



## A Meta-Analysis of the Impact of Anthropogenic Forest Disturbance on Southeast Asia's Biotas

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### ABSTRACT

The impacts of tropical deforestation and forest degradation on SE Asia's biotas have been documented, but a quantitative synthesis is currently lacking. We examined the responses of biodiversity to anthropogenic forest disturbance by comparing key ecological attributes between undisturbed and neighboring disturbed forests. Based on data from four taxonomic groups (vascular plants, invertebrates, birds, and mammals), six broad measures of 'ecological health' (*e.g.*, richness, abundance, and demographics), and a range of different impact types from 120 articles published, we calculated the proportion of pairwise comparisons in which the measure of ecological health was lower in impacted than in pristine sites, as would be expected if forest disturbance was detrimental. The explanatory power of correlates of disturbance sensitivity was assessed using an information-theoretic evaluation of a candidate set of generalized linear models (GLMs). Overall, 73.6 percent (95% CI = 70.8–76.2%) of 1074 pairwise comparisons supported the expectation that forest disturbance was detrimental to ecological health, with mammals being the most sensitive group. The median effect size was for pristine areas to have 22.2 percent higher ecological health than equivalent disturbed areas. The most responsive measure of ecological health was species richness (median = 28.6% higher in pristine), and agricultural areas were the most ecologically degraded (median = 35.6% higher in pristine). However, the GLMs revealed no marked differences overall between taxonomic groups, habitat impact types, or ecological health measures. Our finding implies that the sensitivity of biodiversity to forest disturbance is moderately high, but essentially universal, suggesting urgent forest conservation actions.

*Key words:* biodiversity conservation; extinctions; fragmentation; habitat loss; management; tropics.

ACROSS THE TROPICS, DIRECT AND SYSTEMATIC HUMAN IMPACTS—predominantly habitat loss, fragmentation, and environmental degradation—are operating on a massive scale, and are accelerating (Achard *et al.* 2002, Wright 2005, Sodhi *et al.* 2007). Habitat loss is particularly severe in biologically diverse SE Asia (comprising Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Thailand, Timor-Leste, and Vietnam). Deforestation rates in this region are at least three times higher than in other tropical areas (Sodhi & Brook 2006); this region also supports the highest proportion of endemic bird and mammal species compared to other tropical regions (Meso-America, South America, and sub-Saharan Africa; N. S. Sodhi, M. R. C. Posa, T. M. Lee, D. Bickford, L. P. Koh, and B. W. Brook, pers. comm.), and the greatest number of biodiversity hotspots (Achard *et al.* 2002, Sodhi *et al.* 2004, Sodhi & Brook 2006). There have been numerous studies highlighting the negative effects of anthropogenic forest disturbance on SE Asian biotas (Hill *et al.* 1995, Laidlaw 2000, Liow *et al.* 2001, Lee *et al.* 2007, see Appendix S1).

A number of studies have indicated that tropical forest biotas are vulnerable to disturbance (*e.g.*, Peh *et al.* 2005; Barlow *et al.* 2007a,b), but equally certain is that degraded habitats or areas can continue to sustain a proportion of the primary forest biotas (*e.g.*, Mitra & Sheldon 1993, Warkentin *et al.* 1995, Hughes *et al.* 2002, Sodhi *et al.* 2005). However, broad-scale quantitative syntheses of the impacts of forest disturbance on tropical biodiversity have been few (*e.g.*, Dunn 2004). In particular, certain questions remain poorly resolved: (1) How much more valuable are primary forests for biodiversity in comparison with disturbed forests and does this differ depending on the biodiversity metric used (*e.g.*, species richness vs. demographic traits)? (2) Do different types of disturbance (*e.g.*, fire vs. logging) exert different impacts on forest biotas? (3) Are certain taxa more vulnerable to disturbance than others? Answers to such questions are critical to direct evidence-based conservation, for example, towards areas containing those elements of biodiversity that are most sensitive to disturbance.

