting* capacity (Table 3). The two most highly ranked models using AIC$_c$ accounted for over 80% of the information-theoretical weight and explained up to 8.5% of the deviance in extinction probability (Table 3). Predictions suggested that species with mammal-assisted pollination systems suffered greater extinction probability compared to those assisted by wind (Fig. 2a). There was only weak evidence for a *seed/fruit dispersal mechanism* effect, with species relying on abiotic (wind/water) factors for dispersal possibly suffering slightly greater extinction probability than other species (Fig. 2b). Coastal species appeared to be more resilient to extinction (Fig. 2c), and the effects of vegetative resprouting capability were ambiguous (Fig. 2d).

Contrasting inferences between the GLMM and GLM, which ignores the effects of phylogeny, indicated the importance of considering evolutionary history in comparative extinction studies. The top BIC-selected GLMs explained > 14% of the deviance in extinction probability, and the more complex AIC$_c$-selected models explained > 19% of the deviance. Thus, the hierarchical taxonomic random effect explained between approximately 9% and 12% of the calculated deviance in extinction probability, a result that demonstrates the potential for incorrectly attributing – a much stronger effect of the plausible drivers to this process without controlling for phylogenetic relatedness.

To confirm the potential influence of species extirpated from patches no longer in existence in Singapore, BIC ranked the null model as the most parsimonious ($w$BIC = 0.97; Table 4). By itself, this result would seem to question the validity of the results derived from the entire data set; however, when those extirpated species from patches no longer in existence were considered as the only extinct species in the data set, the model-ranking results were nearly identical (Table 5). The highest BIC-ranked model was again the null ($w$BIC = 0.99; Table 5). Furthermore, the four top-ranked models for both data sets were identical, as well as the top-ranked model according to AIC$_c$ (model PL + DP + HB + HB*DP with $w$AIC$_c$ = 0.80 and 0.38 for the non-existent patch-
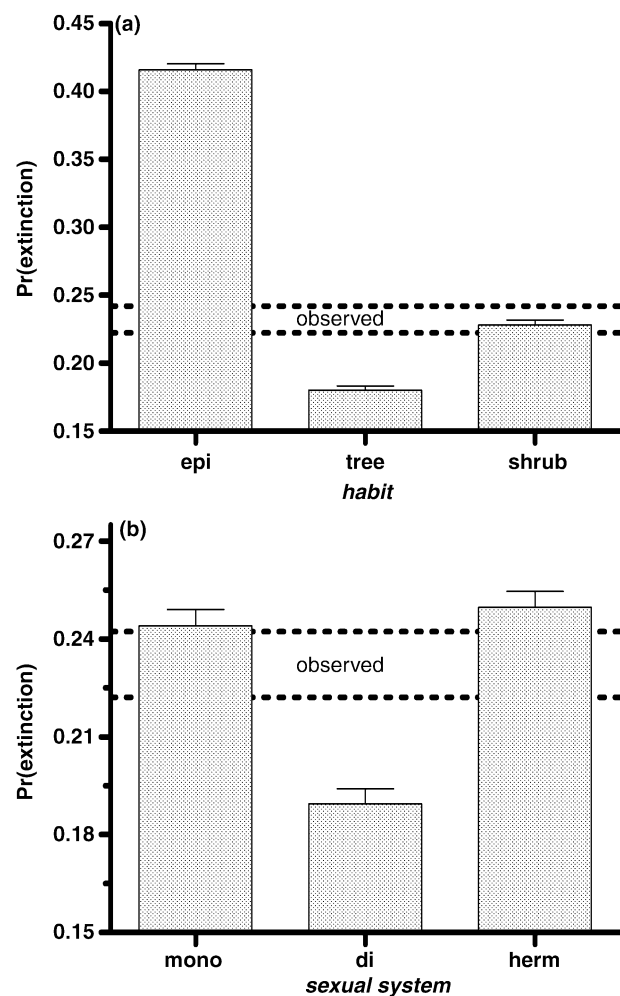


