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Local geographic range predicts freshwater fish extinctions in Singapore

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Summary

1. Identifying the ecological and life-history correlates of local extinction may elucidate mechanisms by which species traits and the environment interact to result in extinctions, and will help to predict and target extinction-prone species for inclusion in conservation programmes. Freshwater habitats are known to be highly threatened in Southeast Asia but the correlates of extinction among tropical freshwater fish remains unclear.

2. To bridge this knowledge gap, we examined extinction correlates of the freshwater fish of Singapore using machine learning methods: conditional inference trees and forests. Singapore is an ideal study site as it has experienced a high degree of habitat loss and has a well-studied ichthyofauna compared with other countries in the region.

3. The local range of a species was the only significant predictor of extinctions: range-restricted species were more likely to go extinct.

4. Other traits found to be important predictors of extinction risk in temperate regions or hypothesized to predict extinctions based on theory included regional geographic distribution, vertical position, feeding guild, body size, number of congeners, air-breathing capability and habitat preference. These factors did not appear to drive extinctions of freshwater fish in Singapore, although forest-dependent species are more likely to have a restricted local range.

5. *Synthesis and applications.* Local extinctions of freshwater fish in Singapore are random with respect to ecological and life-history traits because habitat loss is responsible for the removal of entire populations. The fish fauna of Southeast Asia is so poorly known that intensive field surveys are required to identify hotspots of freshwater fish endemism which may be vulnerable to future extinction. These hotspots should then be incorporated into national conservation plans. Where complete habitat protection is not possible, for example, in existing logging concessions and plantations, local authorities should establish partnerships with management companies to ameliorate impacts on fish fauna. Within Singapore, the Nee Soon Swamp Forest is one such hotspot of fish endemism and must be conserved to protect the last populations of five fish species endemic to this location on the island.

Key-words: body size, conservation, habitat loss, life-history traits, machine learning, Southeast Asia, tropics

Introduction

Anthropogenic land use change is the main threat to the Earth's biota (Millennium Ecosystem Assessment 2005). Despite an increase in conservation efforts, biodiversity losses are not declining (Rands *et al.* 2010). The biodiversity crisis is likely to be most acute in the tropics, which are hyper-biodiverse and at the same time experiencing unabated habitat loss (Bradshaw, Sodhi & Brook 2009). Prospects for conserving biodiversity are particularly dire in Southeast Asia, as this region is being deforested at a rate faster than any other tropical region (Sodhi *et al.* 2010a).

Freshwater bodies cover *c.* 0·8% of the world's surface but freshwater fishes make up about a quarter to almost half of all vertebrate species (Stiassny 1996). Freshwater fish species richness and endemicity are highest in the tropics (Abell *et al.* 2008). Within the tropics, Asia harbours the highest number of freshwater fish families (> 105) compared with South America (74)

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and Africa (60) (Dudgeon 2000). Despite habitat loss threatening the persistence of freshwater fishes in Southeast Asia, the ecology of many species remains unknown (Kottelat & Whitten 1996), and very few studies have investigated the impacts of land use change on freshwater fish communities (Martin-Smith 1998; Iwata, Nakano & Inoue 2003). Our scant knowledge of the ecology of freshwater fish in Southeast Asia hinders conservation efforts in this era of rapid environment change.

Identifying trait correlates of local extinctions is considered a major research priority in the conservation biogeography of freshwater fishes (Olden *et al.* 2010). Conservation biologists strive to identify life-history and ecological traits that correlate with local (e.g. Angermeier 1995; Koh, Sodhi & Brook 2004; Olden, Poff & Bestgen 2008) as well as global extinction risk (e.g. Purvis *et al.* 2000; Reynolds, Webb & Hawkins 2005; Bradshaw *et al.* 2008) so as to allow conservation practitioners to prioritize the management of species that are more likely to become extinct across varying spatial scales. Local extinction risk was found to be correlated with a variety of species traits (Angermeier 1995) and trait synergisms (Olden, Poff & Bestgen 2008) in temperate freshwater fish. However, to the best of our knowledge, no study has investigated the relationship between species traits and local extinction proneness among freshwater fish in the tropics. As long-term population trends are not available for most freshwater fishes in tropical Asia (Dudgeon 2003), species traits, if found to successfully predict extinctions, can be used to identify extinction-prone species and to prioritize long-term population and habitat monitoring programmes in the region.