An increasingly common means of summarizing and combining the results of multiple empirical studies in ecology is through the use of statistical 'meta-analysis'. Meta-analysis, *sensu lato*, is a quantitative scientific review in which the emphasis is placed

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on the statistical synthesis of data from multiple studies, using a range of available techniques of standardization and analysis to evaluate effect sizes for a phenomenon of interest (Mann 1990). It can be particularly useful for identifying the presence and strength of results from a group of studies when the effect size is small or variable, and can help to reconcile apparently contradictory observations within the group (Fernandez-duque & Valeggia 1994). Here we describe a meta-analysis of the literature on the impact of deforestation and habitat degradation on the biota of SE Asia. The wider goal of our analysis is to direct more focused conservation attention to the imperiled biodiversity of this region.

## METHODS

We first generated a list of peer-reviewed research articles published between 1975 and 2007, using this specific query (TS = [bird\* OR mammal\* OR reptile\* OR amphibia\* OR arthropod\* OR plants\* OR lepidoptera\* OR hymenoptera\* OR arachnid\* OR coleoptera\* OR diptera\* OR homoptera\* OR isoptera\*] AND [South-east Asia\* OR Brunei\* OR Cambodia\* OR Indonesia\* OR Lao\* OR Malaysia\* OR Myanmar\* OR Burma\* OR Philippines\* OR Singapore\* OR Thailand\* OR Timor\* OR Vietnam\*] AND [clear-cutting\* OR log\* OR deforestation\* OR fire\* OR agriculture conversion\* OR disturbance\* OR degradation\* OR secondary forest\* OR plantation\* OR fragment\*]), in the data bases of BIOSIS Previews and Web of Science. From this list, we collated a total of 120 individual publications (Appendix S1) from SE Asia, in which ecological attributes had been recorded in pristine and nearby deforested or disturbed sites. From a diverse range of 'ecological health' measures reported across the studies, we *a priori* classified them into six broad but meaningful groups: richness (*e.g.*, total species richness, rarefied number of unique species); abundance (*e.g.*, density per unit area, biomass, number of breeding pairs); structure (*e.g.*, forest height classes, relative frequency of different feeding guilds); diversity (*e.g.*, Shannon's diversity index, Fisher's alpha, evenness measures); demographics (*e.g.*, fecundity, recruitment, survival); and other (*e.g.*, home range size, measures of individual's health) (see Appendix S2 for the list of measures used). Our analysis was based on a total of 1074 pairwise comparisons, for which we assessed: (1) the proportion of cases in which a pristine site had a higher measure of ecological health than equivalent nearby disturbed sites; and (2) the percentage difference in the measure of ecological health between pristine and disturbed sites (where a positive effect size indicated greater health for pristine sites). These statistics were also categorized according to four major taxonomic groups (vascular plants, invertebrates, birds, and mammals) and four main impact types: logged (clear-cut); disturbed (includes secondary, fragmented, and selectively logged forests); fire; and agricultural (includes plantations, cultivations, forest gardens, and mixed-rural). Pristine forests were defined as primary forests with little or no anthropogenic influences. The 95% confidence intervals (CI) were estimated from 10,000 bootstrap resamples (with replacement) of the pairwise proportions.

When analyzing these data statistically, it was necessary to control for autocorrelation and spatial association, which were potentially introduced via measurements of multiple species at the same site, or by different measurements (*e.g.*, abundance, richness) of the same taxa at the same site, or possible observer biases. In each of the analyses described below, we controlled for these forms of pseudoreplication by randomly resampling the full data set, such that only a single measure of ecological health was used from each of the 120 studies. This procedure was repeated 10,000 times and the statistics were calculated using the full probability density functions generated. Some potential biases remain; there may be multiple studies from the same site included in a given resample, thus retaining some nonindependence. Also, more cursory short-term studies of a few taxa are weighted the same as intensive long-term studies of multiple taxa. The latter problem is less applicable to the meta-analysis methods that use both reported effect size and standard errors (see below for the subset analysis).

To test for publication bias (the 'file drawer problem', whereby unexpected or null results may be less likely to be published; Hedges & Olkin 1985), we iteratively added hypothetical data representing a positive effect of disturbance, until the lower 95% CI of pairwise comparisons overlapped with the null expectation of 50 percent. The funnel scatterplot method was also used to visually assess publication bias.