Figure 1 Predicted extinction probabilities for each term considered in the generalized linear mixed-effects model (GLMM) incorporating (a) *habit* and (b) *sexual system* (derived from the two-term model SS + HB based on the BIC-selected uppermost model; see Table 3). The observed extinction probability 95% confidence interval (dotted horizontal lines) was determined by a 10,000 iteration bootstrap of the probabilities predicted by the above model over 1753 species. Changes to extinction probability relative to each term level were calculated by adjusting the original data set so that all species were given the same value for that level (each level value in turn), keeping all other terms in the model as in the original data set. Error bars represent the 10,000 iteration bootstrapped upper 95% confidence limits. Di = dioecious, epi = epiphyte, mono = monoecious, and herm = hermaphrodite or polygamous. See text for the description of variables.

excluded and non-existent patch-only data sets, respectively; Tables 4 and 5). The congruency of these results suggests that complete removal of species during deforestation may not have strongly biased our results. Furthermore, the 64–77% reduction in the number of extirpated species used in the patch-removed analyses (454–163 species in the patch-removed analysis; 454–105 species in the patch-removed-only analysis) and BIC as the principle model ranking metric were likely responsible for the higher support of the null models. Using AIC$_c$, *seed/fruit dispersal*
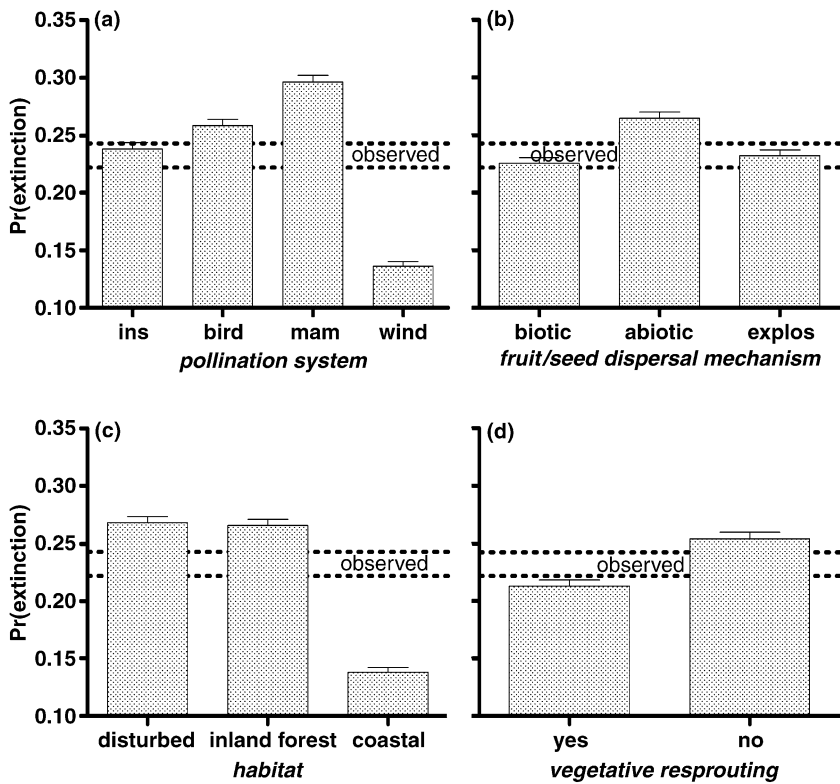
**Figure 2** Predicted extinction probabilities for each term considered in the generalized linear mixed-effects model (GLMM) incorporating (a) *pollination system* and (b) *fruit/seed dispersal*, (c) *habitat* and (d) *vegetative resprouting* (derived from the model with the terms SS + HB + PL + DP + HBT + VG derived from a combination of the upper BIC- and AIC$_c$-supported models; see Table 3). The observed extinction probability 95% confidence interval (dotted horizontal lines) was determined following the bootstrapped procedure as described in Figure 1. Bird = bird pollinated, explos = explosive, or no obvious dispersal mechanism, ins = insect pollinated, mam = mammal pollinated, wind = wind pollinated. See text for the description of variables.

