



## Conservation of amphibians in Borneo: Relative value of secondary tropical forest and non-forest habitats

Graeme R. Gillespie<sup>a,\*</sup>, Eddie Ahmad<sup>b</sup>, Berjaya Elahan<sup>b</sup>, Alice Evans<sup>c</sup>, Marc Ancrenaz<sup>b,e</sup>, Benoit Goossens<sup>c,d</sup>, Michael P. Scroggie<sup>f</sup>

<sup>a</sup> Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia

<sup>b</sup> Kinabatangan Orang-utan Conservation Programme, c/o Sabah Wildlife Department, Sandakan, Sabah, Malaysia

<sup>c</sup> Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom

<sup>d</sup> Danau Girang Field Centre, c/o Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

<sup>e</sup> North of England Zoological Society, Honorary Conservation Fellow, Chester, United Kingdom

<sup>f</sup> Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, P.O. Box 137, Heidelberg, Victoria 3084, Australia

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### ABSTRACT

The impact of degradation of Southeast Asian rainforests and conversion to oil palm plantations on amphibians is unknown. To assess the relative value of secondary forests, oil palm plantations and other non-forest habitats for amphibian conservation, we evaluated amphibian species richness and assemblage composition in secondary lowland forests, compared with oil palm plantations and other non-forest habitats, along the Lower Kinabatangan River, eastern Sabah, Malaysia. Secondary forests retained a large proportion of amphibian species known from lowland primary rainforests. Species richness was higher in secondary forest habitats compared to oil palm plantations and other non-forest habitats. Secondary forests retained a much higher proportion of endemic species than non-forest habitats. We found strong differentiation between the frog assemblages in forest, non-forest and plantation sites. Oil palm plantations retained no microhylid species, few arboreal species and were dominated by habitat generalist and human commensal species. Our findings suggest that, despite a history of disturbance and degradation, remnant secondary forests may play an important role in conserving lowland amphibian diversity. In contrast, oil palm plantations have comparatively low conservation value for amphibians. Our study highlights the value of setting aside adequate areas of representative forest habitats within agricultural landscapes in order to conserve biodiversity, even when those remnants have a history of prior disturbance.

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### 1. Introduction

Ongoing global destruction of tropical forests is a major contributor to biodiversity loss (Wright and Muller-Landau, 2006; Sodhi et al., 2010). Among tropical regions, Southeast Asia currently has one of the highest rates of deforestation (Sodhi and Brook, 2006; Miettinen et al., 2011). Commensurate with this landscape change has been the rapid expansion of secondary forests with varying levels of degradation from selective and commercial logging, and expansion of agriculture, in particular oil palm plantations (McMorrow and Talip, 2001; Fitzherbert et al., 2008). The impacts of these large-scale land use changes on biodiversity are not fully understood, and may further accelerate extinction rates (Sodhi et al., 2010).

In many tropical regions protected areas are inadequate for sustained, broad-based biodiversity conservation (Giam et al., 2011;

\* Corresponding author. Tel.: +61 429091783.

E-mail address: [Graeme.R.Gillespie@gmail.com](mailto:Graeme.R.Gillespie@gmail.com) (G.R. Gillespie).

Mora and Sale, 2011). Conservation of many tropical forest species is increasingly dependent upon human modified habitats, such as production forests, degraded forests and agricultural landscapes (Gardner et al., 2007a,b; Koh and Gardner, 2010; Clough et al., 2011). However, understanding of the conservation value of altered and degraded forests and plantations remains poor for most organisms (Dunn, 2004; Barlow et al., 2007; Gardner et al., 2007a; Sodhi et al., 2010). Whilst evidence exists that some biota persist in modified tropical forests (e.g. Lawton et al., 1998; Medellin and Equihua, 1998; Dunn, 2004; Quintero and Roslin, 2005), there is a lack of consensus regarding the impacts of forest change due to the contrasting responses of different groups of organisms and methodological differences (e.g. Hamer and Hill, 2000; Dunn, 2004; Hill and Hamer, 2004; Lugo and Helmer, 2004). This lack of consensus reflects the relative paucity of studies, ecological variation between taxa, regional and site specific spatial and temporal conditional effects, such as time since disturbance, degree and scale of modification, and the availability of remaining primary forest habitats (Barlow et al., 2007; Gardner et al., 2007a).

Amphibians are considered to be one of the most threatened animal groups globally, having suffered unprecedented rates of decline in recent decades (Stuart et al., 2004). Whilst a range of factors are involved, habitat loss is by far the major cause of declines (Stuart et al., 2004; Gardner et al., 2007a; Sodhi et al., 2008; Gillespie et al., 2011). Amphibian species richness and diversity peaks in tropical forests (Vitt and Caldwell, 2001; Wells, 2007); however, few studies have examined the impact of forest alteration on tropical amphibian communities (Heinen, 1992; Vitt and Caldwell, 2001; Ernst and Rödel, 2005, 2008; Ficetola et al., 2007; Gardner et al., 2007a,b; Wanger et al., 2009a). Resilience of tropical forest amphibians to habitat disturbance may be relatively low, due to adverse microclimatic changes, reduced availability of forest debris (logs and litter) for shelter and foraging, and loss of specialized breeding microhabitats (Vitt and Caldwell, 2001; Hillers et al., 2008; Kudavidanage et al., 2011). Persistence of species may depend on retention of sufficient unmodified habitat (Gillespie et al., 2005; Gardner et al., 2007a; Hillers et al., 2008; Wanger et al., 2009b), as the relatively low dispersal capabilities of amphibians may limit their capacity for recolonisation of disturbed areas (Ficetola et al., 2007). Conversely amphibians may have higher rates of persistence in small habitat fragments compared with other vertebrates due to their small home-range sizes and potentially high local population densities (Vitt and Caldwell, 2001; Rodríguez-Mendoza and Pineda, 2010).

The lowlands of Southeast Asia have been grossly altered in recent decades by timber harvesting and conversion to agriculture, in particular oil palm plantations (McMorrow and Talip, 2001; Sodhi et al., 2010; Miettinen et al., 2011). To date no studies have been undertaken to evaluate impacts on amphibian communities (Barlow et al., 2007; Sodhi et al., 2010). In many lowland regions the only forested areas remaining are secondary or highly degraded (Giam et al., 2011), and often small and fragmented (McMorrow and Talip, 2001; Barlow et al., 2007). Large areas of degraded forests are being converted to oil palm plantations

