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# Conserving Southeast Asian forest biodiversity in human-modified landscapes

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ABSTRACT

Southeast Asia experiences one of the highest rates of deforestation in the tropics due to agricultural expansion, logging, habitat fragmentation and urbanization, which are expected to result in species declines and extinctions. In particular, growing global demands for food, biofuel and other commodities are driving the rapid expansion of oil palm and paper-and-pulp industries at the expense of lowland dipterocarp forests, further jeopardizing Southeast Asian forest biotas. We synthesize recent findings on the effects of land-use changes on plants, invertebrates, vertebrates and ecosystem functioning/services in Southeast Asia. We find that species richness and abundance/density of forest-dependent taxa generally declined in disturbed compared to mature forests. Species with restricted ranges and those with habitat and foraging specialization were particularly vulnerable. Forest loss also disrupted vital ecosystem services (e.g. crop pollination). Long-term studies are needed to understand biotic sustainability in regenerating and degraded forests, particularly in the context of the synergistic or additive effects of multiple agents of biodiversity loss (e.g. invasive species and climate change). The preservation of large tracts of mature forests should remain the principal conservation strategy in the tropics. In addition, reforestation and reintroductions of native species, as well as improved connectivity among forest patches could enhance the conservation value of forest remnants in human-dominated landscapes.

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## 1. Introduction

Ongoing and massive deforestation has been a major threat to tropical biotas (Dirzo and Raven, 2003). Among tropical regions, Southeast Asia (Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Timor-Leste, Thailand, and Vietnam) has one of the highest rate of deforestation (Sodhi et al., 2004, in press a; Sodhi and Brook, 2006). Indeed, unabated and accelerating land-use changes in Southeast Asia could result in massive extinctions (Brook et al., 2003; Cardillo et al., 2006; Lee and Jetz, 2008). It is likely that most of the region's residual biodiversity will be confronted with living in human-modified areas (e.g. cities, agricultural areas; see Fig. 1 and Ziegler et al., 2009). In fact, human population density correlates with deforestation and species endangerment in Southeast Asia (Sodhi et al., in press a). Therefore, in addition to protecting relatively undisturbed forests, conservation biologists have to also develop strategies to make human-dominated areas more hospitable for forest biodiversity (Gardner et al., 2009; Koh and Gardner, 2010).

Here we review the effects of human disturbance (e.g. logging and agriculture) on Southeast Asian biodiversity to illuminate how well native species might survive in human-dominated landscapes with supporting evidence from a recent meta-analysis on this topic (Sodhi et al., 2009; see appendix in this reference for a list of relevant studies). We also highlight the effects of human disturbance on ecosystem functions and services. We end by identifying research and conservation needs. Along with other similar reviews from other regions (Anand et al., 2010; Bond and Parr, 2010; Irwin et al., 2010; Norris et al., 2010; Woinarski, 2010), our synthesis will assist in developing practical conservation strategies for mitigating forest and biodiversity losses in human-modified landscapes.

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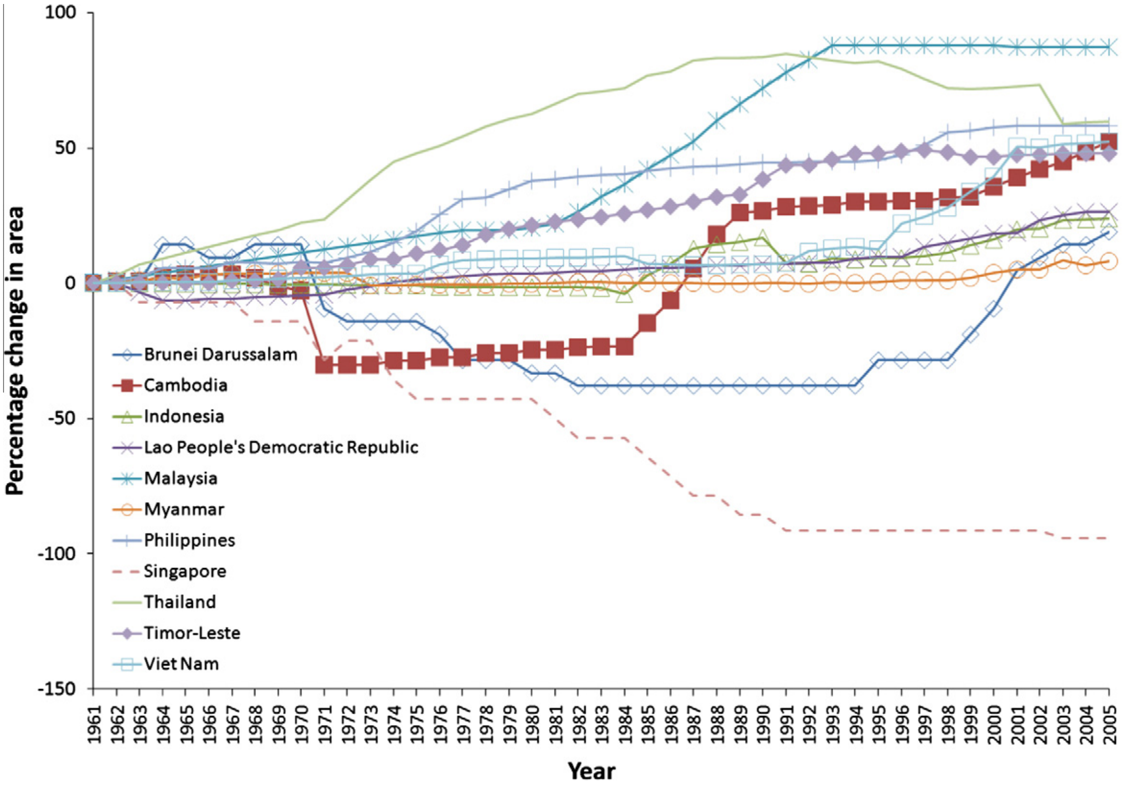