We also undertook an information-theoretic evaluation of a candidate set of generalized linear models (McCullagh & Nelder 1989). These models correlated ecological health to a set of hypothesized predictors. The GLM related the logit of the proportional difference between pristine and nearby disturbed sites (a dimensionless pairwise comparator of ecological health) to the following categorical predictor variables, modeled as fixed-effects: taxonomic group (*Taxon*; Table 1), type of measure of ecological health (*Metric*; Table 2), and impact type (*Type*; Table 3), in the seven possible variable combinations. We also evaluated the null (intercept) model, in which only a mean effect size is estimated (*i.e.*, no correlates exist). As with the pairwise analysis, we controlled for pseudoreplication by selecting a random subset of the full data set, such that only one observation from each *Study* was fitted using GLM, and repeating the fitting procedure a total of 10,000 times.

Model-selection and subsequent inference (using relative weights of evidence) was based on the Akaike information criterion (AIC; Burnham & Anderson 2002), whereby a measure of Kullback–Leibler information (a fundamental conceptual measure of the relative distance of a given model from full reality) is derived and used as an objective basis for ranking the parsimony of models in an *a priori* candidate set. An *a priori* model-building strategy tends to avoid data dredging, which leads to over-fitted models and the 'discovery' of spurious effects (a common fault with stepwise or best subsets model selection, Whittingham *et al.* 2006). The AIC highest ranked models are those which explain the most substantial proportion of variance in the data, yet exclude unnecessary parameters that cannot be justified for inference on the basis of the data (Burnham & Anderson 2001). For the randomized GLM model fits, we calculated the proportion of times each model was selected as the top ranked model ( $\pi_i$ ), based on Akaike's information

TABLE 1. *Impact of deforestation or forest degradation on ecological health, classified according to 'Taxon' (Taxonomic Group). # PC is the number of pairwise comparisons in which some measure of ecological health (see Table 2 for Metric) was compared between pristine and nearby sites impacted by human activity (e.g., logging, fires, conversion for agriculture, etc.). # Studies is the number of individual published studies used to derive the data (some studies presented multiple pairwise comparisons, so TOTAL is less than the sum of individual categories). Effect size is the median percentage difference between pristine and disturbed sites (such that a positive value indicates a higher level of ecological health in pristine sites); also shown (in brackets) are the lower and upper quartiles of the pairwise comparisons. '% LUD' ('lower under disturbance') is the proportion of pairwise comparisons in which the measure of ecological health was lower in impacted vs. pristine sites. % LUD was calculated as the mean of 10,000 bootstrap samples; the 95% CI is the 2.5 and 97.5 percentiles of the bootstrap distribution. In no case does the lower CI overlap with 50% LUD (null expectation of no impact of disturbance).*

Taxon	# PC	# Studies	Effect size (quartiles)	% LUD (95% CI)
Mammals	125	20	39.3 (10.0, 66.0)	81.6 (74.4, 88.0)
Birds	226	40	18.2 (2.1, 46.4)	79.6 (74.3, 85.0)
Plants	275	21	22.8 (-1.9, 41.7)	73.1 (67.6, 78.2)
Invertebrates	448	57	18.6 (-9.1, 47.3)	68.5 (64.3, 72.8)
TOTAL	1074	120	22.2 (-1.3, 48.2)	73.6 (70.8, 76.2)

criterion ( $AIC_c$ ). The percent deviance explained (% DE) was used to represent the structural goodness-of-fit of each model, with 95% CI being estimated as the 2.5 and 97.5 percentiles of the 10,000 sample fits.

Finally, a subset of the full data set (141 pairwise comparisons from 32 individual studies) provided sufficient information on the variance and sample size of the measured effect (abundance, diversity, etc.) to perform a nonparametric standardized difference between means estimation (described in Hedges & Olkin 1985). In this analysis, effect size is estimated as the difference between pairwise group means standardized using the pooled standard deviation of the two groups, and a sample size bias correction is then applied to this estimate. The average effect size ( $d_+$ ) is then calculated using a weighted average based on the variance of these unbiased effect sizes (Hedges & Olkin 1985). As with the other analyses,  $d_+$  was calculated repeatedly, using the randomized subset procedure based on 10,000 sample fits, to control for pseudoreplication.

All analyses were carried out using the R statistical package v2.6 (R Development Core Team 2007).