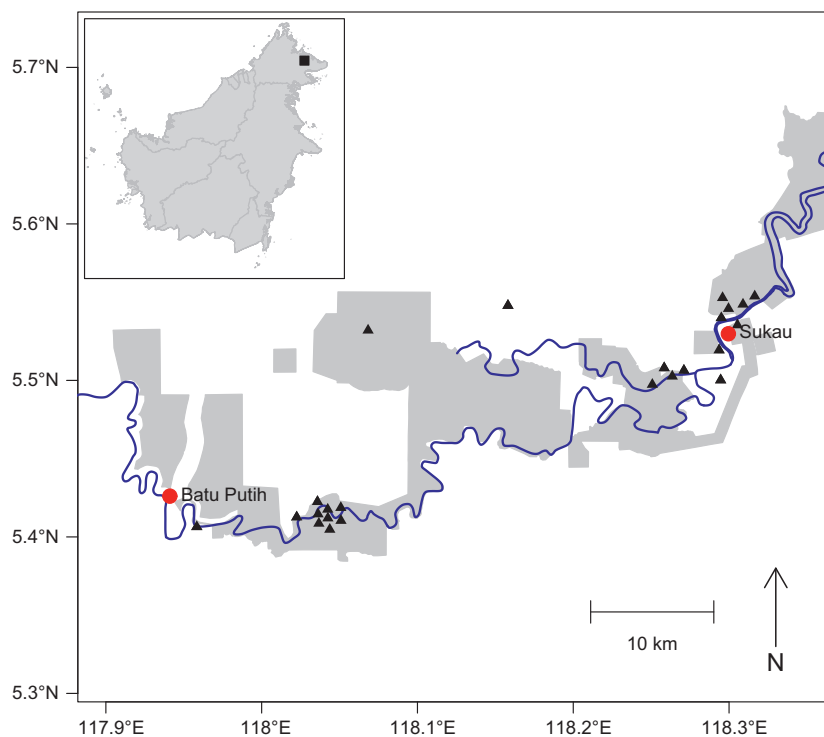
(Koh and Wilcove, 2008a); however, these remnant forests are potentially important reservoirs of biodiversity (Edwards et al., 2010; Giam et al., 2011). To assess the value of secondary forest for amphibian conservation, and the impact of forest clearance and conversion to oil palm plantations, we evaluated amphibian species richness and assemblage composition in secondary lowland forests, compared with nearby oil palm plantations and other non-forest habitats, in eastern Sabah, Malaysia.

## 2. Methods

This study was undertaken in the Lower Kinabatangan River floodplain in eastern Sabah, Malaysia (Fig. 1). The area is mostly flat and low (10–20 m asl), poorly drained and subject to periodic flooding, and is classified as extreme lowland forest (Azmi, 1998). Recent alluvium and finely textured, nutrient-rich deposits occur near the river while gleyic luvisols occur in poorly drained places (Haile and Wong, 1965). There are several low mudstone hills at ca. 40–50 m asl and several karstified limestone outcrops at ca. 100 asl (Azmi, 1998). Due to their poor accessibility, some of these outcrops support the only remnants of primary rainforest in the landscape.

The area is characterized by a warm, wet and humid tropical climate, with mean monthly temperatures ranging between 21 °C and 34 °C. Floods mainly occur between November and March during the west monsoon (Sooryanarayana, 1995) but may also occur in April and May (M. Ancrenaz, pers. obs.). Annual precipitation is approximately 2600–3300 mm (Malaysian Meteorological Services Department, cited in Ancrenaz et al., 2004).

With the exception of some steep limestone outcrops, the entire area was intensively logged, both commercially and illegally, between the 1960s and 1995. Most of the area was subsequently cleared for oil palm plantations (Azmi, 1998). Remnant secondary forest persists along the Lower Kinabatangan River, comprising a



**Fig. 1.** The Lower Kinabatangan River, eastern Sabah, Malaysia, with its position on the island of Borneo (inset). Shaded areas indicate protected forest areas of the Lower Kinabatangan Wildlife Sanctuary. Surrounding unshaded areas are predominantly oil palm plantations with some degraded forest patches. Black dots indicate sampling transects.

series of State forest blocks or 'lots', along with protected forest blocks, called 'Virgin Jungle Reserves', which forms the Lower Kinabatangan Wildlife Sanctuary, gazetted in 2005 by the State Government of Sabah. Adjoining the reserve are other parcels of forest on privately-owned land, not yet cleared. Collectively these remnant forests form a partially fragmented corridor that varies in width on either side of the Kinabatangan River from 0 to 8 km, interspersed with several small villages, roads, gardens and plantations, extending from the coastal mangrove swamps inland in a westerly direction approximately 70 km to dry-land foothill forests.

We identified five broad habitat types for this study: (i) dry forest – rarely inundated during the wet season, including well-drained limestone outcrops; (ii) wet forest – regularly inundated during the wet season, including permanent swamps; (iii) riparian forest – stream banks, comprising the large Kinabatangan River and smaller muddy tributaries; (iv) non-forest – open pasture and gardens, and open marshy areas; and (v) oil palm plantations. We established transects 400 m in length at sites within each habitat between the townships of Batu Putih (N5°24'26"; E117°56'57") and 3 km downstream of Sukau (N5°34'42"; E118°19'54") (Fig. 1). The number of transects in each habitat type was as follows: riparian forest (7); wet forest (6); dry forest (5); plantation (3); and non-forest (3). Transects were a minimum of 400 m apart and we took care where ever possible to place transects away from habitat edges. Transects were generally linear but followed stream banks and ridge lines in some cases in order to maintain habitat-type consistency. Apart from two transects on limestone outcrops (dry forest), all other forest transects were in secondary forest. These outcrops were the only locations in the region retaining any primary forest. Ideally we would also have undertaken sampling in comparable primary, unlogged, floodplain forest; however, this was not possible as there is none of this forest type remaining in the region. Most transects were clustered in two general areas: downstream of Batu Putih and downstream of Sukau. At least one transect was sampled in each of the five habitat types in each of these two general areas. To maximize sampling independence, transects in the same habitat type were placed in different "patches" of habitat. For example, oil palm transects were in different plantations separated by the river and/or areas of forest; transects in dry forest were separated by areas of riparian or wet forest, or non-forest habitats.

In total we undertook 86 censuses across 24 transects. Each transect was sampled either three or four times between August 2008 and May 2010. Most transects were sampled during the monsoon and in the dry season. One transect in each habitat type was not sampled in the monsoon due to inaccessibility; however, these transects were sampled a minimum of twice at the end of the monsoon. Each transect was sampled for frogs after dusk between 1830 and 2100 h, which was the period of maximum frog activity. Two people with head torches slowly walked along each transect documenting all species seen or heard. Apart from single individual records, no attempt was made to quantify the number of individual frogs detected. Sampling effort was therefore constrained by transect length rather than time. However each transect census took between 1.5 and 2 h to complete. Nomenclature follows that of Haas and Das (2011), Bossuyt and Dubois (2001) and Grismer et al. (2007) were also consulted for information on the genera *Philautus* and *Chiromantis*.

The occurrence/non-occurrence of frog species in each of the 86 censuses conducted was used to construct a species accumulation curve for the overall data set. A smoothed version of the species accumulation curve was constructed by carrying out 1000 random re-orderings of censuses to estimate the expected number of observed species after a given number of censuses. The total species richness was estimated from the censuses data using Jackknife and

Chao non-parametric species richness estimators (Chao, 1987; Colwell and Coddington, 1994). These estimates were superimposed on the species accumulation curves for comparison with the observed species richness.