**Fig. 1.** Increase in agricultural area in Southeast Asia from 1961 to 2005 (http://faostat.fao.org/default.aspx). Agricultural area includes all arable and permanent cropland, as well as permanent meadows and pastures. Note that agricultural area has declined in Singapore possibly due to urban expansion.

## 2. Habitat disturbance and biodiversity

Below we highlight the effects of habitat disturbance on major biotic groups.

### *2.1. Plants*

Throughout Southeast Asia, forest areas have been reduced and fragmented considerably by conversion and land-use change. The first organisms to be impacted by deforestation and disturbance are plants. For example, over 95% deforestation in densely-populated Singapore has led to the loss of 26% of the country's original 2277 species of native vascular plants since 1819 (Brook et al., 2003; Sodhi et al., 2008a; Turner et al., 1994). The most extinction-prone of these species possessed the following traits: epiphytic, monoecious, hermaphroditic, forest dependence and reliance on mammal pollinators (Sodhi et al., 2008a). Because Singapore is a landbridge island with low levels of species endemism, these biodiversity losses represent local rather than global extinctions. Nevertheless, considering that some plants live for centuries, many of the currently extant species in Singapore could be the 'living dead' since they are committed to extinction due to unviable populations (Turner et al., 1994). This has been illustrated from an isolated 4 ha fragment of lowland rainforest in Singapore (Singapore Botanic Gardens) where half of the tree species (>5 cm dbh; diameter at breast height) were represented by only one or two individuals, which indicates that these populations are unsustainable (Turner et al., 1996).

Impacts of selective logging, the most common timber extraction system in the region, on tree diversity seem to vary, showing little effect on tree diversity or a negative impact. A study on the effects of selective logging (removal of approximately one third of all trees) on vegetation in Kalimantan (Indonesian Borneo) found that harvesting removed 62% of dipterocarp basal area (Cannon et al., 1994). However, a subsequent study from the same area showed that there was an increase in tree diversity 8 years after selective logging (Cannon et al., 1998). Although there were fewer species of bigger trees (>20 cm dbh) in logged plots than unlogged plots, their mere presence indicates that these species could be reproducing individuals that contribute to regeneration. Similarly, other studies comparing plots 18–20 years after logging also show that tree diversity was not significantly affected, although species composition had been altered and varied among the logged plots (Berry et al., 2008; Verburg and van Eijk-Bos, 2003). Conversely, in a study in Peninsular Malaysia (Pasoh Forest Reserve), the mean canopy height (24.8 versus 27.4 m), mean canopy surface area (12.0 versus 17.4 $m^2$), mean crown size (42.9 versus 94.5 $m^2$) and diversity of trees (Fisher's $\alpha$: 110.1 versus 122.1) were significantly lower in a forest 41 years after logging than a neighboring primary forest (Okuda et al., 2003); these results show that tree structure and diversity in a regenerating forest may match poorly with those in the primary forest, even after more than four decades.

It is likely that impacts of logging vary depending on extraction method used, spatial scale, size and amount of timber harvested and local conditions, with high intensity, short-rotation cycle logging suppressing species diversity. It must also be noted that the observed high tree diversity in logged forest does not equate to high conservation value, as disturbance can facilitate the growth of fast-growing early successional species, while old growth forests may have less diversity and yet contain higher abundances of range-restricted species (Shiel et al., 1999; Slik et al., 2004). Also, if forests come under strong recruitment pressure, logging can exacerbate species loss of late successional species, resulting in species shifts and forest decline. This has been shown in simulations using data from a forest reserve in Sabah (Malaysian Borneo) for dipterocarps (Köhler and Huth, 2004).