## RESULTS

Tables 1 through 3 illustrate the proportion of pairwise comparisons in which the measure of ecological health was lower in impacted versus pristine sites, as would be expected if deforestation or forest degradation was affecting the biota in a detrimental manner. Over-

TABLE 2. *Impact of deforestation or forest degradation on ecological health, classified according to 'Metric'. Metric includes the following categories: richness, abundance, structure, diversity, demographic, and other (see Appendix S2 for the actual measure used for each pairwise comparison). The definitions of the other columns are given in the legend to Table 1.*

Metric	# PC	# Studies	Effect size (quartiles)	% LUD (95% CI)
Richness	312	77	28.6 (5.4, 52.7)	79.5 (75.0, 84.0)
Abundance	388	73	22.0 (-10.0, 53.3)	69.8 (65.2, 74.2)
Structure	73	17	22.1 (3.2, 61.9)	75.3 (65.8, 84.9)
Diversity	185	41	9.5 (-2.2, 31.1)	70.8 (64.3, 77.3)
Demographic	95	11	23.0 (4.0, 45.7)	81.0 (72.6, 88.4)
Other	21	6	-34.9 (-135.8, 37.5)	38.0 (19.0, 57.1)
TOTAL	1074	120	22.2 (-1.3, 48.2)	73.6 (70.8, 76.2)

TABLE 3. *Impact of deforestation or forest degradation on the ecological health, classified according to 'Type'. Type includes the following categories: Logged (clear-cut), Disturbed (includes secondary, fragmented, and selectively logged forests), Fire and Agricultural (includes plantations, cultivations, forest gardens, and mixed-rural). Definitions of other columns are given in the legend to Table 1.*

Type	# PC	# Studies	Effect size (quartiles)	% LUD (95% CI)
Logged	340	49	16.5 (-1.8, 41.8)	74.0 (70.0, 78.2)
Disturbed	490	74	22.4 (-5.2, 47.2)	72.4 (68.4, 76.3)
Fire	71	9	25.9 (3.3, 52.2)	77.5 (67.6, 87.3)
Agricultural	173	35	35.6 (5.0, 57.3)	77.4 (71.1, 83.2)
TOTAL	1074	120	22.2 (-1.3, 48.2)	73.6 (70.8, 76.2)

all, 73.6 percent (95% CI = 70.8–76.2%) of pairwise comparisons supported this expectation, with mammals being the most sensitive group and birds the least (based on medians). The median effect size was for pristine areas to have 22.2 percent higher ecological health than equivalent disturbed areas. The most responsive measure of ecological health was species richness (median = 28.6% higher in pristine), and agricultural areas were the most ecologically degraded (median = 35.6% higher in pristine). The wide interquartile range for some measures showed that the response to disturbance across individual pairwise comparisons was quite variable, indicating site-specific sensitivity (Tables 1–3). The resample statistic (based on 10,000 randomized recalculations, in which each study was represented only once) was almost identical (mean = 74.2%; 95% CI = 68.8–79.6%). Thus, the effect of pseudoreplication by *Study* was negligible. This is also supported visually in Figure 1: the lower left area of the plot, where sample size is small and the effect is the opposite of expectation, is well populated with samples, indicating no inherent publication bias.

The GLM modeling (see below) showed that these small differences in group, measure and impact, were statistically unimportant.