We classified species into three major guilds: arboreal and non-stream-breeding; terrestrial/litter dwelling and non-stream-breeding; and stream-breeding species, based upon our own observations and available literature (Inger et al., 1986; Das, 1996; Inger and Stuebing, 2005; Inger, 2009; Grafe and Keller, 2009). Differences in relative species richness amongst guilds and habitat types were examined by two-way ANOVA. Residuals were plotted against group means to check for normality and equal variances. These analyses were performed using SPSS version 16.0 (SPSS, 1999).

We explored the patterns of variation amongst the frog assemblages of each transect using non-metric multidimensional scaling (NMDS) ordination. The ordination diagram was constructed from the Jaccard dissimilarity matrix of pairwise dissimilarities between transects. Twenty random starting configurations were used for constructing the ordination diagram, with the final configuration that minimized the stress of the ordination configuration being retained for plotting. Statistical comparisons of assemblage dissimilarity between broad habitat types (forest versus non-forest and plantation combined, and forest versus non-forest versus plantation) were made using Analysis of Similarities (ANOSIM) permutation tests (Clarke, 1993) each with 5000 random permutations of the dissimilarity matrix. The NMDS and ANOSIM procedures were implemented using the R package *vegan* (Oksanen et al., 2011).

### 3. Results

We located 31 frog species from 5 families; 15 non-stream-breeding arboreal, 14 non-stream-breeding terrestrial and 2 terrestrial stream breeding species (Table 1). The species accumulation curve from the raw census data suggests that most species likely to occur in the habitats sampled were detected (Fig. 2). Three species, including two *Philautus* and one *Chiromantis* species, were only detected on single occasions and are all believed to be undescribed.

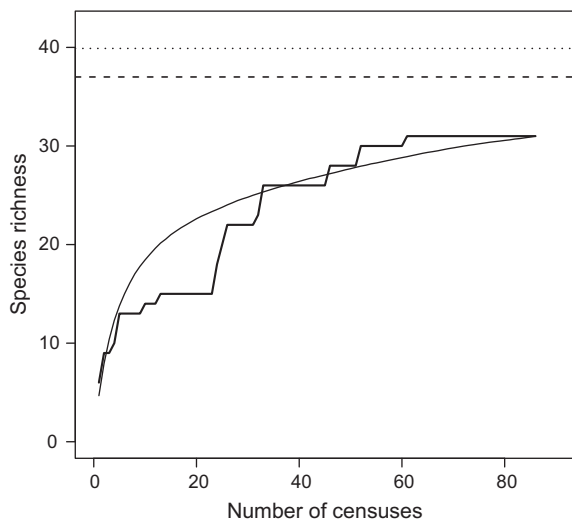
Overall, 29 species were found in forested habitats and 17 in plantations and other non-forest habitats. Thirteen species were restricted to forested habitats and two species were restricted to non-forest habitats. More species were detected in each forest habitat type compared to non-forest and plantation, with the most species (24) being detected in dry forest (Fig. 3). Of the 13 endemic species detected, most were restricted to forest habitats (Fig. 3); only three endemic species were found in non-forest habitats and plantations, all of which also occurred in at least one forest habitat type (Table 1). The higher numbers of species in each forest habitat compared with non-forest and plantation habitats were mostly due to higher numbers of endemic species in forest habitats (Fig. 3).

We found no significant differences in the mean number of species on transects amongst habitat types ( $F_{4,57} = 1.900$ ,  $p = 0.123$ ). However, mean numbers of species within each guild varied significantly across habitat types (guild  $\times$  habitat interaction:  $F_{8,57} = 4.148$ ,  $p = 0.001$ ). Dry forest transects had three times as many arboreal species compared to plantations (Fig. 4). In contrast, dry forest transects had approximately half as many terrestrial species as wet forest, non-forest and plantation transects. At least one stream breeding species was found in each habitat type except dry forest.

Overall, we observed strong differentiation between the frog assemblages found in forest, non-forest and plantations, with no overlap between the minimum convex polygons surrounding

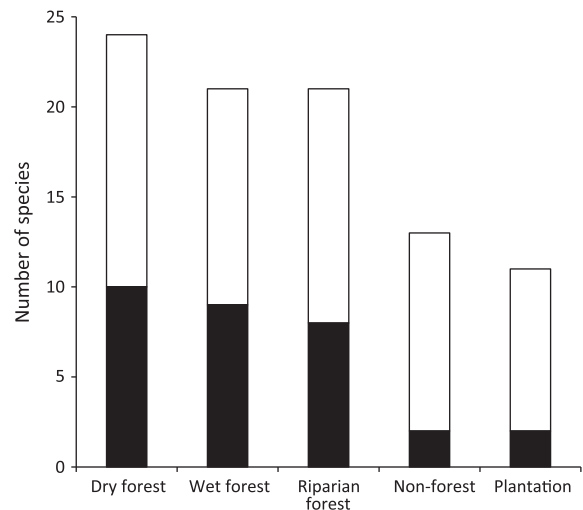
**Table 1**  
Occurrence of species in each habitat sampled. Species abbreviations correspond to those in Fig. 5b.

Species and abbreviations		Dry forest	Wet forest	Riparian forest	Non-forest	Plantation	Endemic	Guild
<b>Bufoidea</b>								
<i>Ingerophrynus divergens</i>	Id	+		+				Terrestrial
<b>Dicroglossidae</b>								
<i>Fejervarya cancrivora</i>	Fc					+		Terrestrial
<i>Fejervarya limnocharis</i>	Fl	+	+	+	+	+		Terrestrial
<i>Limnonectes finchi</i>	Lf	+	+	+		+	+	Terrestrial
<i>Limnonectes ingeri</i>	Li		+	+	+	+	+	Stream
<i>Limnonectes leporinus</i>	Ll		+	+			+	Stream
<i>Limnonectes malaysianus</i>	Ln			+				Terrestrial
<i>Occidozyga baluensis</i>	Ob	+	+				+	Terrestrial
<i>Occidozyga laevis</i>	Ol	+	+	+	+	+		Terrestrial
<b>Microhylidae</b>								
<i>Chaperina fusca</i>	Cf	+	+	+	+			Terrestrial
<i>Kalophrynus pleurostigma</i>	Kp	+						Terrestrial
<i>Kaloula baleata</i>	Kb	+	+	+	+			Arboreal
<i>Metaphrynella sundana</i>	Ms	+	+	+			+	Arboreal
<i>Microhyla borneensis</i>	Mb	+	+	+			+	Terrestrial
<i>Microhyla perpava</i>	Mp	+	+	+			+	Terrestrial
<b>Ranidae</b>								
<i>Hylarana erythraea</i>	He				+	+		Terrestrial
<i>Hylarana glandulosa</i>	Hg	+	+	+		+		Terrestrial
<i>Hylarana nicobariensis</i>	Hn		+	+	+	+		Terrestrial
<i>Hylarana raniceps</i>	Hr	+	+	+	+	+		Arboreal
<b>Rhacophoridae</b>								
<i>Nyctixalus pictus</i>	Np	+					+	Arboreal
<i>Philautus</i> sp. nov. 1	P1	+					+	Arboreal
<i>Philautus</i> sp. nov. 2	P2	+					+	Arboreal
<i>Polypedates colletti</i>	Pc	+		+				Arboreal
<i>Polypedates leucomystax</i>	Pl	+	+		+	+		Arboreal
<i>Polypedates macrotis</i>	Pm	+	+	+	+	+		Arboreal
<i>Polypedates otlophus</i>	Po	+			+			Arboreal
<i>Rhacophorus appendiculatus</i>	Ra	+	+	+		+		Arboreal
<i>Rhacophorus dulitensis</i>	Rd	+	+	+	+		+	Arboreal
<i>Rhacophorus harrissoni</i>	Rh	+		+			+	Arboreal
<i>Rhacophorus pardalis</i>	Rp	+	+	+	+			Arboreal
<i>Chiromantis</i> sp. nov.	Cs		+				+	Arboreal
<b>Total</b>		<b>24</b>	<b>21</b>	<b>21</b>	<b>13</b>	<b>12</b>	<b>13</b>	