In this study, we investigate if species traits may predispose tropical freshwater fish species towards local extinction and assess the relative importance of these traits. Here, local extinction refers to the loss of the entire population of native freshwater fish species (Dulvy, Sadovy & Reynolds 2003). Specifically, we aim to identify the species traits that correlate with freshwater fish extinctions in Singapore, a tropical island-nation in Southeast Asia. Singapore's native freshwater fish assemblage is generally representative of that of Southeast Asia. The 46 species of native freshwater fish fauna of Singapore are dominated by Cyprinidae, the carp family, in common with the freshwater fauna of Southeast Asia (Zakaria-Ismail 1994). Moreover, Singapore, being part of the Malay Peninsula zoogeographic region, has a fish community that is drawn from the two major Southeast Asia regions: Sundaland and Indochina (Yap 2002). The only notable bias is the absence of large river species in Singapore but this is unlikely to affect the representativeness of our study as there is no evidence to suggest that these species respond differently to anthropogenic activities. Singapore has lost 95% of its natural vegetation (Brook, Sodhi & Ng 2003) and its aquatic habitat has been greatly altered by reservoir impoundment and channel concretization. Although Singapore represents an extreme case in terms of habitat alteration and loss, many drainage basins in Southeast Asia may face a similar fate given the current trajectory of rapid development and high rates of habitat loss in the region (Bradshaw, Sodhi & Brook 2009). Moreover, those anthropogenic activities (i.e. deforestation, urbanization, impoundments and flow regulation) that have resulted in the loss of the freshwater fish fauna and their habitat in Singapore are the same ones threatening freshwater fish in Southeast Asia (Dudgeon 1992, 2000). Thus, the results of our study are likely to be relevant at the regional level and will provide a valuable insight into which traits or trait synergisms may predispose freshwater fishes towards local extinction in tropics and guide authorities in Southeast Asia to prioritize conservation efforts towards extinction-prone species.

To perform the analyses, we compiled a trait data set of freshwater fishes (defined as species that complete their life cycle in freshwater) that were historically reported as native to Singapore. The traits selected *a priori* as probable correlates of extinction proneness were: (i) maximum total length, (ii) feeding guild, (iii) air-breathing capability, (iv) habitat preference, (v) vertical position in the water column, (vi) regional geographic range, (vii) local geographic range and (viii) number of congeners (see Table 1). We predicted that the local geographic range (the number of drainages in Singapore from which each species was recorded) and habitat preference (forest-dependent or not) would prove most important in predicting extinctions because many Southeast Asian freshwater fish are known to be restricted to one or a few catchments (Kottelat & Whitten 1996), and habitat loss is likely to extirpate range-restricted species first.

Materials and methods

STUDY SITE

The Republic of Singapore (103°50′E, 1°20′N) is a land-bridge island situated south of Peninsular Malaysia, occupying an area of 710 km^2. It has a fairly uniform equatorial climate throughout the year with a mean daily maximum temperature of 31·5 °C and a mean annual rainfall of 2192 mm (National Environmental Agency 2009).

Singapore's drainages (Fig. 1) have experienced massive environmental change since the start of European occupation in 1819 (Corlett 1992). Natural forest in river catchments was first cleared for pepper *Piper nigrum* L., gambier *Uncaria gambir* (W.Hunter) Roxb., and finally rubber *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg. from the 1800s to the early 1900s. In the latter half of the 20th century, these plantations were cleared for industrial, residential and urban land use. To supply water for human consumption and growing industries, headwaters of major drainages [Sungei (Malay word for river) Kallang, Sungei Kranji, Sungei Seletar and Sungei Whampoa] were impounded to form reservoirs (Fig. 1). In headwater areas, forest streams are now concretized, and further downstream, water flows through a series of concrete canals through urban areas. The alteration of Singapore's natural environment has regrettably led to a catastrophic loss of species (Brook, Sodhi & Ng 2003) but it provides us with a suitable system to study local fish extinctions owing to habitat loss, a phenomenon which is widespread in the tropics and especially in Southeast Asia.