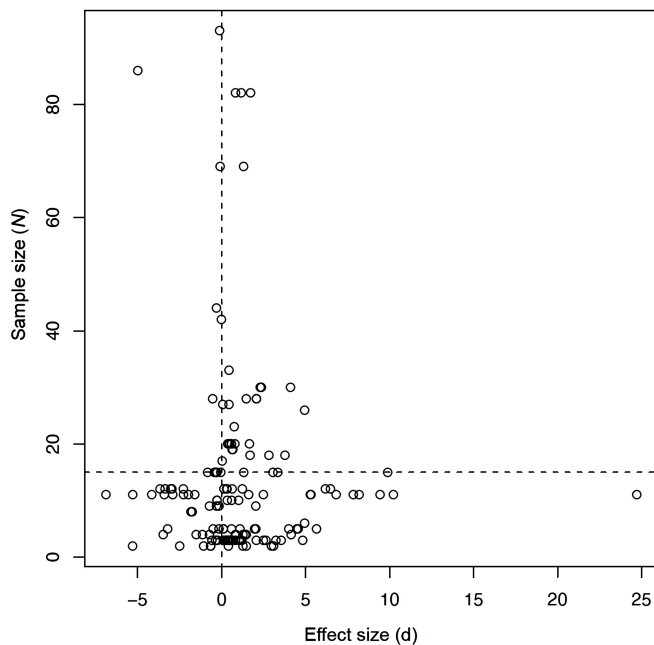


FIGURE 1. A 'funnel' scatterplot, showing standardized effect size ( $d$  = pairwise difference between pristine and disturbed comparisons divided by their pooled standard deviation) on the horizontal axis, plotted against sample size of the study ( $n$ ) on the vertical axis. The vertical dashed line shows an effect size of zero; the dashed horizontal line shows a sample size of 15. Only those 141 comparisons for which both sample size and variance estimates were available are plotted here. The lower left area of the plot is well populated, indicating no publication bias.

The test for publication bias showed that an additional 430 unpublished measures with an unexpected positive effect of disturbance are required for the lower 95% CI to overlap with null expectation of 50 percent. The most parsimonious model for predicting the impact of deforestation or forest degradation on ecological health was the null model (being  $AIC_c - \pi_i$  selected in 74.4% of resamples), with *Metric* (9.2%) and *Taxon* (8.1%) ranked second and third, respectively (Table 4). Moreover, the explanatory power of the two correlate terms (*i.e.*, structural model fit) was weak, with only 10.1 percent of the deviance being captured by the *Metric* model and 6.2 percent by *Taxon*. As such, the null model is effectively the most appropriate fit to these data, in which there was no marked differences overall between taxonomic groups (*e.g.*, birds vs. mammals), the nature of the disturbance to the pristine habitat (*e.g.*, logging vs. fire), or the type of measure of ecological health (*e.g.*, species richness vs. abundance).

We emphasize that the GLM selection of the 'null' result does not imply that deforestation has no impact on ecological health. As described above, there is an impact in about 74 percent of observations. It simply demonstrates that the correlates of the directionality or magnitude of this impact are not strongly related to an organism's taxonomic group (*Taxon*), the measures of disturbance chosen

TABLE 4. Correlates of disturbance. Generalized linear model (GLM) selection results, relating the pairwise ratio of ecological health (see Table 2 for definition), based on the logit of the proportional difference between pristine and nearby disturbed sites, to the following categorical predictors modeled as fixed-effects: taxonomic group ('*Taxon*'; as in Table 1), measure of ecological health ('*Metric*'; as in Table 2), and impact type ('*Type*'; as in Table 3), in the seven possible variable combinations. Also included is the null (intercept) model, in which only a mean effect size is estimated. A random subset of the full data set ( $N = 1074$ ) was selected, such that only one observation from each Study (published paper from which the pairwise comparisons were derived,  $N = 120$ ) was fitted using GLM. This random selection procedure was then repeated 10,000 times.  $AIC_c - \pi_i$  is the proportion of times each model was selected as the top-ranked model, based on Akaike's information criterion ( $AIC_c$ ). The percent deviance explained (% DE) gives the structural goodness-of-fit of each model, with 95% CIs being 2.5 and 97.5 percentiles of the 10,000 sample fits. The number of fitted parameters ( $k$ ) includes the regression intercept, fixed-effects coefficients and residual variance.

Model	$k$	$AIC_c - \pi_i$	% DE (95% CI)
Null (overall mean effect)	2	0.744	0 (0, 0)
<i>Metric</i>	7	0.092	10.1 (8.2, 14.5)
<i>Taxon</i>	5	0.081	6.2 (4.9, 9.2)
<i>Type</i>	5	0.042	6.6 (4.9, 10.1)
<i>Taxon</i> + <i>Type</i>	8	0.020	12.8 (9.9, 19.8)
<i>Taxon</i> + <i>Metric</i>	10	0.013	15.4 (13.3, 19.8)
<i>Metric</i> + <i>Type</i>	10	0.005	15.7 (13.7, 18.6)
<i>Taxon</i> + <i>Type</i> + <i>Metric</i>	13	0.001	21.5 (19.9, 22.3)

(*Metric*), or the type of disturbance (*Type*). Overall, the impact is essentially universal.

