

Forest Fragment and Breeding Habitat Characteristics Explain Frog Diversity and Abundance in Singapore

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ABSTRACT

Habitat loss and fragmentation can have severe negative and irreversible effects on biodiversity. We investigated the effects of forest fragmentation on frog diversity in Singapore because of its high rates of deforestation and the demonstration that frogs are some of the most sensitive species to habitat degradation. We surveyed frog species in 12 forest fragments varying from 11 to 935 ha. We compared differences in species richness, abundance, and Shannon's index in relation to forest fragment size, connectivity (distance between fragments), and breeding habitat heterogeneity. A total of 20 species from 12 genera and five families were encountered in 12 fragments. Larger fragments and those closer to larger fragments had higher species richness. Abundance, however, was not correlated with forest area or connectivity, but we found fewer individual frogs in the larger fragments. We also found that breeding habitat heterogeneity best explained frog species diversity and abundance in forest fragments. Fragments with a high diversity of breeding habitats had more species. We found no evidence to suggest that abundance and diversity are strongly correlated, particularly in disturbed areas, but that breeding habitat heterogeneity is an under-appreciated factor that should be considered when prioritizing areas for anuran conservation. Enriching breeding habitat heterogeneity, creating corridors between fragments, and reforesting degraded areas are some of the most beneficial strategies for preserving urban frog biodiversity.

Key word: amphibians; conservation; deforestation; fragmentation; frogs.

HABITAT LOSS HAS MORE DETRIMENTAL CONSEQUENCES for tropical terrestrial ecosystems to date than any other driver such as climate change and invasive species (Sala *et al.* 2000, Sodhi & Brook 2006, Sodhi *et al.* 2008, Bradshaw *et al.* 2009). We are currently facing an extinction rate perhaps 1000 or more times greater than the background rate derived from the fossil record (Baillie *et al.* 2004), mainly as a result of habitat loss. Within the larger context of a general biodiversity meltdown (Brook *et al.* 2003), amphibians in particular have had the dubious honor among vertebrates of having the highest proportion of species threatened with extinction (Stuart *et al.* 2004, Beebe & Griffiths 2005). According to the 2004 and 2008 IUCN Red Lists of Threatened and Endangered Species, at least 32 percent of the world's amphibian species are now threatened with extinction (Baillie *et al.* 2004, IUCN 2008).

Enigmatic declines of many amphibian populations (Stuart *et al.* 2004), especially in areas isolated from direct human influence, have brought up concerns regarding more novel or widespread stressors (*e.g.*, global climate change, UV radiation, pollution and infectious diseases; Collins & Storfer 2003). An unregulated and extremely large trade in frog meat is another little-known factor that exacerbates the problem (Warkentin *et al.* 2009). However, habitat loss remains the primary cause of recorded global declines for amphibians (Alford & Richards 1999, Blaustein & Kiesecker 2002, Collins & Storfer 2003, Cushman 2006, Gardner *et al.* 2007). Compared with other terrestrial fauna, amphibians are more vulnerable to habitat loss and fragmentation due to their relatively low vagility (Gibbs 1998a, Bowne & Bowers 2004), high

risk of mortality when migrating across inhospitable terrain (Fahrig *et al.* 1995, Carr & Fahrig 2001, Becker *et al.* 2007), low tolerance to environmental extremes (Findlay & Houlihan 1997, Semlitsch 2000), high susceptibility to pathogens, competition or predation from invasive species, and pollution (Hecnar 1995, Bridges & Semlitsch 2000, Stuart *et al.* 2004).

Investigations using richness, abundance, community composition, and dispersal indices of amphibian species' biological response to habitat modification have focused on specific elements related to habitat fragmentation—patch size, isolation, connectivity, edge effects, habitat barriers, and matrix type. As predicted by island biogeography (MacArthur & Wilson 1967), there is strong evidence for a positive relationship between species richness and area (Gibbs 1998b, Kolozsvary & Swihart 1999, Houlihan *et al.* 2000, Vallan 2000, Krishnamurthy 2003, Pineda & Halfiter 2004). Some studies have found an effect of isolation (Lehtinen *et al.* 1999, Parris 2006) or on habitat 'splitting' (Becker *et al.* 2007), another form of habitat fragmentation. Some also show increasing abundance with larger habitat area (Knutson *et al.* 1999, Houlihan *et al.* 2000, Guerry & Hunter 2002), but this may not be true for some species or in some areas. Evidence for the importance of edge effects seems to be equivocal, ranging from no evidence of effect (Gascon 1993, Toral *et al.* 2002), weak effects (Demaynadier & Hunter 1995), to species-specific effects (Schlaepfer & Gavin 2001, Lehtinen *et al.* 2003). Despite numerous amphibian fragmentation studies, there are few in SE Asia (Alcala *et al.* 2004, Gardner *et al.* 2007), a region hosting two of the three 'hottest' biodiversity hotspots, Sundaland and the Philippines (Myers *et al.* 2000), and currently experiencing the highest rate of tropical deforestation and population growth (Hannah *et al.* 1995, Laurance