Agriculture represents an even more intense form of forest disturbance, since it often involves the almost complete removal of trees. In many cases, the loss is permanent, as the land is sown with crops such as rice, tea, and oil palm, on both commercial and smallholder scale (see Koh and Wilcove, 2008). Some traditional swidden agriculture practices result in mosaics of regenerating secondary fallow forests, the oldest of which can be similar to forest that existed prior to cultivation (Schmidt-Vogt, 1998). However, swidden practices across the region are very diverse, and not all result in regeneration of secondary forests. There are also signs that this land-use is evolving to more intensive and permanent cropping systems with changing socio-economic conditions, thus the future of swidden fallow forests is unclear (de Jong and Chokkalingam, 2001). In land abandoned after use for agriculture, the recovery of species in regenerating forest may be poor. In Singapore, Turner et al. (1997) found that the mean species richness in 100-year old secondary forests reached only 60% of that in the primary forest, even after a century of succession. It is possible that either environmental conditions (e.g. soil nutrient levels) were not conducive for the growth of late successional primary forest trees in the secondary forest, or that their seeds did not arrive there due to extirpation of seed dispersers (Castelletta et al., 2000).

### 2.2. Invertebrates

Invertebrates comprise a dominant component of tropical diversity in terms of richness, abundance and biomass (Dunn, 2005). Invertebrates also occupy a wide variety of niches and perform many important ecological functions (e.g. pollination) but receive relatively little attention (no doubt partly due to taxonomic difficulties of identifying most invertebrate taxa). Many invertebrates are likely to respond quickly in terms of population declines or losses to habitat changes due to their short generation times and rapid growth rates (Sodhi et al., in press b). In addition, invertebrates are sensitive to habitat changes resulting from forest disturbance, for instance in terms of changes in light regimes, microclimates, availability of dead wood and soil compaction, making them important indicators of the ecological impacts of habitat disturbance. Below, we consider the persistence of different invertebrate taxa in different forms of anthropogenically modified landscapes, focusing in particular on selective logging, forest fragmentation and agricultural landscapes (particularly oil palm plantations).

#### 2.2.1. Logging

The long-term persistence of species within logged forests is difficult to assess because most studies take place over ecologically brief time periods and relationships between species' responses and logging intensity or time elapsed since logging are rarely known and may be non-linear (Ghazoul and Hill, 2001). Nonetheless, some general patterns may be described for well-studied taxa, particularly Lepidoptera. For this group, selective logging can lead to significant increases in species richness and diversity over small spatial scales (i.e. within a patch), largely through the creation of microhabitats suitable for widespread opportunist species (Hamer et al., 1997; Spitzer et al., 1993, 1997; Vu, 2009). Over larger scales, however, logged forest typically supports fewer species and/or lower diversity than natural forest and becomes increasingly dominated numerically by opportunist species with increasing spatial scale (Hamer and Hill, 2000). This pattern appears to result from changes in vegetation structure and habitat heterogeneity following logging (Holloway et al., 1992), which creates a regenerating forest with few areas of dense shade and few open gaps (Hamer et al., 2003). Species least able to persist within logged forest appear to be those with restricted geographical distributions (Hill et al., 1995; Thomas, 1991) and narrow microhabitat requirements, including both gap and shade specialists (Hamer et al., 2003) and species restricted to the forest canopy (Dumbrell and Hill, 2005). Particular groups of Lepidoptera may also respond differently (Holloway et al., 1992), possibly as a result of differences in life-history traits. For instance among hawkmoths (Sphingidae), capital breeding Smerinthinae (that do not feed as adults and so use only larval resources for egg production and adult energy expenditure) were adversely affected by logging whereas income breeding Macroglossinae (that use both larval and adult resources for reproduction and maintenance) showed the opposite pattern (Beck et al., 2006).

Among other taxa, there are too few studies to date to allow generalizations to be made. Selective logging had little effect on the diversity or composition of dung beetle assemblages 6 years after logging (Holloway et al., 1992), although diversity was lower in logged compared with primary forest after an interval of 1–11 years since logging (Davis et al., 2001). Small-scale species richness for dung beetles in logged forest was generally higher than in individual transects from primary forest due to the presence of composite assemblages that were usually spatially separate in primary forest suggesting that as with Lepidoptera, increased species richness at a fine scale does not necessarily mean that species richness is greater at a larger scale. Stingless bees are affected by local food resources and availability of large trees (dbh > 50 cm) for nesting, but there was no evidence of lower density of nests within logged forest (Eltz et al., 2002; Samejima et al., 2004). Among leaf litter invertebrates, Burghouts et al. (1992) recorded a significant reduction in the absolute and proportional abundance of pseudoscorpions and mites following selective logging and an increase in the proportions of beetles, millipedes and cockroaches. Selective logging appears to have relatively little effect on termite assemblages, although soil-feeding species may be more affected by this level of disturbance than wood-feeders. Species composition also changes, but to a small extent when considered against the background level of compositional differences within the region (Eggleton et al., 1999; Jones et al., 2003).