SPECIES CHECKLIST, EXTANT/EXTINCT STATUS AND TRAIT DATA SET

We compiled a checklist of freshwater fish species that were recorded as native to Singapore from published monographs and papers (Alfred 1966; Lim & Ng 1994; Ng & Lim 1996). As the status of many

Table 1. Definitions of species traits and their hypothesized effects on local extinction risk

Species trait (code)	Definition	Hypothesized effect on local extinction risk
Maximum total length (*MTL*)	Continuous variable: total length measured from tip of the snout to the tip of the tail (cm)	Large-bodied fishes have slow life histories and low population growth rates therefore they are less resilient towards environmental change and more likely to go extinct (Olden, Poff & Bestgen 2008)
Feeding guild (*FEED*)	Categorical variable: herbivore-planktivore; omnivore; invertivore (excluding plankton); piscivore-invertivore; piscivore	Species belonging to feeding guilds at a high trophic level are likely to go extinct, owing to disturbance effects accumulating along the food chain (Purvis *et al.* 2000)
Air-breathing capability (*AIR*)	Categorical variable: air breather; non-air breather	Air breathers are able to survive outside water bodies and disperse across drainages; therefore, they are less likely to go extinct
Habitat preference (*HAB*)	Categorical variable: forest-dependent; forest-independent	Forest-dependent species are more likely to go extinct owing to the high degree of deforestation in Singapore
Vertical position (*VERT*)	Categorical variable: benthic; non-benthic	Benthic species are more likely to go extinct owing to the loss of substratum and benthic vegetation in concretized channels
Regional geographic range (*REGRANGE*)	Continuous variable: the number of freshwater fish zoogeographic zones each species is native to; zoogeographic zones are defined by Zakaria-Ismail (1994)	Species with a wide native geographic range may be better dispersers or exhibit greater habitat flexibility, and are therefore less likely to go extinct
Local geographic range (*LOCRANGE*)	Continuous variable: the number of drainages in Singapore from which each species was recorded historically	Species restricted to one or few drainages are more likely to go extinct compared with species distributed over a larger number of drainages
Number of congeners (*CONG*)	Continuous variable: the number of congeners native to Singapore	As congeners are likely to share similar ecological niches, species with higher number of congeners may be subjected to higher competition and be more extinction-prone under habitat loss (Koh, Sodhi & Brook 2004)

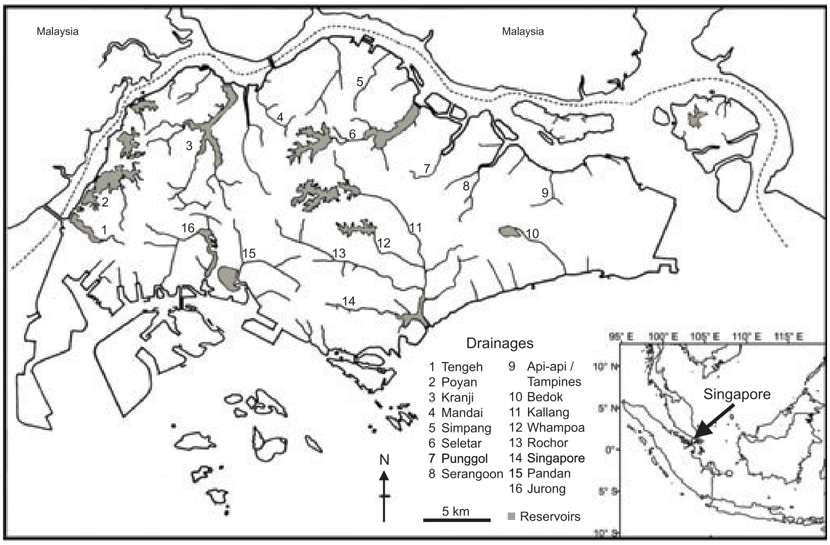

Fig. 1. Map of the major drainages in Singapore (inset: the location of Singapore in insular Southeast Asia).

species were suspect owing to misidentification of specimens and inaccurate collection sources (Alfred 1966), we verified our checklist with a recent revision that clarified suspect records (Baker & Lim 2008). Species that were doubtfully native to Singapore owing to a lack of suitable habitat or previous inference from imported specimens were excluded from our checklist. After the filtering exercise, our data set consisted of 46 species (35 extant; 11 extinct) that complete their entire life cycle in freshwater bodies. Species were considered to be extinct if they were not sighted or collected by ichthyologists within the last 45 years. In addition to consulting published reports and monographs on the last date of sighting/collection, we also checked the catalogue of specimens stored in the Raffles Museum of

Biodiversity Research to confirm the collection dates and hence the extinct/extant status of the species in our data set. Compared with the 30 year cut-off used in a recent study on angiosperm extinctions in Singapore (Sodhi *et al.* 2008), a 45-year time horizon is less likely to erroneously classify extant species as extinct. An examination of the collection dates of extant species revealed that only one species [*Channa gachua* (Hamilton)] had a collection gap of more than 45 years; it was last collected in 1937 before being rediscovered in 1989. As freshwater habitats have been extensively sampled in Singapore since Alfred (1966), we are confident that species not sighted or collected for the last 45 years are indeed extinct.