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1999, Achard *et al.* 2002, Sodhi & Brook 2006, Bradshaw *et al.* 2009). Singapore provides an extreme case of tropical deforestation with almost 95 percent of the former forest cover cleared in the past 200 yr (Brook *et al.* 2003), and an ideal experimental ground for fragmentation studies. The remaining forests in Singapore are highly fragmented and largely degraded, but most are found around the central catchment area (Fig. S1). In Singapore, several studies have focused on the negative effects of forest fragmentation on different taxa (plants, invertebrates, mammals, and birds; Koh & Sodhi 2004, Castelletta *et al.* 2005); however, little is known of its effects on amphibians. Here we investigate the effects of forest fragmentation on frog species richness and abundance in Singapore. Specifically, we hypothesize that patch size, fragment connectivity, breeding habitat diversity, and inter-fragment matrix type will influence abundance and species richness of frog assemblages. Specifically, we predict that the relative importance of fragment area, connectivity, matrix conducive to dispersal, and breeding habitat heterogeneity are positively correlated with frog species richness and abundance. We also assess conservation value of existing forest remnants and regenerating forests for the amphibians of Singapore by evaluating their connectivity and potential for effective restoration.

METHODS

SAMPLING LOCATIONS AND HABITAT TYPES.—We selected 12 forest fragments on Singapore island (Corlett 1997, Turner *et al.* 1997, Castelletta *et al.* 2005; Fig. S1) that ranged in size, forest composition, and disturbance level. Large fragments (> 140 ha) were undisturbed secondary forests that had some primary forest patches, with little or no exotic introductions. Middle-sized fragments (50–140 ha) ranged from more disturbed secondary forests to abandoned plantations with exotic plant introductions and some habitat modification. The smallest fragments (< 50 ha) were generally urban parks with more ornamental plants and relatively fewer native species and much stronger edge effects and disturbance.

ANURAN SAMPLING METHODS.—Visual encounter surveys were chosen as our standard method to census frogs (Crump & Scott 1994) to maximize the number of species observed per survey (Pearman *et al.* 1995). Visual encounter surveys are exceptionally robust sampling methods when replicated in large efforts like our study (Crump & Scott 1994). Surveys were conducted between 1930 and 2230 h, corresponding to the period of greatest anuran vocalization and activity (Marsh & Pearman 1997) with 1 h as our standard sampling unit. Transects within each forest fragment were selected in the vicinity of water bodies (streams and ponds) and forest cover. Each 1-h transect was conducted by two or three trained field personnel with head torches. Frogs were hand-caught, identified to species, measured, sexed, and released at the same site where captured. Individuals that were only heard or were unidentifiable (escaped) were left out of the richness analysis but included in the abundance analysis. Surveys in each fragment were conducted until the species-accumulation curve reached an obvious as-

ymptote (four surveys were conducted after no new species were found), indicating adequate sampling. There is no breeding seasonality for frogs in Singapore, and all fieldwork was done between September 2006 and January 2007.

HABITAT VARIABLES AND ATTRIBUTES.—Four independent variables were investigated to explain variance in species richness and abundance: (1) patch size; (2) weighted connectivity (inverse of isolation); (3) breeding site heterogeneity; and (4) matrix type (for details of these variables see Tables 1, 2, S1 and S2). Patch sizes of the 12 fragments were obtained from published sources (Castelletta *et al.* 2005) and verified with geographic information system coordinates. We further verified area estimates using 1:25,000 topographic maps obtained from the Department of Geography, National University of Singapore. We used weighted connectivity as an index to combine the fragment area and proximity of the other eleven fragments. The weighted connectivity of focal fragment k was calculated as