**Table 3** The five most parsimonious generalized linear mixed-effects models investigating the correlates of extinction (full data set, $n = 1753$ species) according to (a) the Bayesian Information Criterion (BIC) and (b) Akaike's Information Criterion corrected for small sample size (AIC$_c$). The five most highly BIC-ranked models accounted for > 99% of the information-theoretical weight ($w$BIC) of the total of 68 models considered. Terms shown are HT = *height*, SS = *sexual system*, HB = *habit*, PL = *pollination system*, DP = *fruit/seed dispersal mechanism*, VG = *vegetative resprouting*, DT = *distribution*, and HBT = *habitat*. Also shown is the number of parameters ($k$), the negative log-likelihood ($-LL$), the difference in BIC and AIC$_c$ for each model from the most parsimonious model ($\Delta$BIC and $\Delta$AIC$_c$), AIC$_c$ weight, and the percentage deviance explained in the response variable (extinction probability) by the model under consideration.

| Model | $k$ | $-LL$ | $\Delta$BIC | $w$BIC | $\Delta$AIC$_c$ | $w$AIC$_c$ | %DE |
|---|---|---|---|---|---|---|---|
| (a) BIC-ranked | | | | | | | |
| ~SS + HB | 9 | −391.916 | 0.000 | 0.809 | 11.347 | 0.002 | 3.67 |
| ~1 | 5 | −406.865 | 3.213 | 0.162 | 33.093 | $3.446 \times 10^{-8}$ | 0.00 |
| ~SS + HB + VG | 10 | −391.913 | 6.675 | 0.029 | 13.393 | $6.531 \times 10^{-4}$ | 3.67 |
| ~PL + DP + HB | 12 | −390.235 | 16.669 | $1.941 \times 10^{-4}$ | 14.155 | $4.463 \times 10^{-4}$ | 4.09 |
| ~HT + HB | 12 | −391.130 | 18.462 | $7.921 \times 10^{-5}$ | 15.946 | $1.822 \times 10^{-4}$ | 3.87 |
| (b) AIC$_c$-ranked | | | | | | | |
| ~PL + DP + HB + HB*DP | 16 | −379.006 | 20.881 | $3.363 \times 10^{-5}$ | 0.000 | 0.529 | 6.85 |
| ~DT + SS + HB + HBT + VG + PL + DP + HB + HB*DP | 23 | −372.256 | 54.016 | $1.508 \times 10^{-12}$ | 1.241 | 0.284 | 8.51 |
| ~HT + DP + HB + HB*DP | 18 | −379.366 | 34.959 | $2.073 \times 10^{-8}$ | 4.902 | 0.046 | 6.76 |
| ~HT + DT + HB + HBT + VG + PL + DP + HB*DP | 26 | −371.032 | 71.567 | $2.328 \times 10^{-16}$ | 5.193 | 0.039 | 8.81 |
| ~HT + DT + SS + HB + HBT + VG + DP + HB*DP | 25 | −372.322 | 67.494 | $1.785 \times 10^{-15}$ | 5.632 | 0.032 | 8.49 |

*mechanism*, *habitat*, and *pollination system* were identified as having important contributions to explaining extinction risk (Tables 4 and 5).

## DISCUSSION

Our ability to launch remedial management actions for threatened species, such as population augmentation and directed protection of individuals or populations, has been hampered in the past by our lack of understanding of the process of extinction in tropical plants, especially via habitat loss. Therefore, studies of extinction proneness that compare ecological and life-history traits between extinct and extant species are essential for generating mechanistic hypotheses, as well as for identifying species at risk given the impossibility of conducting experiments on the appropriate temporal and spatial scales.