As an alternative response variable, we also fitted a binomial GLM, where the variable was coded a 1 if ecological health was higher in a pristine site, and 0 otherwise. In this case, the best ranked model was again the null ( $AIC_c - \pi_i = 73.1\%$ ), followed by *Taxon* (14.3%), *Metric* (9.2%), and *Type* (3.2%). The explanatory power of these terms (goodness of structural model fit) remained poor, with only 10.2 percent of the deviance being captured by the *Metric* model. As such, the overarching conclusion of a consistent negative impact of deforestation or forest degradation on biodiversity holds.

We were also able to examine, using a subset of the data (595 pairwise comparisons from 75 individual studies), the effect of time since disturbance on the impact of deforestation or forest degradation on ecological health (Appendix S1). The sign of the coefficient for the time since disturbance model was positive, as expected—that is, the longer since a site was disturbed, the greater the chance for recovery, and hence the lower residual impact of the disturbance. However, the effect was weak: for this reduced data set, the best-supported model was again the null ( $AIC_c - \pi_i = 0.812$ ). The *Type* + *Time* (since disturbance) model ranked second ( $AIC_c - \pi_i =$

0.078), but was 10.4 times less well supported than the null. The other models received no credible support from the data.

The results of our nonparametric standardized difference analysis on those 141 comparisons for which sample size and variance estimates were published, revealed a  $d_+ = 0.655$  (95% CI = 0.217–1.081), which, according to Cohen's (1977) guidelines on interpreting  $d_+$ , constitutes a medium-large effect size ( $d_+ = 0.2$  being small, 0.5 being medium and  $> 0.8$  being large). A statistical interpretation of the frequency distribution of corresponding z-scores for this more detailed (*i.e.*, sufficient information on the variance and sample size of the measured effect) data set is that ecological health would be lower in 74.7 percent (95% CI = 58.7–86.0%) of the disturbed vs. pristine areas. This is a remarkably similar result to the pairwise analyses based on all 1082 comparisons, and further strengthens the quantitative justification for an overall impact of deforestation on major taxa and multiple key ecological measures.

## DISCUSSION

Previous studies from the tropics show that pristine forests can be especially critical for biodiversity (*e.g.*, Hughes *et al.* 2002; Dunn 2004; Barlow *et al.* 2007a, b). Our broad-scale analyses, integrating the findings of 120 individual papers, indicate that deforestation and forest degradation has a widespread impact on SE Asia's biotas (a median of 22.2% difference in ecological health compared to pristine areas), regardless of taxonomic group, impact type or the measure of biodiversity. This may be because over the past few decades, many of the region's formerly pristine forests have experienced large-scale disturbance for the first time (Sodhi & Brook 2006). For example, in the Malay Archipelago, 85 percent of the logging that has occurred in primary forests took place from 1981 to 1990 (see Sodhi *et al.* 2007). Considering that natural disturbances, such as forest fires, have been rare in SE Asia (Sodhi & Brook 2006), the biotas of the region may be less adaptable to anthropogenic changes than for example in the boreal region. Indeed, recent detailed studies reveal that SE Asia's biotas are extremely sensitive to human-induced disturbances (Peh *et al.* 2005, Brook *et al.* 2006, Posa & Sodhi 2006, Soh *et al.* 2006). Our comprehensive meta-analysis reinforces the generality of these findings. It also shows that deforestation and disturbance may negatively affect the demographics of SE Asian biotas (Table 2; see also Cahill & Walker 2000), indicating that large-scale regional deforestation may depress reproductive success. This may be an additional mechanism, beyond direct loss of habitat, which could exacerbate the already massive regional extinctions predicted for the region this century on the basis of species-area projections (Brook *et al.* 2003). Our pooling of different categories of disturbance (*e.g.*, fragmentation grouped together with selective logging in our 'disturbed' impact type) may have masked some of the disturbance-specific impacts; however, the similarity in results among different categories suggests that such biases will be minimal. Agricultural areas seem to be the most detrimental to SE Asian biodiversity. Since mixed-rural habitats (*sensu* 'countryside') were included in this category, it is possible that SE Asian biodiversity is more sensitive to countryside

expansion than that in the Neotropics (*e.g.*, Hughes *et al.* 2002, Sekercioglu *et al.* 2007). However, more data are needed to study the effects of different types of forest disturbance on tropical biotas. Similarly, more data are needed to determine if different types of agriculture (*e.g.*, oil-palm vs. rubber plantations) impact SE Asian forest biodiversity differently.