$$\sum_{i=1, i \neq k}^{12} (A_i/A_T)/D_{ik}$$

where A_i is the area of fragment i , A_T is the total area of all fragments and D_{ik} is the shortest distance between fragments i and k . Breeding site heterogeneity was a measure of breeding site diversity in each fragment. Five types of breeding sites were defined (Table 1) based on known frog reproductive ecologies (Lim & Lim 1992, Inger & Stuebing 2005) and the breeding site heterogeneity score was a simple additive function (ranging from 0 to 5) of the number of different breeding habitats found in the particular forest fragment (see Table 1). The habitat matrix surrounding each site and separating it from the nearest fragment was categorized into two classes: (1) ‘urbanized area’ defined matrix that had undergone urban modification (*e.g.*, asphalt roads, cement walks, and houses); and (2) ‘vegetation’ defined matrix that had not undergone such modification and was > 50 percent forested area, grassland, or reservoir. This predictor (*matscore*; Table S1) was used for detecting possible corridors and connectivity between fragments.

ANALYSES.—We used general linear models implemented using the *glm* function in R (R Development Core Team 2007). We adopted

TABLE 1. Breeding site categorization for the breeding heterogeneity score (brhet; determined from sum of total number of different breeding site categories contained in each forest fragment [ranging from 0 to 5]).

Category	Description
Short stream	Running water < 100 m long and < 2 m wide
Long stream	Running water > 100 m long and > 2 m wide
Small pond	Still water < 100 m ²
Large pond	Still water > 100 m ²
Reservoir	Artificial reservoir

information-theoretic methods to contrast models incorporating different of habitat variables on amphibians in the forest fragments in Singapore because of the known advantages of these methods over stepwise approaches (Weakliem 2004, Whittingham *et al.* 2006). Models were built using Gaussian error structures and identity link functions. This approach compares the fits of a suite of candidate models using Akaike's information criterion (AIC), a measure of the relative Kullback–Leibler information lost when a model is used to approximate reality (Burnham & Anderson 2004). To determine the intercorrelations among our chosen predictor candidates, we calculated Spearman's rank correlations.

Our three model sets (Table S1) were built based on each of four measured habitat variables. Our model set is presented in Table S1, where the response was: (a) species richness; (b) \log_{10} abundance; or (c) Shannon's diversity index (H' ; higher values indicate more unique species, or greater species evenness). All predictor variables were highly intercorrelated (Table S2). In general, larger forest fragments had more, different breeding sites, were closer to other fragments, and surrounded by vegetation. More isolated fragments had fewer breeding site types and were surrounded by urban matrix. Given these high intercorrelations, and the low sample size (12 fragments total), we could not contrast complex, multiterm models. Indeed, approximately ten data per term are recommended for adequate inference (Wintle *et al.* 2005). As such, each model set has five total candidate models (four single-term models and the intercept-only model). To determine if more complex models were excluded in error, we also included a two-term model comprising the highest-ranked terms for each response—in all cases the two-term model performed worse than a single-term model (results not shown); hence, we are justified in considering the single-term models only. Fragment area and weighted connectivity were \log_{10} -transformed before analysis to account for nonnormality. Akaike's information criterion corrected for small samples (AIC_c) was used to assess relative model support, and AIC_c weights ($wAIC_c$) provided relative weight of any particular model which varied from 0

(no support) to 1 (complete support) relative to the entire model set (Burnham & Anderson 2002). For each model considered, we also calculated the percentage deviance explained (% DE) as a measure of explanatory power.

RESULTS

Seventy-six visual encounter survey transects were done for the 12 sites, ranging from five to nine per site. A total of 638 individual frogs from 20 species representing five families (Rhacophoridae, Bufonidae, Megophryidae, Microhylidae, and Ranidae) and 12 genera were encountered in the forest fragments we examined in Singapore. The number of species in each site ranged from 1 in Mount Faber to 14 in Bukit Timah (Table 2), with mean species richness higher in larger, undisturbed secondary forests than in smaller urban parks. Ten species were found exclusively in larger (> 140 ha) forest fragments: *Megophrys nasuta*, *Leptobrachium nigrops*, *Rana baramica*, *Rana laterimaculata*, *Limnonectes malesiana*, *Limnonectes plicatella*, *Occidozyga laevis*, *Nyctixalus pictus*, *Kalophrynus pleurostigma*, and *Microhyla butlerii*. The species *Polypedates leucomystax*, *Kaloula pulchra*, *Bufo melanostictus*, and *Microhyla heymonsi* were ubiquitous across sites and were almost always found even in the smallest urban parks. *Rana catesbiana* was the only exotic species encountered (Lim & Lim 1992).