**Table 4** The five most parsimonious generalized linear mixed-effects models investigating the correlates of extinction with extinct non-existent-habitat-patch-species removed ($n = 1497$ species) according to (a) the Bayesian Information Criterion (BIC) and (b) Akaike's Information Criterion corrected for small sample size ($AIC_c$). The five most highly BIC-ranked models accounted for > 99% of the information-theoretical weight ($w$BIC) of the total of 68 models considered. Terms shown are HT = *height*, SS = *sexual system*, HB = *habit*, PL = *pollination system*, DP = *fruit/seed dispersal mechanism*, and VG = *vegetative resprouting*. Also shown is the number of parameters ($k$), the negative log-likelihood ($-LL$), the difference in BIC and $AIC_c$ for each model from the most parsimonious model ($\Delta$BIC and $\Delta AIC_c$), $AIC_c$ weight, and the percentage deviance explained in the response variable (extinction probability) by the model under consideration.

| Model | $k$ | $-LL$ | $\Delta$BIC | $w$BIC | $\Delta AIC_c$ | $w AIC_c$ | %DE |
|---|---|---|---|---|---|---|---|
| (a) BIC-ranked | | | | | | | |
| ~1 | 5 | −172.291 | 0.000 | 0.969 | 20.109 | $3.431 \times 10^{-5}$ | 0.00 |
| ~SS + HB | 9 | −162.651 | 7.044 | 0.029 | 8.999 | 0.009 | 5.60 |
| ~SS + HB + VG | 10 | −161.940 | 12.206 | 0.002 | 9.632 | 0.006 | 6.01 |
| ~SS + DP | 9 | −168.713 | 19.195 | $6.581 \times 10^{-5}$ | 21.121 | $2.069 \times 10^{-5}$ | 2.08 |
| ~PL + DP + HB | 12 | −159.243 | 19.968 | $4.470 \times 10^{-5}$ | 8.370 | 0.012 | 7.57 |
| (b) $AIC_c$-ranked | | | | | | | |
| ~PL + DP + HB + HB*DP | 16 | −150.891 | 29.544 | $3.723 \times 10^{-7}$ | 0.000 | 0.798 | 12.42 |
| ~HT + DP + HB + HB*DP | 18 | −150.433 | 41.783 | $8.189 \times 10^{-10}$ | 3.284 | 0.155 | 12.69 |
| ~PL + DP + HB | 12 | −159.243 | 19.968 | $4.470 \times 10^{-5}$ | 8.370 | 0.012 | 7.57 |
| ~HT + PL + DP + HB + HB*DP | 21 | −149.869 | 60.393 | $7.450 \times 10^{-14}$ | 8.505 | 0.011 | 13.01 |
| ~SS + HB | 9 | −162.651 | 7.044 | 0.029 | 8.999 | 0.009 | 5.59 |

**Table 5** The five most parsimonious generalized linear mixed-effects models investigating the correlates of extinction using only those extinct species from non-existent habitat patches ($n = 1442$ species) according to (a) the Bayesian Information Criterion (BIC) and (b) Akaike's Information Criterion corrected for small sample size ($AIC_c$). The five most highly BIC-ranked models accounted for > 99% of the information-theoretical weight ($w$BIC) of the total of 68 models considered. Terms shown are HT = *height*, SS = *sexual system*, HB = *habit*, PL = *pollination system*, DP = *fruit/seed dispersal mechanism*, VG = *vegetative resprouting*, DT = *distribution*, and HBT = *habitat*. Also shown is the number of parameters ($k$), the negative log-likelihood ($-LL$), the difference in BIC and $AIC_c$ for each model from the most parsimonious model ($\Delta$BIC and $\Delta AIC_c$), $AIC_c$ weight, and the percentage deviance explained in the response variable (extinction probability) by the model under consideration.