#### 2.2.2. Forest fragmentation and degradation

Forest is increasingly being reduced to isolated remnants and so the ability of species to persist within remnants is an issue of concern. Despite this, there are relatively few data to assess the responses of different invertebrate taxa to forest fragmentation in Southeast Asia. On Borneo, species richness and diversity of butterflies declined significantly with declining fragment area and endemic species were not recorded within small remnants (<4000 ha) but these sites nonetheless made a significant contribution to regional biodiversity (Benedick et al., 2006). Species richness and diversity of ants in relatively large forest remnants (median size ca. 40 km$^2$) were significantly lower than in intact forest, reaching only ca. 50% of the species number collected in contiguous forest. Species density was also lower in the fragments and community composition was substantially altered, with an increase in the abundance of wide-ranging opportunistic species with decreasing fragment size (Brühl et al., 2003). Genetic diversity of two species of ant was also lowered in forest remnants although Benedick et al. (2007) found little effect of fragmentation on genetic diversity of the butterfly *Mycalesis orseis*. In heavily degraded landscapes of Singapore, fragmentation over the past 200 years has resulted in the loss of approximately 60% of the original butterfly fauna (Brook et al., 2003). In this landscape, the remaining forest reserves are important for preserving butterfly diversity, supporting approximately 75% of current butterfly richness, compared with urban parks and more isolated forest remnants (Koh and Sodhi, 2004).

In limestone karst forests, endemic land snails are increasingly being threatened by degradation from a variety of human activities such as mining, logging and agriculture and burning (Clements et al., 2006; Clements, 2008a). In Sabah, the abundance of prosobranch snails in disturbed karst plots was found to be significantly lower than pulmonate snails in the same plots (Schilthuizen et al., 2005). Given prosobranch snails generally include many karst-endemic species (e.g. Clements et al., 2008b), karst forest degradation could therefore eventually lead to their extinctions.

### 2.2.3. Agriculture

The main consideration for the future persistence of invertebrates within agricultural landscapes in Southeast Asia is their response to conversion of forest such as to oil palm. A recent meta-analysis (Danielsen et al., 2009) concluded that the persistence of invertebrates within oil palm plantations was much greater than that of vertebrates, with little adverse effect on a range of taxa and higher species richness of ants, bees and moths in oil palm than in forest. However, these data were not corrected for sampling effort and may have been biased by higher rates of species accumulation within oil palm. Moreover, some studies have recorded significant adverse impacts of conversion of forest to oil palm. For instance, Koh and Wilcove (2008) showed that 83% of butterfly species recorded from natural rain forest were absent from oil palm plantations. Furthermore, the proximity of natural forests to some oil palm estates had only a minor, albeit positive, effect on butterfly species richness (Koh, 2008). In addition, species diversity of isopods was 50% lower in oil palm than in forest despite a threefold increase in abundance within oil palm (Hassall et al., 2006) and species richness of arboreal ants within oil palm was <15% of that within forest (Pfeiffer et al., 2008). Faunal composition may also be adversely affected even if there is relatively little impact on species richness. For instance, conversion of forest to oil palm had a significant adverse impact on beetles, with more herbivores and fewer predators in oil palm compared to forest (Chung, 2000). Abundance and biomass of arthropods within arboreal ferns (*Asplenium* spp.) were also 70–80% lower within oil palm plantations, although beetles, cockroaches and woodlice were more common within oil palm than in forest (Turner and Foster, 2009).

In a land-use intensification gradient on the island of Sulawesi, ranging from rainforest, logged forest, to different agroforestry types, species richness of bees, wasps and their parasitoids peaked at intermediate levels of canopy cover, whereas canopy beetles and ants showed no significant correlation with canopy cover (Steffan-Dewenter et al., 2007; see also Clough et al., 2010). Functional consequences along this canopy cover gradient were a decrease in plant biomass and carbon storage, as well as a decrease in decomposition rates and soil arthropod abundance, while herbivory did not change and parasitism (of bees and wasps) peaked at intermediate levels (Kessler et al., 2009; see also Section 3). Overall, a reduction in shade tree cover from 80% to 40% in agroforestry caused only a minor quantitative loss in biodiversity and maintained high levels of ecosystem functioning, while doubling farmer's net income (Steffan-Dewenter et al., 2007).

## 2.3. Birds

The world's highest estimate of long-term loss of forest bird species due to deforestation is reported from highly deforested Singapore in Southeast Asia (>90% forest cover loss from 1923 to 2000, 67% bird species lost; Castelletta et al., 2000), and extinctions are even reported for small, still well-forested Indonesian islands (Trainor, 2007). Based on estimates of forest loss and the species area-relationship, Brook et al. (2003) projected that 16–32% of Southeast Asian forest bird species will become extinct by 2100. Currently, of 274 resident forest bird species confined to the lowlands of the Sundaic region (excluding Palawan), 83 and 26 are adversely affected by fragmentation and logging respectively (Lambert and Collar, 2002). Even though logged forests can support similar or even higher species richness of birds than undisturbed forests, this is likely due to improved suitability for common forest edge species (Johns, 1996). Endemic forest species of insular Southeast Asia have been shown to be adversely affected by deforestation (Maas et al., 2009; Posa and Sodhi, 2006). Certain groups of forest species such as understorey insectivores (e.g. flycatchers), terrestrial insectivores, large canopy frugivores and/or bark foragers (e.g. woodpeckers; Styring and Ickes, 2001) are disproportionately affected both by logging and forest fragmentation (Cleary et al., 2007; Danielsen and Heegaard, 1995; Lambert, 1992; Lambert and Collar, 2002). In logged forests, bird communities tend to recover after several decades (Wong, 1986; Yap et al., 2007), but again, sensitive species such as woodpeckers may take much longer (Styring and Ickes, 2001).