We collated species-specific data for eight traits that are potential correlates of extinction as indicated by theory and/or previous studies (Table 1) from published monographs, papers, books and online data bases (Appendix S1, Supporting information). We are cognizant of the fact that species traits other than the ones we have investigated may drive local extinctions (e.g. longevity and fecundity). However, data were unavailable in the literature for these traits, hence precluding their inclusion in our analysis. On the other hand, the eight traits that we examined are available in literature and therefore can be readily used in assessing extinction-prone species in other Southeast Asian regions. We recognize that fish may display trait variations across their geographic ranges; therefore, we based trait assignments on local publications whenever possible. Regional or generalized data [e.g. data obtained from FishBase (http://www.fishbase.org)] were only used if local data were not available. Our complete data set is made freely available (Appendix S2, Supporting information) so that it can be used by conservation practitioners to assemble a larger regional or global data set to address questions critical to effective conservation.

ANALYSIS

We used a recursive partitioning technique known as conditional inference trees (Hothorn, Hornik & Zeileis 2006) to test for the association of traits or trait synergisms with local extinctions of freshwater fish in Singapore. Recursive partitioning, which includes the more commonly used classification trees (CART; Breiman *et al.* 1984), is a nonparametric technique that splits a data set into binary groups repeatedly based on the association between the predictor variables and the response variable to generate a decision tree. Classification tree modelling is sometimes preferred to logistic regression in modelling binary outcomes because tree modelling does not require the data to be parametric and it deals with nonlinear interactions as well as higher order interactions (i.e. trait synergisms) in predicting the outcome (Sodhi *et al.* 2010b). In addition, tree modelling allows for the detection of nonlinear, threshold effects. However, conventional classification trees may lead to overfitting and are associated with biases towards variables with many categories (in our study, the variable *FEED*, which has five categories) when tree pruning is performed to avoid the problem of overfitting (Hothorn, Hornik & Zeileis 2006). Conditional inference classification trees, perform as well as conventional classification trees but unlike them, do not require tree pruning as they employ a statistical stopping criterion to decide if the recursion needs to stop (Hothorn, Hornik & Zeileis 2006). We therefore used conditional inference trees, which separate variable selection and splitting procedures, to generate optimal trees free from the abovementioned biases. The tree was generated using a minimum splitting criterion of two (there must be a minimum of two cases for the algorithm to attempt a split), and Monte Carlo $P < 0{\cdot}05$ (P-value must be lower than 0·05 for the algorithm to implement a split). To test the sensitivity of the analysis towards parameter settings, we generated a second tree using a minimum splitting criterion of four and Monte Carlo $P < 0{\cdot}10$, and compared the results generated by the two trees.

To generate robust results as well as to determine the relative importance of each species trait in predicting extinction (Sodhi *et al.* 2010b), we modelled local extinctions using conditional inference forests (Hothorn, Hornik & Zeileis 2006). This is an ensemble machine learning method which combines the predictions from many individual trees to generate robust and unbiased predictions. We constructed an unbiased conditional inference forest of 1000 trees following the parameter settings suggested by Strobl *et al.* (2007) and determined the relative importance of each species trait by computing its conditional permutation importance value. The conditional permutation importance value of species trait j is generated by first randomly permuting the species trait (X_j) within groups of observations with the same value for a third correlated species trait k and then generating new predictions based on the permutated species trait and the other non-permutated species traits. Finally, the conditional permutation importance value of species trait j is computed by taking the difference between the prediction accuracy before and after permuting X_j, averaged over all trees (Strobl *et al.* 2008).