SPECIES RICHNESS.—The breeding site heterogeneity (*brhet*) model was the most highly ranked ($wAIC_c = 0.976$; Table S1). The second highest-ranked model ($wAIC_c = 0.010$; Table S1) accounted for 53 percent of the deviance (% DE), but as mentioned above, these variables were correlated (Table S2). The top-ranked model predicts frog species richness as a function of *brhet*:

$$richness = 1.60 + 1.92 brhet$$

where the estimated standard errors are 0.98 and 0.32 for the intercept and slope estimates, respectively. Species richness increases

TABLE 2. Summary statistics of forest fragments in Singapore. Average abundance here is number frogs/hour of visual encounter survey transect. See text for details.

Forest fragments	Area (ha)	Weighted connectivity ($\times 10^3$)	Breeding site heterogeneity	Matrix type	Species richness	Shannon index	Average abundance
Nee Soon Nature Reserve	935	1.1	5	Veg	12	2.22	7.0
MacRitchie Nature Reserve	484	3.6	5	Veg	11	1.84	14.8
Bukit Timah Nature Reserve	145	5.3	5	Veg	14	2.04	11.6
Bukit Batok West Park	102	0.2	1	Urb	4	1.17	2.4
Holland Woods	69	0.3	3	Urb	5	1.56	8.5
Lornie Forest	58	1.8	3	Veg	4	1.20	5.6
Mount Faber Park	49	0.4	0	Urb	1	0.00	4.0
Bukit Batok Nature Park	38	0.6	3	Urb	6	1.60	11.4
Kent Ridge Park	32	0.1	2	Urb	6	1.15	8.8
Telok Blangah Hill Park	29	0.6	1	Urb	6	1.11	10.0
Yishun Park	27	0.2	1	Urb	3	0.92	2.2
Labrador Nature Park	11	0.1	1	Urb	5	0.83	7.8

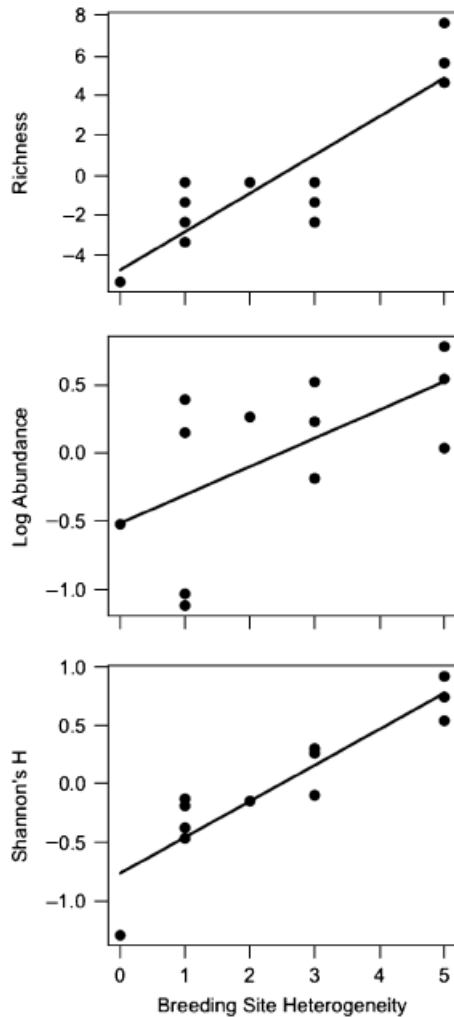


FIGURE 1. Partial residual plots of frog species richness (top row), abundance (middle row), and Shannon's diversity index (bottom row) as a function of breeding site heterogeneity (see Methods for details).

with breeding site diversity (Fig. 1), but considering area alone as a predictor provided the lowest relative statistical evidence and explanatory power.

ABUNDANCE.—The breeding site heterogeneity model was again the most highly ranked (Table S1), but with a weaker weight ($wAIC_c = 0.479$) explaining only 37 percent of the deviance in abundance. Isolation ($lconn$) had the next highest relative support ($wAIC_c = 0.225$) and a slightly lower explanatory power (% DE = 28%). As for richness, area provided the weakest prediction of abundance (Table S1).

SHANNON'S DIVERSITY INDEX.—Consistent with richness and abundance responses, the breeding site heterogeneity model was the highest-ranked model correlating with Shannon's diversity

index ($wAIC_c = 0.998$), explaining 84 percent of the deviance in data (Table S1). The remaining models had considerably weaker support.