Agricultural habitats such as rubber and oil palm plantations or cacao and coffee agroforests may be richer in bird species than open habitats, but the species similarity with forests is often very low (Aratrakorn et al., 2006; Danielsen and Heegaard, 1995; Peh et al., 2005; Sodhi et al., 2005a; Waltert et al., 2004). Only 27% of recorded forest bird species were also found in coffee plantations in Sumatra (Philpott et al., 2008). Nevertheless, high densities of tall shade trees and proximity to natural forest tend to improve conservation value of agroforests (e.g. in cacao; Abrahamczyk et al., 2008; Clough et al., 2009). The maintenance of tall forest trees in otherwise modified landscapes (oil palm, cacao, rubber) and the protection of forest fragments could be essential for the subsistence of still widespread, disturbance-tolerant forest bird species where their primary habitat cannot be extensively protected (Abrahamczyk et al., 2008; Castelletta et al., 2005; Clough et al., 2009; Peh et al., 2006; Sodhi et al., 2005b). However, small fragments (<100 ha) continue to lose species decades after isolation and are colonized by generalist nest predators such as house crows (*Corvus splendens*) (Sodhi et al., 2005c, 2006a). Few studies have been conducted to determine the effects of forest disturbance on montane birds, but available data shows that their richness and density declines in human-dominated areas such as tree plantations and urban areas (Soh et al., 2006).

## 2.4. Amphibians and reptiles

Compared to other vertebrate taxa and studies from the Neotropics and Africa, few studies have addressed the impacts of human-dominated landscapes on the herpetofauna of Southeast

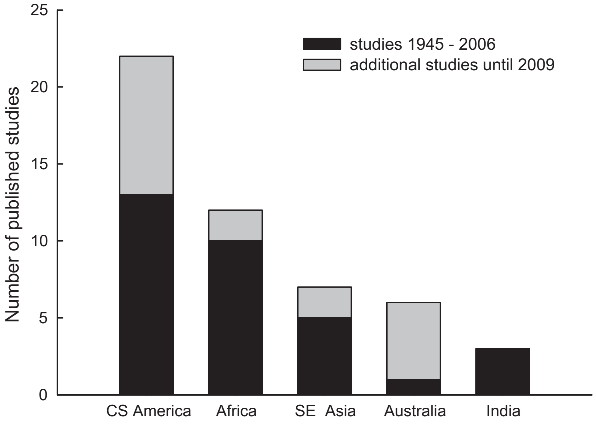

**Fig. 2.** Number of published studies on the impact of land-use change on amphibians and reptiles between 1945 and 2006/2009. We used the same search string in the ISI Web of Science as a comprehensive review on the topic in 2006 (Gardner et al., 2007) to make results comparable. We combined studies from Madagascar with Africa and those from the Philippines with Southeast Asia (*SE Asia*). *CS America* = Central and South America.

Asia (Fig. 2). These studies report declines in amphibian species richness as habitat disturbance (or fragmentation increases; Alcala et al., 2004), while reptile species richness remains similar or increases (Gillespie et al., 2005; Inger and Colwell, 1977; Wanger et al., 2009; but see Alcala et al., 2004; Bowman et al., 1990; Inger, 1980; Wanger et al., in press). Species composition was distinctly different in pristine habitats, but similar between disturbed habitats (Gillespie et al., 2005; Inger and Colwell, 1977). Habitats studied include secondary forests, rubber and cacao plantations, traditional gardens, rice-fields and open areas. However, rapidly expanding oil palm plantations have received no attention in herpetological studies. As in the Neotropics (e.g. Luja et al., 2008; Whitfield et al., 2007), species responses are mostly attributed to changes in leaf litter thickness and temperature through reduced canopy cover (Alcala et al., 2004; Inger, 1980; Wanger et al., 2009). Overall, resilience of forest herpetofauna to habitat disturbance seems to be lower in amphibians than reptiles and depends on sufficient pristine habitat remaining in the area (Gillespie et al., 2005; Wanger et al., 2009).