For both analyses, in addition to the eight species traits, we also included family (*FAM*) as a ninth predictor variable to test if there is a phylogenetic effect on extinctions. Receiver operating characteristic (ROC) curves, which demonstrate the trade-off between sensitivity (tree positive rate) and 1-specificity (false positive rate) given different cut-off probabilities, were plotted for each model to determine (i) the optimal cut-off value (maximizing sensitivity and specificity) for classifying modelled extinction probabilities into extant or extinct categories and (ii) the diagnostic accuracy of the models [via area under ROC curve statistic (AUC)]. ROC curves and the AUC statistic have been used to evaluate the diagnostic accuracy of species distribution models (Gibson *et al.* 2004). The AUC ranges from 0·5 in models that are no more accurate than chance to 1 in models that demonstrate perfect accuracy in discriminating between extant and extinct species. The overall model fit was quantified by the classification accuracy (percentage of species correctly classified as extant or extinct), specificity (percentage of species correctly classified as extant) and sensitivity (percentage of species correctly classified as extinct). The

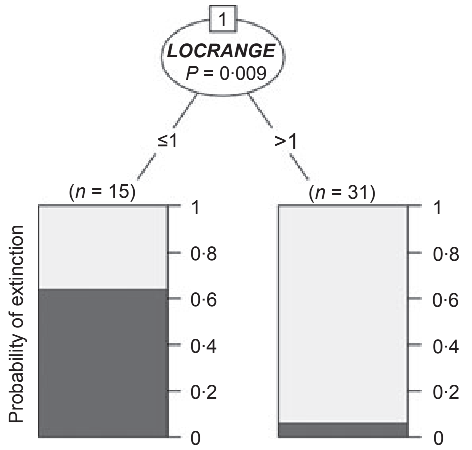

Fig. 2. Conditional inference tree for predicting freshwater fish extinctions in Singapore. Local geographic range (*LOCRANGE*) was the only predictor of extinction. The P-value represents the significance level of the split based on 9999 Monte Carlo simulations. The dark-grey barplots at the terminal nodes represent the empirically derived probability of extinction as determined by the *LOCRANGE* value (number of drainage(s) from which the species was recorded).

Cohen's kappa statistic was used to assess the strength of association between the observed and predicted classes. All analyses were performed in R v. 2·10·1 (R Development Core Team 2009); conditional inference trees and forests were implemented using the package PARTY (Hothorn, Hornik & Zeileis 2006) and ROC/AUC analyses were conducted using the package ROCR (Sing *et al.* 2005).

Results

The optimal conditional inference tree revealed that local geographic range (*LOCRANGE*) is the only predictor of freshwater fish extinctions in Singapore (Fig. 2). Changing parameter settings of the tree algorithm did not alter the results. For species restricted to a single drainage, the empirically derived probability of extinction was 64·3%, whereas the extinction probability for species historically recorded in two or more drainages was 6·3%. The tree model demonstrated high diagnostic accuracy (AUC = 0·84; Fig. S1, Supporting information). The model was slightly better at correctly predicting the status of extant species (85·7% accurate) compared with extinct species (81·8% accurate) using a cut-off extinction probability of 0·643 (Fig. S1, Supporting information). Overall, the model provided a high classification accuracy (84·8%) and showed a high association with the observed status (Cohen's kappa = 0·62, $P < 0·0001$; Table 2).

Using conditional inference forests, *LOCRANGE* was again selected as the only predictor of freshwater fish extinctions. The conditional permutation importance scores suggested that *LOCRANGE* was the best predictor variable because it was the only variable that resulted in a reduction of classification accuracy when randomly permutated (Table 3). Randomly permuting the other variables either had no effect on the model performance (*MTL* and *FAM*) or improved model performance (*AIR*, *VERT, HAB*, *CONG*, *REGRANGE* and *FEED*). The forest model displayed a high diagnostic accuracy (AUC = 0·93). Using a cut-off extinction probability of 0·224, the sensitivity and specificity of the forest model was 90·9% and 85·7%. Consequently, classification accuracy (87·0%) and strength of association between observed and predicted species status (Cohen's kappa = 0·68, $P < 0·0001$) of the forest model was higher than that of the tree model (Table 2).

The relationship between species traits and extinction may be obscured by the possible correlation between species traits and the local geographic range, that is, a subset of ecological and life-history traits may influence the extent of a species' range, which in turn drives local extinction (Olden, Poff & Bestgen 2008). To test this possibility, we generated a conditional inference tree and a conditional inference forest to examine the correlation between species traits and local geographic range. Habitat (*HAB*) was found to be the best predictor of local geographic range: forest-restricted species tend to occupy fewer drainages (tree model: $R^2 = 0·41$; forest model: $R^2 = 0·46$; Fig. S2 and Table S1, Supporting information).