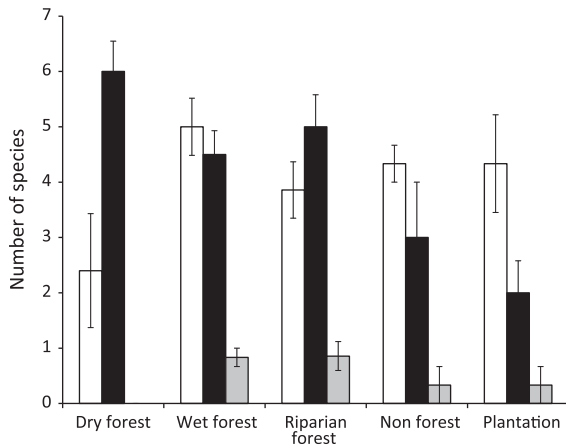
**Fig. 2.** Species accumulation curves generated from the transect census data showing actual and smoothed versions of the original data, and Jackknife and Chao non-parametric species richness estimates.

transects in plantation, non-forest and the forest habitats in the best-fitting NMDS ordination configuration (Fig. 5a). This differentiation in assemblage structure between the habitat types was also reflected in the results of the ANOSIM tests. There was a strong and highly significant difference between the assemblage composition amongst habitat types (ANOSIM  $R = 0.418$ ,  $p = 0.0002$ ). A similarly

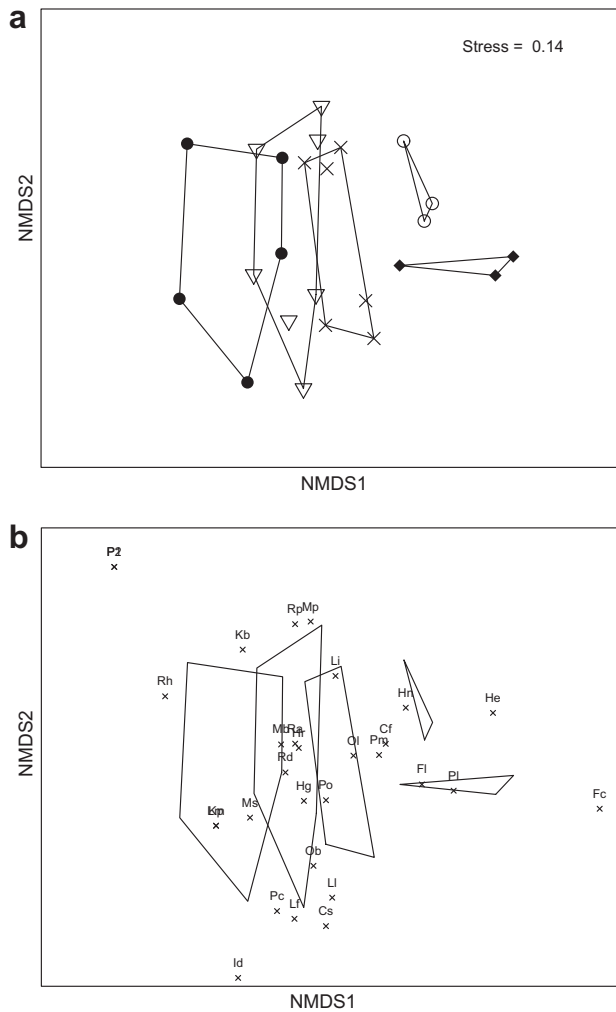


**Fig. 3.** Total number of species found in each habitat type. Solid bars – Bornean endemic species; open bars – non-endemic species.

significant difference was also found between all forest transects combined and plantation and non-forest transects combined (ANOSIM  $R = 0.592$ ,  $p < 0.0002$ ). The distribution of species in the ordination space illustrates the strong affinities of certain species with particular habitat types, such as *Hylarana erythraea*, *Hylarana nicobariensis*, *Fejervarya cancrivora*, *Fejervarya limnocharis*, *Polypedates leucomystax* with plantation and non-forest habitats



**Fig. 4.** Means and standard errors of number of species detected across sampling sites within each habitat type. Open bars – arboreal species; solid bars – terrestrial species; gray bars – stream-breeding species.



**Fig. 5.** NMDS of species composition amongst all sampling sites. (a) Habitat polygons. Solid circles – dry forest sites; open triangles – riparian forest; crosses – wet forest; open circles – oil palm plantation; solid diamonds – other non-forest sites. (b) Habitat polygons with species distributions in the ordination space. Species abbreviations are listed in Table 1.

(Fig. 5b). In contrast, species on the left side of the plot, such as *Philautus* spp., *Rhacophorus harrissoni*, *Limnonectes leporinus* and

all the Microhylidae, are all strongly associated with forest habitats, and rare or absent in non-forest or plantation habitats.

#### 4. Discussion

Most of our current knowledge of Bornean amphibians is derived from the Malaysian states of Sabah and Sarawak, and Brunei Darussalam (see Lloyd et al., 1968; Inger et al., 1986; Inger and Voris, 1993; Das, 1996, 2006; Inger and Stuebing, 2005; Grafe and Keller, 2009; Haas and Das, 2011), with very few published accounts from the larger Indonesian region of Kalimantan (see Iskandar et al., 2004; Bickford et al., 2008). However, most studies have been undertaken in upland or foothill forests, and there are few published accounts of amphibian species communities or assemblage composition in particular habitats other than riparian habitats (see Lloyd et al., 1968; Inger and Voris, 1993; Grafe and Keller, 2009; Keller et al., 2009). Our discovery of three likely undescribed anuran species in a relatively accessible area of lowland forest shows that current knowledge of amphibian biodiversity and patterns of species richness and assemblage composition in the region is by no means comprehensive.

