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# Quantifying the impacts of commercial logging and forest conversion to oil palm on biodiversity and conservation planning

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Abstract. Strong global demand for tropical timber and palm oil has driven large-scale logging and subsequent clearance of tropical forests. Given that the majority of tropical landscapes have been or will likely be logged, the protection of biodiversity within tropical forests thus depends  
40 on whether species can persist in these economically exploited lands, and if species cannot persist, whether we can protect enough primary forest from logging and clearance. Our knowledge of the impact of logging and clearance to oil palm on biodiversity is limited to a few taxa, often sampled in different locations with complex land-use histories, hampering attempts to plan cost-effective conservation strategies and to draw conclusions across taxa. Spanning a land-  
45 use gradient of primary forest, once- and twice-logged forests, and oil palm plantations, we compiled an extensive dataset in Sabah, Malaysian Borneo for nine vertebrate and invertebrate taxa to quantify (i) the biological impacts of logging and oil palm, (ii) cost-effective methods of protecting biodiversity, and (iii) whether there is congruence in response among taxa. Logged forests retained high species richness, including most of the species found in primary forest. In  
50 contrast, clearance to oil palm dramatically reduces species richness, including most primary-forest species. Using a systematic conservation planning analysis, we show that efficient protection of primary-forest species is achieved with land portfolios that include a large proportion of logged-forest plots. Protecting logged forests is thus a cost-effective method of protecting much of the biodiversity in the tropics, particularly when conservation budgets are  
55 limited. Six indicator groups (birds, leaf-litter ants, beetles, aerial hymenoptera, flies, and true bugs) proved to be consistently good predictors of the response of the other taxa to logging and oil palm. Our results confidently establish the high conservation value of logged forests and the low value of oil palm. We also show that several taxonomic groups are, in fact, good indicators

of general animal biodiversity. This suggests that the practice of focusing on only a few taxa in  
60 studies of logging and oil palm may not be as problematic as feared.

Key words: cost-effective conservation; DNA metabarcoding; indicator taxa; oil palm plantation  
agriculture; selective-logging; timber concessions; Southeast Asia; tropical rain forest.

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## INTRODUCTION

Tropical rainforests are the global hotspots of terrestrial biodiversity, yet they are increasingly  
impacted by selective logging and habitat conversion to agricultural plantations (Laporte et al.  
2007, Asner et al. 2009, Gibbs et al. 2010). Demand for wood products and agricultural  
commodities is accelerating (DeFries et al. 2010), and this is likely to result in tropical  
70 landscapes that increasingly consist of a mosaic of timber concessions, plantations, and shrinking  
areas of undisturbed, old-growth habitat. To achieve the greatest benefit from limited  
conservation funding, it is therefore vital to understand the relative biodiversity value of each of  
these three broad habitat types (Wilson et al. 2010, Fisher et al. 2011b).

The importance that biodiversity conservation strategies should place on old-growth (primary)  
75 forest, logged forest and plantations depends mainly upon two factors: (1) the relative impacts of  
logging and habitat conversion on biodiversity; and (2) the trade-off between the biodiversity  
benefit of protecting each habitat and the economic cost of doing so (i.e. the ‘opportunity cost’ of  
offsetting the profit that would be returned if each habitat were converted to a more financially  
productive land-use). However, most studies that examine impacts of land-use change on  
80 biodiversity and conservation value provide only an incomplete assessment of these issues in

several key respects.

First, because conducting comprehensive multi-taxon surveys is costly and time-consuming (Lawton et al. 1998, Gardner et al. 2008), studies on the impacts of logging and habitat conversion have typically focused on very few taxa. As a result of limited availability of taxonomic expertise (Gotelli 2004, May 2010, Cardoso et al. 2011), these studies are also heavily biased towards a small number of relatively well-studied and easily sampled groups (Gardner et al. 2009). For example, with an estimated 2.5-3.7 million species in the tropics, arthropods comprise the vast majority of rainforest fauna (Hamilton et al. 2010, Basset et al. 2012), yet knowledge of the impacts of land-use change is very limited for most arthropod taxa (Kozłowski 2008, Cardoso et al. 2011), with most assessments focusing on a few groups (e.g., ants, dung beetles, and butterflies and moths; Fitzherbert et al. 2008, Foster et al. 2011) and with some studies seeking to subvert this bias by assessing changes in arthropod abundance of rarely sampled taxa but not by identifying individuals to (morpho-)species level (e.g., Burghouts et al. 1992, Turner and Foster 2009, Edwards et al. 2012a). Moreover, most of the commonly censused taxa are mobile and/or have long generation times (e.g. birds, mammals). Assessments dominated by these taxa may give inflated estimates of the biodiversity value of particular habitats as a result of spillover from adjacent primary forest (Koh 2008, Lucey and Hill 2012), or because extinction debts in long-lived species are repaid over longer timescales than those typically studied (Gibson et al. 2011, Wearn et al. 2012, de Lima et al. 2013). Some less well-studied groups, again including several arthropod taxa, may also be particularly susceptible to land-use change because of very high habitat specificity (Dunn 2005).