We found that there were only 226 entries from 34 studies (Appendix S2) that either considered the exotic, introduced, invasives, or vagrant (*e.g.*, exclude or include them from their analyses) or that it was not an issue at all because the metric was for single or two species. Even though we used all species and hence likely included invasives for some studies, we believed that the effects reported by us may actually be more conservative, in part, because invasive species are rarely present in pristine forests (Teo *et al.* 2003).

Our study also shows that the negative effects of deforestation may be partially mitigated if forests are allowed to regenerate; the overall ecological health in disturbed areas was 5.6 percent higher (median) than logged forests. However, the poor overall explanatory power of disturbance type, coupled to the observation that recovery in regenerated to original forest communities depends largely if large primary tracts of 'source' populations exist (Yap *et al.* 2007), suggests that afforestation alone may not be an adequate conservation strategy. Further, regenerating forests in SE Asia are also rapidly disappearing (Sodhi *et al.* 2007), thus the prospects for full biotic recovery may appear low in most areas subject to intensive human development. Clearly, deforestation and extensive reclearance of secondary forests does not bode well for sensitive SE Asian forest species, and may have long-term consequences for ecosystem functioning (*e.g.*, pollination and seed dispersal; see Zakaria & Nordin 1998).

A potential source of bias inherent in some of the studies that we include in our meta-analysis is that the extent of undisturbed and disturbed habitats is different (see methods for handling of other potential biases). For example, if an old growth forest in a protected area has a larger geographical area than a secondary forest fragment with which it is being compared, based on the species-area relationship, one would expect the old growth forest to contain a greater number of species than the forest fragment. It would follow then, in such cases of area-asymmetric pairwise comparisons, the null expectation is in the direction of a negative impact of deforestation or forest degradation on biodiversity. Until recently, most studies did not statistically consider this bias, although most attempted to do so in their sampling design, for example, by having sites that are of similar sizes (Gotelli & Colwell 2001). By excluding uncorrected studies, we would greatly reduce our already small sample size and hence compromise the statistical power of our analysis. Nevertheless, selected studies, through the use of accumulation curves that control for unequal sampling area/effort, minimize this likely bias and should be used more widely (Peh *et al.* 2005, Posa & Sodhi 2006).

The spatial scale of the unit of sampling and analysis could also affect the directionality of effects being measured. For example, in their meta-analysis of the effects of logging on various taxonomic groups across the tropics, Hamer and Hill (2000) and Hill and Hamer (2004) showed that 11 of 12 studies in which

the unit of sampling and analysis was < 1 ha reported increases in species diversity following disturbance, whereas 10 of 15 larger scale studies (> 3.1 ha) reported higher diversity in undisturbed than disturbed forests. Biologically, this is explained by the different extent of heterogeneity in species distributions between disturbed and undisturbed habitats. Because species distributions are typically more heterogeneous in undisturbed than disturbed habitats, species diversity at smaller spatial scales (*e.g.*, point diversity; *sensu* Whittaker 1972) is likely to be lower in the former than the latter. However, because of the consistency of our results across different measures, we argue that these biases are minimal in our analysis.

In conclusion, our study supports the theory that deforestation in SE Asia alters the abundance and to a lesser extent the distribution of forest biotas. This may result in fragmentation and reduction of geographical range sizes potentially compromising the persistence of narrow range species. However, more ecological research is needed to determine the long-term viability of forest biotas in disturbed areas and to pin-point their individual susceptibilities and persistence. It is our hope that improved empirical evidence on the biodiversity impacts of forest exploitation will spur actions directed towards better and more widely adopted forest conservation practices in SE Asia, such that the dire prediction of catastrophic losses of biotas (Brook *et al.* 2003), will never become a reality.

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## SUPPORTING INFORMATION

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

APPENDIX S1. *The 120 individual studies from SE Asia in which ecological attributes were recorded in pristine and nearby deforested/disturbed sites, with 1074 pairwise comparisons reported across four taxonomic groups, six broad measures of 'ecological health', and four different impact types.*

APPENDIX S2. *A total of 120 individual studies from SE Asia with more information on the metric and location for 1074 pairwise comparisons.*

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