Table 2. Measures of classification accuracy to establish the fit of conditional inference tree and forest models in predicting freshwater fish extinctions in Singapore ($n = 46$)

	Model	
Accuracy measure	Conditional inference tree	Conditional inference forest
Classification accuracy (%)	84·8	87·0
Specificity (%)	85·7	85·7
Sensitivity (%)	81·8	90·9
Cohen's kappa (*P*-value)	0·62 (<0·0001)	0·68 (<0·0001)

Table 3. Species traits ranked by their relative importance in predicting extinction in the conditional inference forest model

Rank	Species traits	Conditional permutation variable importance score
1	Local geographic range (*LOCRANGE*)	0·104
2	Maximum total length (*MTL*)	0
3	Family (*FAM*)	0
4	Air-breathing capability (*AIR*)	−0·001
=	Vertical position (*VERT*)	−0·001
5	Habitat preference (*HAB*)	−0·001
6	Number of congeners (*CONG*)	−0·002
7	Regional geographic range (*REGRANGE*)	−0·002
8	Feeding guild (*FEED*)	−0·002

A positive conditional permutation variable importance score refers to a reduction in the classification accuracy of the model when the test variable is permutated. A variable importance score of *c.* 0 means that there is negligible change to the classification accuracy of the model when the test variable is permutated, suggesting that the variable is not predictive of extinctions.

Discussion

Local geographic range emerged as the only predictor of freshwater fish extinctions in Singapore. The other ecological and life-history traits demonstrated limited utility in predicting extinctions despite offering plausible theoretical explanations and/or being identified as correlates of local extinction proneness in studies of freshwater fish elsewhere. For example, Olden, Poff & Bestgen (2008) found that the smallest and largest fishes were at the greatest risk of extinction in the lower Colorado River basin and suggested that large-bodied fishes are prone to extinctions because they have slow life histories and low maximum population growth rates, and are therefore intrinsically less resilient towards environmental change. It is however still unclear why extinction risk is higher for small-bodied fishes. A possible reason is that small-bodied fishes are likely to have lower dispersal ability (Gaston 1994) and, therefore, are restricted in its range and hence more likely to go extinct. However, we failed to find a correlation between body size and extinction status in our study.

Regional geographic range has also been shown to correlate with local extinction risk in other taxa (birds: Sodhi *et al.* 2010b; butterflies: Koh, Sodhi & Brook 2004) but the relationship remains untested with regard to freshwater fishes. The regional geographic range of the species may be a result of evolved traits that determine a species' dispersal ability or habitat flexibility (Bradshaw *et al.* 2008). Species with a wide regional geographic range may be better dispersers or exhibit greater habitat flexibility or tolerance, and are therefore less sensitive to environmental change. Related to dispersal ability and habitat flexibility are the two traits, habitat preference and air-breathing capability. We hypothesized that forest-dependent species are more likely to go extinct owing to (i) their habitat specificity, and (ii) the almost-complete conversion of primary forests in Singapore. We also expected air-breathing species, such as *Anabas testudineus* (Bloch) and *Clarias batrachus* (Linnaeus) to be less prone to extinction as they are able to survive out of the water (Johnels 1957) and therefore able to disperse to nearby drainages when their original habitats become uninhabitable. However, like body size, these three traits – regional geographical range, habitat preference and air-breathing capability – were not predictive of extinction in our analysis. Family was not correlated with extinction status, suggesting that there is negligible phylogenetic signal in predisposing species towards extinction. However, we recognize that our measure of phylogenetic relatedness was coarse, and further analyses, if a detailed phylogenetic tree for the species in the data set becomes available, will be useful in confirming the effect of phylogeny on extinction risk.

Nevertheless, our conditional inference tree and forest models were highly accurate, correctly predicting the status of 39 and 40 of 46 species, respectively. Freshwater fish species were more likely to be extinct if they were historically restricted to a single drainage. Of the 11 species that went extinct, nine were restricted to a single drainage. While two of these nine species were recorded from single unknown drainages, seven went extinct from the Seletar drainage. These seven species were historically recorded from Mandai Road, and the streams north and west of the Seletar reservoir. These sites, formerly freshwater swamp forests adjoining the existing Nee Soon Swamp Forest (Mandai Road Swamp Forest; Corner 1978), have been cleared (Ng & Lim 1992) resulting in the extinction of species endemic to the area.