DISCUSSION

Our results underscore and augment previous findings on birds, butterflies, moths, and freshwater mollusks in Singapore (Koh & Sodhi 2004, Castelletta *et al.* 2005, Clements *et al.* 2006). We confirm the obvious negative effects of forest fragmentation on the diversity of frogs previously shown in other areas (Findlay & Houlahan 1997, Kolozsvary & Swihart 1999, Houlahan *et al.* 2000), but we add new insights into the complex relationships of species richness and abundance in disturbed areas, especially concerning breeding site heterogeneity. Although fragment area is known to affect frog abundance and richness (Dupuis & Steventon 1999, Knutson *et al.* 1999, Houlahan *et al.* 2000, Guerry & Hunter 2002, Trenham & Shaffer 2005, Cushman 2006, Sodhi *et al.* 2008), it was an inferior predictor of species richness, abundance, and evenness compared with the more direct measure of breeding habitat heterogeneity (also see Zimmerman & Bierregaard 1986).

Although the basic species–area relationship is well established (MacArthur & Wilson 1967), fragmentation is associated with other, more complex changes to habitats. For example, the abiotic conditions of the perimeter of the fragments are modified because edge habitats are more exposed to the sun, wind, and climatic extremes. Temperature is elevated and the air and leaf litter humidity greatly reduced (Kapos 1989, Kapos *et al.* 1997). These altered conditions are unfavorable for the physiological needs of many frogs (Schlaepfer & Gavin 2001, Neckel-Oliveira & Gascon 2006), and many species are only able to survive in the interior of forest fragments. This edge effect inevitably increases with decreasing fragment area as the perimeter:area ratio increases. Additionally, small fragments often suffer more disturbances, are more vulnerable to invasive species (Saunders *et al.* 1991, Hobbs & Huenneke 1992, Halme & Niemela 1993), and have a lower threshold for local extirpation (Ferraz *et al.* 2003). Thus, the measure of breeding site heterogeneity provides a more direct mechanism between species loss and environmental degradation than does area alone.

Like a previous study in the Amazon (Zimmerman & Bierregaard 1986), we also find that deviations from the typical species–area curve might be the new normal state for frogs and other species most tied to specific kinds or heterogeneity of breeding sites. Many species are closely associated with specific types of water bodies (Bousbouras & Ioannidis 1997, Semlitsch 2000); hence, a fragment with more types of breeding habitats, regardless of its size, will likely contain more species. Eight of the ten species that were exclusively found in large, undisturbed forests breed only in forest streams, while the other two are tree-hole or ephemeral forest-pool breeders. Other species (*M. heymonsi*, *M. butleri*, *Rana erythraea*, *Rana chalconota*) that use ponds and ephemeral puddles to breed were found mainly in smaller, disturbed forests patches and urban parks. These findings are of critical importance for the restoration of small forest fragments where habitat and

breeding site heterogeneity augmentation can help conserve amphibian biodiversity.

We also observed a positive relationship between fragment size and species abundance of anurans, despite finding that abundance was sometimes higher in certain smaller, highly disturbed fragments with low species richness (*i.e.*, the high variance and residuals contributed to the weak effect found). Higher abundance in some disturbed fragments has also been found in other fragmentation studies on small mammals, birds, and invertebrates (Bowers & Matter 1997, Debinski & Holt 2000). Debinski and Holt (2000) attributed this superficially counter-intuitive observation to crowding effects, where population density rises immediately following fragmentation. But this explanation may not be sufficient to explain our results because of the long time since fragmentation in Singapore. The ability of some species to use both urbanized matrix and forest fragments may also lead to the prevalence of these species. Certain species have evolved to survive well in disturbed areas (Beebe 1979, Gascon *et al.* 1999) where they can do well under conditions that favor them over less competitive and more specialized species. Although there is a general decline in diversity in smaller disturbed sites, abundance of some weedy species may increase.