Our study area does not contain any clear-flowing rocky/stony streams, typical of foothill and montane environments, which in Borneo, support a rich guild of obligate stream-breeding anurans (Inger et al., 1986; Grafe and Keller, 2009; Inger, 2009; Das, 2006), so detection of very few stream-breeding species in our study is not unexpected. Excluding stream-breeding species, we recorded most of the previously described frog species that have been recorded in lowland regions (below 400 m elevation) of Sabah. Another nine species previously recorded from lowland floodplain and swamp forests in Sabah could potentially occur in our study area (see Inger and Stuebing, 2005; Haas and Das, 2011). Several of these species have also been reported from secondary forest, such as *Ingerophrynus quadriporcatus* and *Rhacophorus reinwardtii* (Haas and Das, 2011). The combined total number of described frog species that could potentially occur in the Lower Kinabatangan region where the present study was undertaken is therefore at least 40. This estimate is similar to the uppermost species richness estimate inferred from our data (Fig. 2), which suggests that the actual species richness in the habitats that we sampled may be similar to the total number of described, lowland, non-stream breeding species, in eastern Sabah. However, this estimate is not necessarily a good measure of the potential species richness of the whole Lower Kinabatangan area, as it is possible that certain habitat types that have not been surveyed, may support species that are rare or absent in the habitat types that we actually surveyed. Nevertheless, in terms of species richness, our results are similar to most previous studies in lowland Borneo, when obligate stream-breeding species are excluded. Most of these previous studies were conducted in less-disturbed habitats compared to the Lower Kinabatangan (e.g. Lloyd et al., 1968; Inger et al., 1986; Tan, 1992; Inger and Voris, 1993; Das, 1996; Grafe and Keller, 2009). Therefore, it appears that to date, the Lower Kinabatangan Wildlife Sanctuary may have retained a large proportion of its original anuran species richness despite extensive alteration from past timber harvesting.

No historic amphibian data are available for the Lower Kinabatangan area prior to logging, so site-specific assessments of changes in species richness and assemblage composition due to logging or other disturbances are not possible. The potential for more undescribed species to be discovered in Sabah is high (see Das, 2006; Grafe and Keller, 2009 and this study); some species may already have been extirpated from secondary forests such as those in our study area prior to discovery. Other changes may have occurred at the community level, such as changes in abundance of

species, or contractions or expansions in habitats used, and changes in assemblage composition of specific habitats. Some species currently present may be undergoing long-term population declines as a result of environmental changes instigated by historic disturbances. Studies of impacts of logging on amphibians in Borneo, or elsewhere in Southeast Asia, are few. Iskandar (1999a,b) found that intensively logged forests contained only about 20% of the frog abundance found in unlogged forests of the same area of Sumatra, their abundance being correlated with the amount of leaf litter. In contrast, in northeast Kalimantan, Borneo, Iskandar (2004) found that relative abundance of amphibians and reptiles in unlogged plots was less than half that of selectively logged plots, but that species composition was similar. In Danum Valley, Sabah, Wong (2006a, cited in Meijaard et al., 2005) found that unlogged forest had more species than conventionally-logged forest but fewer species than selectively-logged forest. Selective logging appeared to attract disturbance-tolerant species, while also maintaining most species present in primary and 30-year-old regenerating logged forest. A range of post disturbance responses have been reported in tropical amphibian communities in other tropical regions, including: up to 40% loss of old-growth species in secondary forests (Gardner et al., 2007b; Kudavidanage et al., 2011) to virtually full recovery of communities (Hilje and Aide, 2011); reductions or losses of specific guilds, such as litter-dwelling species (Ernst and Rödel, 2005; Gardner et al., 2007b; Kudavidanage et al., 2011); and differential population responses of species with contrasting life histories (Ernst et al., 2007). The longer-term impacts of disturbance on amphibian communities and their recovery potential is likely to be influenced by inherent ecological characteristics of the community; nature and intensity of disturbance; frequency of, and time since disturbance; geographic extent, and availability and distribution of undisturbed refugia (de Maynadier and Hunter, 1995; Gardner et al., 2007a,b). Given the nature of the disturbance history of remaining Lower Kinabatangan forests and those elsewhere in Southeast Asia, changes to amphibian communities are expected. However, more robust comparative studies of primary and disturbed forest are required to properly ascertain the nature and severity of these changes.

In contrast to secondary forest habitats, oil palm plantations and other non-forest habitats supported fewer species, and differed markedly in assemblage composition. Amphibian assemblages of oil palm plantations and other non-forest habitats were dominated by terrestrial, non-endemic, generalist species, typical of human modified landscapes (Inger and Stuebing, 2005; Gillespie et al., 2005; Meijaard et al., 2005). Microhylids were absent from plantations and other non-forest habitats, and there were also less arboreal species, particularly rhacophorids. We found a single specimen of *Rhacophorus appendiculatus* on one plantation transect, and single specimens of *Rhacophorus dilutensis* and *Rhacophorus pardalis* on one non-forest transect. These three species were much more abundant within forest habitats and no evidence of breeding was found in non-forest habitats. Both of these transects were within 100 m and 300 m of forest edges respectively, and it is possible that the presence of these species at these sites resulted from local dispersal from nearby forested habitats. Exclusion of these individuals from the analysis further increases the apparent differences in species richness and assemblage composition between forest, non-forest habitats and palm oil plantations. Further investigation is required to ascertain the full extent to which these species may use plantations and other non-forest habitats.

The differences in species richness and assemblage composition between forested, non-forest and plantations are undoubtedly underpinned by marked differences in habitat structure and microclimatic characteristics amongst these environments. Oil palm plantations are structurally less complex than primary or second-

ary rainforest, lacking many microhabitats important to tropical amphibian species, such as leaf litter and a diversity of arboreal and terrestrial aquatic or moist breeding microhabitats, and are subject to greater microclimatic flux (Danielsen and Heegaard, 1995; Chung et al., 2000; Peh et al., 2006). Leaf litter and coarse woody debris are important for sheltering, foraging and reproduction of many tropical forest amphibians (Gardner et al., 2007b; Vitt and Caldwell, 2001). High amphibian species richness in tropical forests is underpinned by availability of a wide variety of reproductive niches provided by the diversity of aquatic microhabitats, stratified between the forest floor and lower canopy (Crump, 1974; Duellman, 1988; Vitt and Caldwell, 2001). Most of these microhabitats are absent in oil palm plantations due to the almost complete absence of forest plant species (Donald, 2004). The simple structure and open canopy of plantations results in greater temperature flux between day and night, increased evaporation rates and lower humidity (Fimbel et al., 2001), conditions which are likely to adversely affect many tropical forest amphibians (Vitt and Caldwell, 2001; Kudavidanage et al., 2011). The generally simple structure, lack of plant diversity and changed micro-climate of plantations also alters the availability of invertebrate prey (Chung et al., 2000), and reduces availability of shelter from predators. These conditions favor some species, which in turn may disadvantage others through changed competition and predator-prey relationships (Fitzherbert et al., 2008). Brühl and Eltz (2010) found that ground ant communities of oil palm plantations in Sabah were severely reduced in species richness compared with the forest interior and were dominated by invasive non-forest species, which may explain the complete absence of microhylid frogs, which are mostly ant and termite specialists (Wells, 2007), from non-forest habitats examined in our study. Oil palm plantations are also subject to a continuous cycle of disturbance as they are cleared and replanted every 25–30 years (Corley and Tinker, 2003). Furthermore, a variety of pesticides are used extensively in palm oil plantations (Friends of the Earth, 2004; Fernandez and Behari, 2006), which are likely to adversely impact various amphibian life stages (Relyea, 2005; Hayes et al., 2006; Wanger et al., 2010).