Our models displayed a high degree of accuracy in classifying extinct species. Of the 11 extinct species, only one [*Systomus dunckeri* (Ahl)] was misclassified by the conditional inference forest and two [*Eugnathogobius oligactis* (Bleeker) and *Systomus dunckeri* (Ahl)] was misclassified by the conditional inference tree. The misclassified species were recorded from two drainages. Our models were also able to classify the status of extant species with a high degree of accuracy: both models erroneously classified only 5 of 35 extant species as extinct. These five species [*Clarias leiacanthus* Bleeker, *Nemacheilus selangoricus* Duncker, *Pangio muraeniformis* (de Beaufort), *Parakysis longirostris* Ng & Lim, *Pseudomystus leiacanthus* (Weber & de Beaufort)] were misclassified because they were all restricted to the intact Nee Soon Swamp Forest, a freshwater swamp in the Seletar drainage. These species would probably be extinct if this patch of freshwater swamp was cleared.

Our results suggest that freshwater fish extinctions in Singapore are driven by loss of entire populations after habitat conversion and are random with respect to the ecological and life-history traits we have investigated. This is contrary to previous studies, which demonstrated correlations between local extinction risk and life-history traits in freshwater fish (Olden, Poff & Bestgen 2008) and other taxa (Koh, Sodhi & Brook 2004; Sodhi *et al.* 2008, 2010b). The interaction between the high degree of endemism (almost a quarter of freshwater fish species are restricted to a single drainage in Singapore; freshwater fish are restricted to drainages while terrestrial organisms can disperse across the landscape) and habitat destruction may explain our results. In Singapore, entire catchments were deforested and portions of drainages were dredged, thereby resulting in the loss of entire populations restricted to these areas irrespective of species traits, for example, the extinction of the seven species of fish restricted to the swamp forests at Mandai after the area was drained.

Methodological differences may also help to explain the difference in results. Olden, Poff & Bestgen (2008) investigated the frequency of extinctions across segments of the Lower Colorado Basin as the response variable, while we investigated whether a species has completely gone extinct from Singapore. In addition, previous studies (Koh, Sodhi & Brook 2004; Olden, Poff & Bestgen 2008; Sodhi *et al.* 2008, 2010b) did not include local geographic range as a predictor for extinction proneness. On the other hand, our study may have missed out on traits that correlate with extinction proneness. For example, fecundity and longevity, acting in synergy with body size to drive the frequency of local extinctions in the lower Colorado River basin (Olden, Poff & Bestgen 2008), were not investigated in our study owing to the lack of data for these traits. However, given the high accuracy demonstrated by our models and that potential predictors were carefully chosen based on theory and past studies, it is unlikely that the effect of local geographic range will be swamped by the inclusion of new species traits.

In our study, habitat preference was the best predictor of local geographic range; species that are forest-dependent were observed to be restricted to fewer drainages. This is not unexpected as forest-dependent species are, by definition, unable to inhabit to drainages in non-forested habitats. Moreover, Singapore was almost completely deforested by the start of the 1900s (Corlett 1992), further restricting forest-dependent species to the drainages where forests were not cleared.

The results of our study can inform policies aimed towards conserving the native freshwater fish of Singapore. Species with restricted local ranges are most likely to go extinct locally, suggesting that habitat loss threatens the persistence of species irrespective of ecological and life-history traits. In Singapore where the geographic range of each freshwater fish species is generally well-known, conservation action should focus on the five species (listed before) that are currently restricted to Nee Soon Swamp Forest, the last remnant patch of freshwater swamp forest in Singapore. Although the legal protection of this forest patch (Tan *et al.* 2010) secures its immediate future, the population trends of these species remain poorly known. Besides the continued protection of this unique habitat, we suggest that the local parks authority undertake long-term monitoring studies to elucidate the population trends of species restricted to the Nee Soon Swamp Forest for their permanent conservation.