The frogs *P. leucomystax*, *K. pulchra*, *B. melanostictus*, *R. erythraea*, and *M. heymonsi* were commonly seen and heard across small and heavily disturbed fragments, sometimes even found in highly urbanized areas. These five species are highly adaptable and tolerate disturbance and severe habitat alteration. The Asian toad, *B. melanostictus*, was by far the most abundant species in Singapore. Besides exuding a skin secretion toxic to predators and having a toxic tadpole stage, it has thick and relatively impermeable skin, making it less susceptible to drying and increasing its survival probability in drier microhabitats (Zug *et al.* 1993, Inger & Stuebing 2005). *Kaloula pulchra* is another frog associated with human settlement that is found in sewers, drainage tiles, garbage debris, and most places where water accumulates. They also have defensive skin secretions that deter predators as well as antipredator tadpole behaviors. Upon agitation, *K. pulchra* inflates, exudes a sticky paste, suddenly deflates, and escapes (Inger & Stuebing 2005). *Polydectes leucomystax* is an adaptable arboreal species and lays its eggs on vegetation above water. Eggs hatch into tadpoles before dropping into the water below. *Rana erythraea* is also highly adaptable, able to endure polluted ditches and freshwater ponds, and its tadpoles exhibit predator avoidance. The last common urban species, *M. heymonsi*, is small and needs only a waterlogged lawn in which to breed. In general, all common frogs in Singapore have many larval and adult adaptations that have enabled them to take advantage of human disturbed conditions.

The matrix separating fragments was another parameter affecting diversity of anurans. Fragments joined by forest corridors seem to encourage interfragment movement and could possibly maintain diversity between sites that were joined. In contrast, urbanized matrixes presented barriers preventing dispersal (Fahrig *et al.* 1995, Findlay & Houlahan 1997, Knutson *et al.* 1999, Houlahan *et al.* 2000, Carr & Fahrig 2001). Although we have no direct measures or observations of these matrix effects, the data suggest isolation and matrix type effects.

Rana catesbeiana was the only exotic frog species encountered in Singapore (Lim & Lim 1992). Initially imported from America and bred locally in farms for human consumption, it was later released by residents into the wild for religious traditions (the Buddhist Vesak Day). *Rana catesbeiana* is aggressive and territorial (Emlen 1968) posing a potential threat to native frog species. Although we found no evidence of direct negative effects (*e.g.*, predation of native species), these introduced animals compete for the same food and breeding resources as native species.

Conservation outcomes may seem bleak in Singapore (Brook *et al.* 2003), but our work demonstrates that conservation implemented on the central catchment area (consisting of BTNR, MNR, and NSNR) is paying off. A total of 20 anuran species were encountered, compared with the 23 species initially recorded by Lim and Lim in 1992. Ten species, all forest specialists, are found exclusively in the central catchment area including the locally endangered *K. pleurostigma*. We did not encounter two of the least-known frogs in Singapore, *Theloderma horridum* and *Pelophryne brevipes*, also locally endangered species that are restricted to the largest forest patches, but we refrain from declaring them locally extinct until more surveys are conducted.

Overall, we suggest that forest fragments on the island of Singapore, although small, are still worth conserving. They provide the last refuges for plant and animal species and offer an opportunity to avert extirpations. Fragments can also act as sources for recolonization of nearby areas undergoing succession, providing valuable habitat for migratory animals, be made more valuable through linking corridors to other fragments, and enhance the likelihood for the persistence of other species (Turner & Corlett 1996). Our analyses showed that breeding habitat heterogeneity is also the most important factor determining frog species richness and should be directly targeted for enrichment projects. This can be as simple as adding bamboo or PVC cylinders in forest habitats, creating additional drainage ditches and seepage areas, and improving water quality of existing ponds and waterways.

Maintaining connectivity among forest fragments also depends on protecting fragments and corridors from degradation over wide areas. A strategic landscape-based approach including both protected areas and land vetted for restoration or mitigation will be important to achieve effective frog conservation in Singapore. Large-scale networks of linked forest fragments including breeding sites are perhaps the only effective means of conserving frog biodiversity (Semlitsch 2000). Perhaps the largest conservation problem Singapore faces is the small amount of remaining undisturbed forest cover. The forest left intact on the island is tiny; only 1564 ha located in the central catchment area (*ca* 3% of original) remains. Other fragments are either small, heavily disturbed, or both. While ongoing urbanization and economic development will almost certainly not be compromised for biodiversity conservation, the best solution now is to preserve and enrich remaining fragments and to rehabilitate degraded areas in Singapore, linking quality habitats for a diversity of organisms. We encourage habitat and breeding site heterogeneity augmentation as some of the most effective interventions to restore and protect amphibian biodiversity.

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SUPPORTING INFORMATION

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

TABLE S1. *General linear models and summary statistics for species richness, log₁₀ abundance, and Shannon's diversity index.*

TABLE S2. *The Spearman rank correlation showing high inter-correlation of predictor variables used in this study.*

FIGURE S1. Map of Singapore showing locations of the 12 forest fragments.

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