Our findings suggest that oil palm plantations, as with other non-forest habitats, do not contribute substantially to amphibian conservation. This is consistent with studies of other taxonomic groups that have found reduced diversity/and or major shifts in community composition in oil palm plantations, including: tree shrews, squirrels and bats (Danielsen and Heegaard, 1995), large mammals (Maddox et al., 2007), birds (Danielsen and Heegaard, 1995; Peh et al., 2006; Azhar et al., 2011), lizards (Glor et al., 2001), butterflies (Koh and Wilcove, 2008b), beetles (Chung et al., 2000; Davis and Philips, 2005), ants (Brühl and Eltz, 2010), and terrestrial isopods (Hassall et al., 2006). Furthermore the types of differences we observed are also consistent with the general patterns seen across other taxonomic groups; i.e. plantations generally support fewer species than forest, and species composition of plantations differs from forest habitat, with few forest species being found within plantations (Fitzherbert et al., 2008).

The conversion of secondary forests to agricultural production, including oil palm plantations (Fitzherbert et al., 2008; Koh and Wilcove, 2008a,b; Sodhi et al., 2010), has greatly reduced available habitat for many forest-dependent species, especially those that are endemic or restricted to lowland regions. In addition to not supporting resident populations of many species, large continuous plantations, such as oil palm, are likely to impose barriers to dispersal, recolonisation and gene flow, thus limiting the viability of amphibian populations in forest remnants. Sabah currently retains only about 50% of its original forest cover. Most of this remaining forest has been degraded or significantly altered through timber production, such that only about 20% of the original forest cover

is considered intact, much of which is in upland areas. Most lowland forests elsewhere in Malaysia and Indonesia have also been cleared or heavily degraded (Sodhi et al., 2010). We can therefore infer that most endemic lowland forest-dependent anuran species in the region have suffered population declines and range contractions commensurate with these percentages.

Conservation of lowland amphibian biodiversity in Borneo is therefore now highly dependent upon remnant secondary forests; this is most likely the case throughout much of Southeast Asia (Gillespie et al., 2005; Giam et al., 2011). Our findings suggest that other remnant, and semi-degraded, forest areas in Southeast Asia are also likely to be important reservoirs of amphibian diversity. Conservation of primary forest should remain a priority, but degraded forests and multiple use forests are increasingly being recognized as playing important roles in biodiversity conservation (Clough et al., 2011; Giam et al., 2011). The value of remnants is expected to be influenced by disturbance history and habitat type, along with size and degree of isolation from other remnants or larger areas of habitat. Often remnant forest areas are set aside because the topography is unsuitable for agriculture or because timber harvesting is not commercially viable. Limestone outcrop habitat in the Lower Kinabatangan is an example of this default conservation; however, despite the forest on some of these outcrops being relatively intact, we found comparatively few frog species there. These outcrops are well drained and comparatively dry, which may reduce their suitability for many anuran species. Consequently, the relative value of forest remnants for amphibian conservation seems highly dependent upon local habitat characteristics. Nevertheless, our findings highlight the value of setting aside and preserving adequate areas of forest, representing a range of habitats, within plantation landscapes in order to retain some of the original amphibian diversity.

Our findings provide some directions for future research. Firstly, similar studies in other parts of Southeast Asia will help determine the generality of our findings, given that our study was limited to a single catchment. Further studies will also increase our knowledge of the conservation status of various amphibian species, and the impacts of habitat alteration upon them. Secondly, whilst becoming increasingly difficult in lowland regions of Southeast Asia, due to the lack of available primary forest habitats, comparative studies with minimally disturbed primary rainforest are required in order to properly assess changes in anuran assemblages in secondary forests brought about by historic disturbances. Thirdly, obligate stream-breeding anuran species make up a significant proportion of Bornean amphibian diversity and may be more sensitive to forest disturbance, due to hydrological, physical and chemical changes to breeding habitats brought about by more distal disturbances upslope and in catchment headwaters (de Maynadier and Hunter, 1995; Gillespie, 2002; Meijaard et al., 2005; Durnham et al., 2007). Studies are required to evaluate how this guild responds to these habitat changes.

The value of forest remnants and their long term viability for amphibian conservation is likely to be influenced by size of remnants, levels of connectivity and habitat characteristics (Gardner et al., 2007a; Hillers et al., 2008). Because of their trophic niche, small size, potentially high population densities and low dispersal capabilities, the viability of anuran populations may be higher in small, isolated fragments than for many other vertebrates; however understanding of these relationships for tropical amphibians is poor (Gardner et al., 2007a,b). More detailed studies are required in Southeast Asia on the relationships between disturbance regimes, habitat structure, patch size and connectivity, and post disturbance recovery rates for tropical Asian amphibian assemblages in order to make informed conservation and management decisions at the landscape scale.

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## References

- Ancrenaz, M., Calaque, R., Lackman-Ancrenaz, I., 2004. Orangutan nesting behavior in disturbed forests of Sabah, Malaysia: implications for nest census. *Int. J. Primatol.* 25, 983–1000.
- Azhar, B., Lindenmayer, D.B., Wood, J., Fischer, J., Manning, A., McElhinny, C., Zakaria, M., 2011. The conservation value of oil palm plantation estates, small holdings and logged peat swamp forest for birds. *Forest Ecol. Manage.* 62, 2306–2315.
- Azmi, R., 1998. Natural Vegetation of the Kinabatangan Floodplain. Part 1: An Introduction to the Natural Vegetation Including a Preliminary Checklist of the Region. WWF Malaysia, Kota Kinabalu, Sabah.
- Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci. USA* 104, 18555–18560.
- Bickford, D., Iskandar, D., Barlian, A., 2008. A lungless frog discovered on Borneo. *Curr. Biol.* 18, R374–R375.
- Bossuyt, F., Dubois, A., 2001. A review of the frog genus *Philautus* Gistel, 1848 (Amphibia, Anura, Ranidae, Rhacophorinae). *Zeylanica* 6, 1–112.
- Brühl, C.A., Eltz, T., 2010. Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). *Biodivers. Conserv.* 19, 519–529.
- Chao, A., 1987. Estimating the population size for capture–recapture data with unequal catchability. *Biometrics* 43, 783–791.
- Chung, A.Y.C., Eggleton, P., Speight, M.R., Hammnd, P.M., Chey, V.K., 2000. The diversity of beetle assemblages in different habitat types in Sabah. *Malaysian Bull. Entomol. Res.* 90, 475–496.
- Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Clough, Y., Barkmann, J., Jührbandt, J., Kessler, M., Wanger, T.C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D.D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C.H., Seidel, D., Steffan-Dewenter, I., Stenclly, K., Vidal, S., Weist, M., Wielgoss, A.C., Tscharnke, T., 2011. Combining high biodiversity with high yields in tropical agroforests. *Proc. Natl. Acad. Sci. USA* 108, 8311–8316.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. (Series B)* 345, 101–118.
- Corley, R.H.V., Tinker, P.B., 2003. *The Oil Palm*, fourth ed. Blackwell Science Ltd., Oxford.
- Crump, M.L., 1974. Reproductive Strategies in a Tropical Anuran Community, vol. 61. University of Kansas Museum of Natural History Miscellaneous Publications, pp. 1–67.
- Danielsen, F., Heegaard, M., 1995. Impact of logging and plantation development on species diversity: a case study from Sumatra. In: Sandbukt, Ø. (Ed.), *Management of Tropical Forests: Towards an Integrated Perspective*. Centre for Development and the Environment, University of Oslo, pp. 73–92.
- Das, I., 1996. Spatio-temporal resource utilization by a Bornean rainforest herpetofauna: preliminary results. In: Edwards, D.S., Booth, W.E., Choy, S.C. (Eds.), *Tropical Rainforest Research*. Kluwer Academic Publishers, Dordrecht, pp. 315–323 (current issues).
- Das, I., 2006. Crocker Range National Park, Sabah, as a refuge for Borneo's montane herpetofauna. *Amphibian Reptile Conserv.* 4, 3–11.
- Davis, A.L.V., Philips, T.K., 2005. Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. *Environ. Entomol.* 34, 1081–1088.
- de Maynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environ. Rev.* 3, 230–261.
- Donald, P.F., 2004. Biodiversity impacts of some agricultural commodity production systems. *Conserv. Biol.* 18, 17–37.
- Duellman, W.E., 1988. Patterns of species diversity in anuran amphibians in the American tropics. *Ann. Missouri Bot. Garden* 75, 79–104.
- Dunn, R.R., 2004. Recovery of faunal communities during tropical forest regeneration. *Conserv. Biol.* 18, 302–309.
- Durnham, J.B., Rosenberger, A.E., Luce, C.H., Rieman, B.E., 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10, 335–346.