| Model | $k$ | $-LL$ | DBIC | $w$BIC | $DAIC_c$ | $w AIC_c$ | %DE |
|---|---|---|---|---|---|---|---|
| (a) BIC-ranked | | | | | | | |
| ~1 | 5 | −122.898 | 0.000 | 0.989 | 9.743 | 0.003 | 0.00 |
| ~SS + HB | 9 | −114.281 | 9.013 | 0.011 | 0.681 | 0.272 | 7.01 |
| ~SS + HB + VG | 10 | −114.069 | 15.155 | $5.060 \times 10^{-4}$ | 2.315 | 0.120 | 7.18 |
| ~SS + DP | 9 | −120.456 | 21.396 | $2.233 \times 10^{-5}$ | 13.029 | 0.001 | 1.99 |
| ~DT + HB + HBT | 9 | −121.853 | 24.194 | $5.513 \times 10^{-6}$ | 15.824 | $1.401 \times 10^{-4}$ | 0.85 |
| (b) $AIC_c$-ranked | | | | | | | |
| ~PL + DP + HB + HB*DP | 16 | −106.675 | 39.699 | $2.368 \times 10^{-9}$ | 0.000 | 0.382 | 13.20 |
| ~HT + DP + HB + HB*DP | 9 | −114.281 | 9.013 | 0.011 | 0.681 | 0.272 | 7.01 |
| ~PL + DP + HB | 10 | −114.069 | 15.155 | $5.060 \times 10^{-4}$ | 2.315 | 0.120 | 7.18 |
| ~HT + PL + DP + HB + HB*DP | 12 | −112.410 | 24.958 | $3.763 \times 10^{-6}$ | 3.130 | 0.080 | 8.53 |
| ~SS + HB | 13 | −111.833 | 30.369 | $2.515 \times 10^{-7}$ | 4.050 | 0.050 | 9.00 |

Using a unique data set where the extinction fate of species was known rather than inferred from indices of risk (e.g. IUCN Red List category, see Sekercioglu *et al.*, 2004), we determined that only a relatively small amount of the variation in extinction probability could be explained by plausible life history correlates. Similarly, Wilson *et al.* (2007) argued that because of complex biological, environmental, and anthropogenic interactions, it is difficult to predict invasiveness traits in plants. There are at least three plausible explanations of our low explanatory power: (1) our choice of extinction correlates failed to incorporate the main factors determining extinction; (2) the loss of plant species in Singapore is largely due to physical removal during deforestation, irrespective of life-history traits; or (3) the process of extinction in tropical angiosperms is more random than previously assumed and driven primarily by stochastic forces operating after large-scale population reduction (caused by [2]). We carefully chose traits based on previous studies (see Methods), so we doubt that the poor explanatory power was due to inappropriate traits being used. While it is likely that some species were entirely eliminated during the act of deforestation, we argue that extinction

is less predictable for species that vanished subsequently (explanation [3]). Indeed, recent work has found empirical evidence for the decoupling of the processes causing extinction and decline (Brook *et al.*, 2006b) – the so-called 'small and declining species paradigms' proposed by Caughley (1994). Thus, extinction risk defined mainly by the extent of population decline may be driven more by life-history characteristics such as size, dispersal capacity, and degree of specialization than the ultimate extinction event itself (Brook *et al.*, 2006b). However, another complicating factor is that there simply may not have elapsed enough time from the disturbance to ultimate extinction given the relatively recent deforestation of Singapore (see also below). Thus, life-history traits are expected to correlate increasingly with extinction over time. Our study also highlights the importance of phylogenetic controls when analysing data such as ours.