### 2.5. Mammals

Large-scale species extinctions in Southeast Asian mammals are projected due to habitat loss; around 21–48% of mammals are predicted to be extinct by 2100 (Brook et al., 2003). For example, on the Indonesian island of Sumatra, the Sumatran orang-utan (*Pongo abelii*) would probably be first great ape to go extinct (Wich et al., 2008) in the coming decades (Knop et al., 2004; Meijaard and Wich, 2007). Based on the latest 2009 IUCN Red List, more mammal species in Southeast Asia appear closer to extinction following a reclassification of their 2007 threat status to a higher threat category (http://www.iucnredlist.org/). These statistics are not surprising as a meta-analysis by Sodhi et al. (2009) revealed that mammals are generally more sensitive (in terms of richness, abundance and demographics) to forest disturbance than taxa such as vascular plants, invertebrates and birds. Here, we discuss three main threats contributing to the imperilment of Southeast Asia's mammal fauna.

#### 2.5.1. Logging and fragmentation

While clear-felling can extirpate entire mammal populations, selective logging appears to have varying effects on mammal populations (Meijaard and Sheil, 2008). In Sabah, Heydon and Bulloh (1997) found that densities of forest-dwelling frugivorous ungulates such as mousedeer were adversely affected by selectively logging, while primates generally retained their numbers in the long run even with 73% of trees removed from a concession as long as logging is prohibited before full forest regeneration (Johns, 1992). Sumatran (*Pongo abelii*) and Bornean orang-utan (*P. pygmaeus*) populations decline temporarily after reduced-impact logging (Johnson et al., 2005; Knop et al., 2004; Marshall et al., 2006; Morrogh-Bernard et al., 2003), but can rebound with sufficient fruit availability (Knop et al., 2004) and strict adherence to sustainable logging practices (Ancrenaz et al., 2005). For small carnivores such as civets, populations can still persist in low numbers in selectively-logged forests (SLFs), though they do better in unlogged forests (Colón, 2002; Veron et al., 2006). Similarly, a study within two SLFs in Sumatra showed that larger carnivores such as tigers preferred primary over degraded forests (Linkie et al., 2008). Conversely, another study within one SLF in Malaysia yielded a higher population density estimate of tigers (2.59 adults/100 $\text{km}^2$; Rayan and Shariff, 2009) than that of an unlogged primary forest (1.66 adults/100 $\text{km}^2$; Kawanishi and Sunquist, 2004). Elsewhere in Malaysia, surveys from newly logged forests adjacent to unlogged forests also yielded higher species richness, particularly for small mammals (Laidlaw, 2000).

Few empirical studies have quantified the negative impacts of forest fragmentation on mammals in the region. Laidlaw (2000) made a comparative study of the mammal species richness of seven protected areas (70–304 ha) and their adjoining logged forests in Peninsular Malaysia (states of Pahang and Selangor). The size of the natural forest area was the most important variable affecting mammal richness, with a sharp fall observed from 164 to 70 ha of natural forest (Laidlaw, 2000). Similarly Pattanavibool and Dearden (2002) compared the mammal richness of two contiguous wildlife sanctuaries in Thailand. With larger fragment sizes and greater connectivity, Om Koi had ten more mammal species than Mae Tuen, and only Om Koi retained large mammals like the Asiatic elephant (*Elephas maximus*); this suggests that fragmentation impacts negatively upon mammal richness in these study areas.

#### 2.5.2. Expansion of monoculture plantations

Massive conversion rates in Indonesia (linked to agricultural industries and opportunistic settlers arriving from Indonesia's transmigration program) have caused Sumatran elephant and tiger populations in Riau to plummet to around 216 (84% reduction) and 192 (70% reduction) individuals, respectively (Uryu et al., 2008). The use of fire to clear natural forests for plantations has also devastated mammals (e.g. Morrogh-Bernard et al., 2003; Nellemann et al., 2007; Nyhus and Tilson, 2004; Wich et al., 2008); post-fire surveys conducted in Bukit Barisan Selatan National Park (BBSNP) on Sumatra found that certain mammal populations were absent or declined in burnt areas, in part due to direct mortality, loss of food sources and displacement (Kinnaird and O'Brien, 1998). Encroachment from plantations in BBSNP are so severe that by 2010, core habitats are not expected to support any elephant herds and probably can only support single families of tiger and rhino (Kinnaird et al., 2003). Although agroforests were once touted as complementary conservation areas buffering core protected areas (Mackinnon et al., 1986; Nyhus and Tilson, 2004), the encroachment and unregulated expansion of plantations are now considered major threats to mammals (e.g. rhinos, tigers, elephants and orang-utans) as they are a primer for poaching and illegal logging activities (Wich et al., 2008). Encroaching plantations can also disrupt mammalian movement patterns around forest edges; surveys have shown that tigers, elephants and rhinos appear to avoid forest boundaries by up to 3 km (Kinnaird et al., 2003). Satellite images further substantiate the alarming expansion of agroforestry systems in Sumatra—around 28% of BBSNP has been converted mainly to *Coffea robusta* plantations (Kinnaird et al., 2003). This has caused a surge in elephant crop raids and tiger attacks, and consequently retaliatory killings of problem elephants and tigers (Nyhus and Tilson, 2004). In other countries such as Malaysia, Laidlaw (2000) showed that mammalian richness in a Virgin Jungle Reserve (VJR) adjacent to monoculture plantations was lower than in VJRs adjacent to logged and unlogged natural forests. Fitzherbert et al. (2008) similarly reported that species richness of bats and primates in rubber and oil palm plantations were relatively lower than primary forests.