Despite focusing on local extinctions in Singapore, the results of our study have broad implications for conservation in the other parts of Southeast Asia. It is important to understand local extinctions because they are the first steps towards extinctions at larger spatial scales (regional and global) and therefore help to inform conservation actions before a species become globally extinct (Dulvy, Sadovy & Reynolds 2003). As the fish assemblage (Zakaria-Ismail 1994; Yap 2002) and human impacts (Dudgeon 1992, 2000) in Singapore are generally representative of that in other parts of Southeast Asia, our results are likely to be applicable to other Southeast Asian regions. The major mechanism driving local extinctions in Singapore is habitat loss removing entire populations of range-restricted species. Local extinctions are therefore likely to reflect those in other parts of Southeast Asia if habitat loss, primarily driven by the expansion of oil palm agriculture (Wilcove & Koh 2010), remains unchecked. This is corroborated by an existing study which attributed local freshwater fish extinctions at Gombak River in Malaysia to habitat loss (Zakaria-Ismail 1994).

Regionally, our results suggest that it is important to elucidate the geographic ranges of species for the effective conservation of the Southeast Asian freshwater fish fauna. Successive losses of local populations across Southeast Asia will engender the regional extinction of freshwater fish. For the many freshwater fish species that are restricted to only Southeast Asia (e.g. the *c.* 70 cyprinid genera not found anywhere else; Zakaria-Ismail 1994), regional extinction is equivalent to global extinction. By determining species ranges, conservation managers will be able to identify species which are restricted to one or a few drainages in Southeast Asia and are therefore more likely to become globally extinct as habitat loss proceeds. However, as many drainages in Southeast Asia have not been sufficiently sampled and the exact distribution of freshwater fish species remains unknown (Kottelat & Whitten 1996), a major priority is to conduct extensive surveys of drainages so as to elucidate spatial patterns of species richness and endemism. Before the completion of an extensive assessment of species ranges, we suggest that surveys proceed concurrently with conservation efforts in peat swamp forests because they are known to harbour a substantial number of freshwater fish species that are restricted to only a few specific drainages in Southeast Asia (Kottelat & Whitten 1996) and are threatened owing to a high rate of habitat loss (Miettinen & Liew 2010).

Previous studies have suggested that the life-history and ecological correlates of extinctions may be used as generalized rules of thumb to earmark extinction-prone species for conservation action (Bradshaw *et al.* 2008). However, our results indicate that the immediate conservation of Southeast Asian freshwater fish fauna does not require an extensive knowledge in the life history and ecology of individual species. Effective conservation can be achieved by the complete protection of habitats with high endemic species richness after they have been identified via an assessment of species ranges, which is likely to require less time and financial resources compared with comprehensive studies aimed towards uncovering the life-history and ecological characteristics of every species in Southeast Asia. Where complete protection is not possible, for example, in existing logging concessions and plantations, local authorities should aim to establish partnerships with logging or plantation companies to ameliorate impacts on fish fauna via reconciliatory approaches such as establishing multiple-use modules (Noss & Harris 1986) and riparian buffers (Moyle & Sato 1991). Non-governmental conservation organizations and local wildlife authorities should also monitor the population trends of species that are restricted to one or few drainages in Southeast Asia as the local extinctions of their populations are equivalent to global extinctions of these species.

Although we did not examine the impact of invasive species on freshwater fish extinctions, it is unlikely to affect our results as there is no evidence that invasive species have caused population reductions or extinctions of native fish species in Singapore (Ng, Chou & Lam 1993). However, given that invasive species has contributed to extinctions in other regions (e.g. the invasive Nile perch precipitating extinctions of cichlids endemic to Lake Victoria; Rahel 2002) and that the impacts of invasive species in Southeast Asia are still unclear (Dudgeon 1992), the stocking of exotic species should be avoided in drainages with high endemic species richness should these species have negative, but presently unidentified, impacts on native fish fauna following the precautionary principle.

Freshwater habitats and its biota are under tremendous threat from unabated habitat loss in Southeast Asia. In regions where the degree of habitat loss is high, for example, in Singapore, extinctions appear to be dependent on the local geographic range but not other ecological and life-history traits. Given the rate at which freshwater ecosystems in Southeast Asia are being altered, it is imperative to identify range-restricted species and to reduce habitat loss in drainages of high endemism for the long-term preservation of the region's unique freshwater ichthyofauna.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Full list of references used to assemble the data set.

Appendix S2. Full data set used in the analysis.

Table S1. Species traits ranked by their relative importance in predicting a species' local geographic range in the conditional inference forest model.

Figure S1. Receiver operating characteristic (ROC) curves for models.

Figure S2. Conditional inference tree for predicting the local geographic range of a species.

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