- Edwards, H.J., Elliott, I.A., Pressey, R.L., Mumby, P.J., 2010. Incorporating ontogenetic dispersal, ecological processes and conservation zoning into reserve design. *Biol. Conserv.* 143, 457–470.
- Ernst, R., Rödel, M.-O., 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86, 3111–3118.
- Ernst, R., Rödel, M.-O., 2008. Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. *J. Trop. Ecol.* 24, 111–120.
- Ernst, R., Konrad, T., Linsenmair, K.E., Rödel, M.-O., 2007. The impacts of selective logging on three sympatric species of *Leptodactylus* in a Central Guyana rainforest. *Amphibia-Reptilia* 28, 51–64.
- Fernandez, J., Behari, R., 2006. The Politics of Paraquat. Tenaganita and Pesticide Action Network Asia and the Pacific, Penang.
- Ficetola, G.F., Furlani, D., Colombo, G., De Bernardi, F., 2007. Assessing the value of secondary forest for amphibians: *Eleutherodactylus* frogs in a gradient of forest alteration. *Biodivers. Conserv.* 17, 2185–2195.
- Fimbel, R.A., Grajal, A., Robinson, J. (Eds.), 2001. *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*. Columbia University Press, New York.
- Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielson, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? *Trends Ecol. Evol.* 23, 538–545.
- Friends of the Earth, 2004. *Greasy Palms: The Social and Ecological Impacts of Large-Scale Oil Palm Plantation Development in Southeast Asia*. [www.foe.co.uk](http://www.foe.co.uk).
- Gardner, T.A., Barlow, J., Peres, C.A., 2007a. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biol. Conserv.* 138, 166–179.
- Gardner, T.A., Ribeiro Jr., M.A., Barlow, J., Ávila-Pires, T.A.S., Hoogmoed, M., Peres, C.A., 2007b. The value of primary, secondary and plantation forests for a neotropical herpetofauna. *Conserv. Biol.* 21, 775–787.
- Giam, X., Clements, G.R., Aziz, S.A., Chong, K.W., Miettinen, J., 2011. Rethinking the 'back to wilderness' concept for Sundaland's forests. *Biol. Conserv.* 144, 3149–3152.
- Gillespie, G.R., 2002. Impacts of sediment loads, tadpole density, and substratum on the growth and development of tadpoles of the Spotted Tree Frog *Litoria spenceri*: an in-stream experiment. *Biol. Conserv.* 106, 141–150.
- Gillespie, G.R., Howard, S., Lockie, D., Scroggie, M., Boeadi, 2005. Herpetofaunal richness and community structure of offshore islands of Sulawesi, Indonesia. *Biotropica* 37, 279–290.
- Gillespie, G.R., Scroggie, M.P., Roberts, D., Cogger, H., McDonald, K.R., Mahony, M.J., 2011. The influence of uncertainty on conservation assessments: Australian frogs as a case study. *Biol. Conserv.* 144, 1516–1525.
- Glor, R.E., Flecker, A.S., Benard, M.F., Power, A.G., 2001. Lizard diversity and agricultural disturbance in a Caribbean forest landscape. *Biodivers. Conserv.* 10, 711–723.
- Grafe, T.U., Keller, A., 2009. A Bornean amphibian hotspot: the lowland mixed dipterocarp rainforest at Ulu Temburong National Park, Brunei Darussalam. *Salamandra* 45, 25–38.
- Grismer, L.L., Thy, N., Chav, T., Holden, J., 2007. A new species of Chiromantis Peter 1854 (Anura: Rhacophoridae) from Phnom Samkos in the northwestern Cardomom Mountains, Cambodia. *Herpetologica* 63, 392–400.
- Haas, A., Das, I., 2011. *Frogs of Borneo*. <http://frogsofborneo.org/index.html> (accessed December 2011).
- Haile, N.S., Wong, N.P.Y., 1965. *The Geology and Mineral Resources of Den. Peninsula Sabah*. Printing Office, Kucing, Sarawak, Malaysia.
- Hamer, K.C., Hill, J.K., 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conserv. Biol.* 14, 1435–1440.
- Hassall, M., Jones, D.T., Taiti, S., Latipi, Z., Sutton, S.L., Mohammed, M., 2006. Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. *Eur. J. Soil Biol.* 42, 197–207.
- Hayes, T.B., Case, P., Chu, S., Chung, D., Haefele, C., Haston, K., Lee, M., Mai, V.P., Marjua, Y., Parker, J., Tsui, M., 2006. Pesticide mixtures, endocrine disruption, and amphibian declines: are we underestimating the impact? *Environ. Health Perspect.* 114, 40–50.
- Heinen, J.T., 1992. Comparison of the leaf litter herpetofauna in abandoned cacao plantations and primary rainforest in Costa Rica—some implications for faunal restoration. *Biotropica* 24, 431–439.
- Hilje, B., Aide, T.M., 2011. Recovery of amphibian species richness and composition in a chronosequence of secondary forests, northeastern Costa Rica. *Biol. Conserv.* 146, 170–176.
- Hill, J.K., Hamer, K., 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *J. Appl. Ecol.* 41, 744–754.
- Hillers, A., Veith, M., Rödel, M.-O., 2008. Effects of forest fragmentation and habitat degradation on west African leaf-litter frogs. *Conserv. Biol.* 22, 762–772.
- Inger, R., 2009. Contributions to the natural history of seven species of Bornean Frogs. *Fieldiana Zool.* 116, 1–25.
- Inger, R.F., Stuebing, R.B., 2005. *A Field Guide to the Frogs of Borneo*. Natural History Publications, Kota Kinabalu, Malaysia.
- Inger, R.F., Voris, H.K., 1993. A comparison of amphibian communities through time and from place to place in Bornean forests. *J. Trop. Ecol.* 9, 409–433.
- Inger, R.F., Voris, H.K., Frogner, K.J., 1986. Organisation of a community of tadpoles in rain forest streams in Borneo. *J. Trop. Ecol.* 2, 193–205.
- Iskandar, D.T., 1999a. Amphibian declines monitoring in the Leuser Management Unit, Aceh, North Sumatra, Indonesia. *Froglog* 34, 2.
- Iskandar, D.T., 1999b. *Training on Monitoring Methods in Amphibians and Reptile Fauna at Soraya and Gunung Air Station, Leuser National Park*. Institute of Technology, Bandung, Indonesia (unpublished report).