#### 2.5.3. Infrastructure development

In the tropics, the construction of roads (especially highways) is known to fragment major forest complexes and consequently disrupt behavioral patterns and habitat use of most mammal species (Laurance et al., 2009; Ngoprasert et al., 2007; but see Austin et al., 2007). In addition, major roads increase the probability of direct mortality due to vehicular traffic and provide greater accessibility to poachers targeting threatened mammals (e.g., Mohd Azlan, 2006; Mohd Azlan and Lading, 2006; Pattanavibool and Dearden, 2002; Wich et al., 2008). In Sumatra, tiger occurrences have actually been shown to negatively correlate with distance to public roads (Linkie et al., 2006). The construction of hydroelectric dams has also resulted in flooding of natural forests (and logging of surrounding catchment areas; Sharma, 2008) despite these being important habitats for threatened mammals. The establishment of human settlements around forest reserves also contracts mammal home ranges; a regression model showed that leopard habitat use in a Thai National Park increased with distance from human settlements (Ngoprasert et al., 2007).

## 3. Habitat disturbance and ecosystem-services/functioning losses

In this section we briefly discuss the effects of disturbance on ecosystem processes (both services and functioning). Conservation strategies should aim to protect not only rainforests and biodiversity but also ecosystem services, which are defined as benefits people obtain from ecosystems (Millennium Ecosystem Assessment, 2005). Major challenges in managing ecosystem services in human-dominated tropical landscapes are that they are not independent of each other and attempts to optimize a single service (e.g. reforestation) lead to losses in other services (e.g. food production; Rodríguez et al., 2006). In rapidly transforming Southeast Asia, biodiversity conservation, maintaining resilient ecosystems and ensuring sustainable ecosystem goods and services require new concepts (e.g. Bengtsson et al., 2003; Tylianakis et al., 2008a) with interaction effects of major global-change drivers being little appreciated (Brook et al., 2008; Tylianakis et al., 2008b). The effective conservation of most ecosystem services requires a landscape perspective (Chazdon et al., 2009). Agricultural land-use is often focused on few species and local processes, but in dynamic, human-dominated landscapes, only a diversity of species can insure resilience (i.e. the capacity to re-organize after disturbance). Biodiversity and associated ecosystem services can be maintained only in complex landscapes with near-natural habitat supporting a minimum number of species dispersing across natural and managed systems (Tscharntke et al., 2005). For example, in Indonesian agroforestry systems, high levels of pollination and yield in coffee (Klein et al., 2003) and pumpkin (Hoehn et al., 2008) depend on a high diversity of bee species, which is only available in heterogeneous environments including nearby forests providing natural bee habitats (Liow et al., 2001). Including the environmental heterogeneity, which is typical for natural ecosystems, into models may lead to a better explanation of diversity-functioning relationships, as shown for bees and coffee pollination in Indonesia (Fig. 3).

Further studies in Indonesian landscapes analyze the relative role of managed versus natural habitat and the great contribution of beta diversity compared to alpha diversity (e.g. Kessler et al., 2009; Schulze et al., 2004; Tylianakis et al., 2008a). The landscape context may be even more important for local biodiversity and associated ecosystem services than differences in local management (e.g. between organic versus conventional farming; between crop fields with versus without near-natural field margins) because the organisms colonizing agroecosystems from the landscape-wide species pool may compensate for agricultural intensification at a local scale (Tscharntke et al., 2005). The concept of functional biodiversity links species diversity to ecosystem functioning through resource-use patterns (Tscharntke et al., 2008). Based on a global data-base, bird assemblages in tropical agroforest ecosystems were found to comprise disproportionately more frugivorous and nectarivorous, but fewer insectivorous bird species compared with forest (Tscharntke et al., 2008). According to Clough et al. (2009), greater species richness of shade trees in Indonesian agroforestry was associated with higher richness of frugivores and nectarivores, while distance to forest decreased richness of these functional groups. In a comparison of functional Hymenoptera diversity in Ecuadorian and Indonesian landscapes, insect predators of plant-feeding arthropods were more diverse in Ecuadorian agroforest and forest compared with rice and pasture, while in Indonesia bee diversity was higher in forested habitats (Tscharntke et al., 2008).