Nonetheless, we found evidence for a weak to moderate influence of two main correlates – *sexual system* and life-history *habit* – on extinction probability. Epiphytes were found to be more extinction prone (Fig. 1a), probably because of factors such as the loss of preferred hosts (big trees), microclimate changes brought about by fragmentation, and/or overexploitation for the horticultural trade (Turner *et al.*, 1994). Our finding that species restricted to inland forests are more vulnerable to extinction following deforestation than those occurring in (or preferring) now heavily disturbed habitats such as coastal areas is consistent with the conclusions of other studies (e.g. Turner *et al.*, 1994; Castelletta *et al.*, 2000; Brook *et al.*, 2003; Thomas, 2004; Soh *et al.*, 2006). For example, Brook *et al.* (2003) reported that across a wide range of taxonomic groups (e.g. plants, butterflies, mammals), species inhabiting primary or secondary rainforest suffered higher rates of extinction (33%) than species tolerant of open or forest-edge habitats (7%) in Singapore. A probable explanation for this trend is that forest-dependent species may be more sensitive to changes in habitat quality, increased predation rates, and dispersal barriers than species that are adapted to colonizing disturbed habitats. On the other hand, coastal plants may be more persistent due to their inherent abilities to deal with environmental perturbations (e.g. high wind speed and sunlight, low relative humidity, and salt spray).

In contrast to other studies examining extinction in plants (Thompson, 1994; Walker & Preston, 2006), we found no strong evidence that allometry was an important predictor of risk. This lack of a relationship may result from the lag time between population reductions and extinction given that many of the taller species also have the highest longevity (Duncan & Young, 2000). Remnant populations of long-lived species may not be viable in the long term and are ultimately committed to extinction (i.e. living dead, Turner *et al.*, 1994), a possibility supported by the relatively higher extinction risk for tree/treelet species (Fig. 1a). This phenomenon has been illustrated by a study of plant extirpations from an isolated 4-ha fragment of lowland rainforest in Singapore (Singapore Botanic Gardens) (Turner *et al.*, 1996). In Turner *et al.*'s study, although shorter-lived shrubs suffered higher rates of local extinction than long-living trees, half of the extant tree species were represented by only one or two individuals.

Animals that provide the ecosystem services of pollination and seed dispersal for plants (Sekercioglu *et al.*, 2004) often suffer extinctions following habitat disturbance (Laurance, 1991; Castelletta *et al.*, 2000; Koh & Sodhi, 2004; Koh *et al.*, 2004b), and plants reliant on these extinct pollinators and seed dispersers would consequently be expected to have higher risks of coextinction (Koh *et al.*, 2004a,b). As predicted, we found that species dependent on animals, particularly mammals, for pollination were more prone to extinction (Fig. 2a). However, we found no strong evidence that plants relying on animals for seed dispersal are more extinction-prone. These findings are especially noteworthy given the comparative lack of specificity of pollination and seed dispersal systems in tropical Asia (Corlett, 2004) and the lack of evidence in other studies for dispersal syndrome as an indicator of plant extinction proneness in temperate systems (Walker & Preston, 2006). The species possessing life-history traits that allow populations to persist following habitat disturbance should intuitively be able to withstand its effects. However, no clear effect of vegetative propagation on extinction proneness was found (Fig. 2d). Genetic erosion in monoecious and hermaphrodic species that may self-fertilize may be one of the factors increasing their susceptibility to extinction (Fig. 1b). However, other factors such as the number of gametes produced could also be important (see Wilson & Harder, 2003).

Although over 2700 tropical plant species are considered threatened (www.iucnredlist.org), we suspect that this is an underestimation. Our study underscores the need for similar studies using species traits to help predict extinction risk for tropical plants. We found that epiphytic, monoecious, and hermaphroditic species and those restricted to inland forests are likely to have higher probabilities of extinction. Species dependent on mammal pollinators also probably have higher extinction probabilities. Plant species possessing such traits, especially if endemic to an area under threat, should be considered as a priority for pre-emptive conservation actions such as implementing protected areas, reforestation, and population augmentation. Given their rich diversity and the sensitivity of many species to habitat disturbance, it is clearly important that plants receive due attention in conservation projects that attempt to maintain or restore tropical ecosystems. Plants can also be a good surrogate group for other taxa such as insects, thus highlighting the importance of these findings for conservation efforts (Sætersdal *et al.*, 2003).

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