- Iskandar, D.T., 2004. *The amphibians and reptiles of Malinau region, Bulungan research forest, East Kalimantan: Annotated checklist with some notes on ecological preferences of the species and local utilization*. CIFOR. Available from: [http://www.cifor.org/mla/\\_ref/publication/amphibian.htm](http://www.cifor.org/mla/_ref/publication/amphibian.htm).
- Iskandar, S.D., Hallman, G., Henkel, H.-W., Kosuch, J., Rudhimanto, L., Veith, M., Sound, P., Wulffraat, S., 2004. Amphibians of the Kayan Mentarang National Park (East Kalimantan, Indonesia): estimating overall and local species richness. *Trop. Zool.* 17, 1–12.
- Keller, A., Rödel, M.-O., Linsenmair, K.E., Grafe, T.U., 2009. The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. *J. Anim. Ecol.* 78, 305–314.
- Koh, L.P., Gardner, T.A., 2010. Conservation in human modified landscapes. In: Sodhi, N.S., Ehrlich, P.E. (Eds.), *Conservation Biology*. Oxford University Press, pp. 236–261.
- Koh, L.P., Wilcove, D.S., 2008a. Oil palm: disinformation enables deforestation. *Trends Ecol. Evol.* 24, 68.
- Koh, L.P., Wilcove, D.S., 2008b. Is oil palm agriculture really destroying tropical biodiversity? *Conserv. Lett.* 1, 60–64.
- Kudavidanage, E.P., Wanger, T.C., de Alwis, C., Sanjeeva, S., Kotagama, S.W., 2011. Amphibian and butterfly diversity across a tropical land-use gradient in Sri Lanka; implications for conservation decision making. *Anim. Conserv.* <http://dx.doi.org/10.1111/j.1469-1795.2011.00507.x>.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleston, P., Hammond, P.M., Hodda, M., Holt, R.D., Laresen, T.B., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification on tropical forest. *Nature* 391, 72–76.
- Lloyd, M., Inger, R.F., King, F.W., 1968. On the diversity of reptile and amphibian taxa in a Bornean rain forest. *Am. Natural.* 102, 497–515.
- Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecol. Manage.* 190, 145–161.
- Maddox, T.M., Gemita, E., Wijamukti, S., Selampassy, A., 2007. *The Conservation of Tigers and Other Wildlife in Oil Palm Plantations*. Jambi Province, Sumatra, Indonesia. ZSL Conservation Report No 7. Zoological Society of London, London, United Kingdom.
- McMorrow, J., Talip, M.A., 2001. Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. *Global Environ. Change* 11, 217–230.
- Medellin, R.A., Equihua, M., 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural Weldon in Chiapas, Mexico. *J. Appl. Ecol.* 35, 13–23.
- Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S., O'Brien, T., 2005. *Life after Logging: Reconciling Wildlife Conservation and Production Forestry in Indonesian Borneo*. CIFOR, Bogor.
- Miettinen, J., Shi, C., Liew, S.C., 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biol.* 17, 2261–2270.
- Mora, C., Sale, P.F., 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Mar. Ecol. Prog. Ser.* 434, 251–266.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Simpson, G.L., Solymos, P., Stevens, M.H., Wagner, H., 2011. *Vegan: Community Ecology Package for R*. Version 1.16-6.
- Peh, K.S.H., Sodhi, N.S., de Jong, J., Sekercioglu, C.H., Yap, C.A.-M., Lim, S.L.-H., 2006. Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia. *Divers. Distrib.* 12, 572–581.
- Quintero, I., Roslin, T., 2005. Rapid recovery of dung beetle communities following habitat fragmentation in central Amazonia. *Ecology* 86, 3303–3311.
- Relyea, R.A., 2005. The lethal impact of Roundup on aquatic and terrestrial amphibians. *Ecol. Appl.* 15, 1118–1124.
- Rodríguez-Mendoza, C., Pineda, E., 2010. Frog diversity and riparian remnants. *Biol. Lett.* 6, 781–784.
- Sodhi, N.S., Brook, B.W., 2006. *Southeast Asian Biodiversity in Crisis*. Cambridge University Press, Cambridge, UK.
- Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H., Bradshaw, C.J.A., 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS One* 3 (2), e1636.
- Sodhi, N.S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tscharnkte, T., Posa, M.R.C., Lee, T.M., 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol. Conserv.* 143, 2375–2384.
- Sooryanarayana, S., 1995. Floods in Malaysia: patterns and implications. *Malays. J. Trop. Geogr.* 26, 35–46.
- SPSS Inc., 1999. *Statistical Package for the Social Sciences*. SPSS Inc., Chicago, USA.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783–1786.
- Tan, F.L., 1992. Ecological distribution of amphibians and reptiles in lowlands of Crocker Range National Park, Sabah. In: Ismail, G., Mohamed, M., and Omar, S. (Eds.), *Forest Biology and Conservation in Borneo*. Centre for Borneo Studies Publication No. 2, Yayasan Sabah, Kota Kinabalu, pp. 496–497.
- Vitt, L.J., Caldwell, J.P., 2001. The effects of logging on reptiles and amphibians of tropical forests. In: Fimbel, R.A., Grajal, A., Robinson, J. (Eds.), *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*. Columbia University Press, New York, pp. 239–259.



- Wanger, T.C., Iskander, D.T., Motzke, I., Brook, B.W., Sodhi, N.S., Clough, Y., Tschardtke, T., 2009a. Effects of land-use change on community composition of tropical amphibians and reptiles in Sulawesi, Indonesia. *Conserv. Biol.* 24, 795–802.
- Wanger, T.C., Saro, A., Iskandar, D.T., Brook, B.W., Sodhi, N.S., Clough, Y., Tschardtke, T., 2009b. Conservation value of cacao agroforestry for amphibians and reptiles in Southeast Asia: combining correlative models with follow-up field experiments. *J. Appl. Ecol.* 46, 823–832.
- Wanger, T.C., Rauf, A., Schwarze, S., 2010. Pesticides and tropical biodiversity. *Front. Ecol. Environ.* 4, 178–179.
- Wells, K.D., 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago.
- Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. *Biotropica* 38, 287–301.