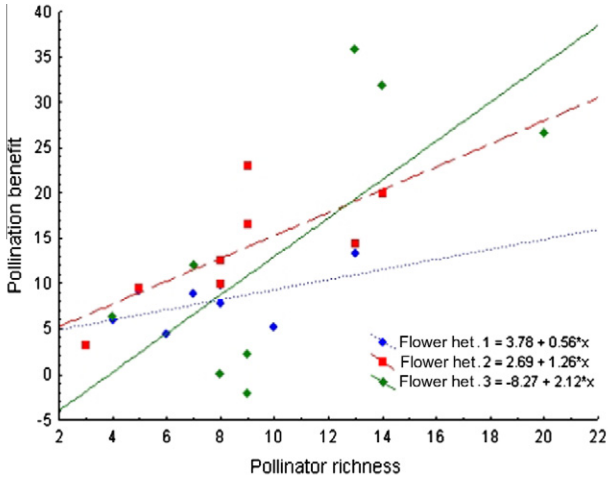

**Fig. 3.** Relationship between bee pollinator species richness, heterogeneity in coffee flower density and pollination benefit (difference between percent fruit set in open and bagged control treatments) in Indonesian agroforestry. The slope of the diversity-functioning relationship increases with increasing levels of resource heterogeneity. Flower heterogeneity was calculated as the CV (coefficient of variation) in flower abundance between the three experimental coffee shrubs. In Indonesia, agroforests with high bee diversity had higher rates of coffee pollination (Klein et al., 2003), and the slope of this relationship increased with increasing spatial heterogeneity in the density of coffee flowers within plots. The overall model explained 49.2% of the variance in enhanced fruit set (adapted from Tylianakis et al. (2008a)).

In conclusion, research in Indonesia (e.g. Steffan-Dewenter et al., 2007) shows that conservation of biodiversity and associated services needs to integrate socio-economic and ecological views at local and landscape scales to better identify ecological-economic trade-offs. However, more research is needed to understand how ecosystem processes are affected by forest disturbance.

## 4. Research needs

Chazdon et al. (2009) have identified research requirements for biodiversity in human-dominated tropical landscapes. Based on the above review, we identify the following research needs for conserving Southeast Asian forest biodiversity in human-dominated landscapes. Long-term studies are needed to understand biotic sustainability in regenerating and degraded forests. These studies should include data on habitat use, dispersal and population viability. Better understanding of the minimum amount of forests (i.e. thresholds) required to retain forest species richness in human-dominated areas is needed. Information is also needed about the mechanisms of species losses in isolated forests. Specifically, data are needed on the synergistic or additive effects of biodiversity loss drivers such as forest degradation, invasive species, drought, wildfires and climate change on forest biodiversity in human-dominated landscapes (Brook et al., 2008; Cleary, 2003; Slik et al., 2002). How ecosystem functioning and services (e.g. seed dispersal and flood protection) are compromised due to land-use changes need to be better illuminated. Similarly, better comprehension of socio-economic and political drivers of habitat loss is needed. More data are also needed to evaluate the success of various conservation measures (e.g. protected areas [e.g. Lee et al., 2007] and corridors). Further, research should be devoted towards refining existing mechanisms that can potentially generate economic incentives (e.g. compensation for avoided deforestation [through reduced emissions from deforestation and degradation or REDD]; payment for ecosystem services) for rural people to retain natural forests for biodiversity conservation. Overall, as Chazdon et al. (2009) point out, biological knowledge on tropical forest biodiversity needs to be urgently improved to better understand its fate in human-modified landscapes.

## 5. Conservation recommendations

One generalization drawn from our review is that the majority of Southeast Asian forest biodiversity is negatively affect by forest disturbance, thus preserving and protecting large tracts of mature forests should be the principal conservation strategy (see also Sodhi et al., in press a,b). However, forest remnants in human-modified landscapes can be augmented through reforestation, reintroductions, implementation of corridors and upgrading of their protected status to increase their conservation value. Clearly, better logging practices, with longer rotation cycles, incorporation of specific biodiversity guidelines for timber concessions and preservation of remnants in logged forests as source populations are needed (Dennis et al., 2008). In order to ameliorate the effects of agricultural expansion on biodiversity in surrounding protected areas, existing certification guidelines (e.g. by the Roundtable for Sustainable Palm Oil [RSPO] and International Coffee Organization [ICO]) need to be improved (e.g. RSPO indicators relevant to wildlife protection should be better identified) and enforced (Laurance et al., in press). Whilst engaging them to fund the protection of important wildlife habitats (e.g. through conservation payments) in return for environmentally friendly accreditation, non-governmental organizations should also assist plantations to implement guidelines for sustainability (Clements and Posa, 2007). Ultimately, there should also be no further conversion of secondary forests for agriculture (Koh and Wilcove, 2008); pre-existing cropland and degraded habitats should be utilized for plantation development (e.g. 900,000 ha of wastelands in Riau can potentially be utilized for agriculture; Uryu et al., 2008). The protection of tropical forests has ecological, social and economic dimensions (Tscharntke et al., 2007). Thus, better understanding the ecological and socio-economic determinants of land-use change in this region is the key for more sustainable human development and conservation objectives (Sodhi et al., 2006b, 2008b).

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