Second, the taxonomic limitations of existing datasets impair efforts to determine whether or not there are patterns of congruence across multiple taxonomic groups in responses to logging

and habitat conversion. To avoid potential confounding issues such as methodological  
105 differences in the spatial and temporal scale of sampling and data analysis (Hamer and Hill 2000,  
Hill and Hamer 2004), patterns in responses should ideally be assessed by comparing an  
ecologically broad range of taxa at standardized sampling locations. Whilst such multi-taxa data  
have been collected for some land-uses (e.g. primary forest, secondary forest regrowth on  
abandoned agricultural lands, timber plantations and agriculture in South America, Southeast  
110 Asia, and Africa; Lawton et al. 1998, Schulze et al. 2004, Barlow et al. 2007), for selective  
logging, assessments have been restricted to one or two taxonomic groups (e.g., Thiollay 1992,  
Mason 1996, Marsden 1998, Whitman et al. 1998, Willott 1999, Willott et al. 2000, Ghazoul  
2002, Peters et al. 2006, Edwards et al. 2011b, Woodcock et al. 2011) and rarely for the impact  
of multiple rotations of logging (Edwards et al. 2011b, Woodcock et al. 2011). Yet selective  
115 logging is a pervasive threat across the tropics, with over 400 million hectares in the permanent  
timber estate (Blaser et al. 2011) and with 20% of tropical forests logged at some level of  
intensity between 2000 and 2005 (Asner et al. 2009). Biological impacts of selective logging also  
tend to be more subtle and complex than those of habitat conversion (Gibson et al. 2011).  
Accordingly, the absence of standardized, multi-taxon information on responses to selective  
120 logging is an important constraint on understanding the long-term trajectories of community  
recovery in logged forest (Adum et al. 2013), the effects of different harvesting regimes (Davis  
2000, Edwards et al. 2012c, Edwards et al. 2013, Ramage et al. 2013a) and the most appropriate  
protected area networks to maximize species coverage (Wilson et al. 2010).

Finally, most previous research on the effects of logging and forest conversion has generally  
125 focused on the magnitude of change in biodiversity metrics but has not considered whether or  
not the biodiversity benefits of a given land-use outweigh the opportunity cost of not converting

to a lower diversity but more profitable land-use (Moore et al. 2004, Polasky et al. 2008). An understanding of this trade-off can greatly enhance the practical value of conservation research: for instance, most species of bird and dung beetle encountered in a primary forest can be  
130 conserved by protecting twice-logged forest at a fraction of the cost of primary forest, because primary forests have a far higher timber value than do intensively logged forests (Fisher et al. 2011b; see also Ji et al. 2013 for similar results with Arthropoda). However, it is uncertain whether or not this finding holds across multiple invertebrate taxonomic groups. More importantly, both Fisher et al. (2011) and Ji et al. (2013) did not incorporate the opportunity  
135 costs of not converting either unlogged or logged forest to agricultural plantations in their analyses of this tradeoff. This transition frequently occurs, threatening both primary and logged forests (Gibbs et al. 2010, Gaveau et al. 2012), sometimes to different degrees, and has a major impact on opportunity costs because oil palm plantations return high profits (Edwards et al. 2011a, Fisher et al. 2011a).

140 Here, we address each of the above limitations of previous research on logging and habitat conversion. We avoid taxonomic biases by combining conventional biodiversity censuses with DNA metabarcoding (Ji et al. 2013). Metabarcoding allows us to identify diverse but rarely studied arthropods to the level of Operational Taxonomic Units (OTUs, approximately equivalent to species, Yu et al. 2012), and we complement this with morphologically identified  
145 datasets of scavenging mammals, birds, dung beetles, and leaf-litter ants to provide the most comprehensive assessment to date of the animal compositions of primary forest, logged forest and agricultural plantations. We first investigate changes in commonly used measures for understanding the impacts of anthropogenic disturbance on biodiversity (e.g., species richness and composition). We then use decisions derived from conservation planning software to

150 determine which management strategies conserve the greatest biodiversity across a range of  
conservation budgets, of key land-use transitions (Fisher et al. 2011b, Ji et al. 2013), and of  
alternative conservation priorities. Finally, we use the results from each assessment of  
conservation value (richness, composition, conservation planning) to identify taxa that could be  
used as effective predictors of the responses of other taxa to logging and forest conversion to  
155 agriculture, and any taxa that would have to be surveyed individually. Our principal questions  
are thus:

- 1) What are the impacts of logging and oil palm cultivation on biodiversity?
- 2) What conservation strategy is the most efficient way to protect animal biodiversity when it is  
possible to protect some combination of unlogged forest and logged forest?
- 160 3) Which taxa, if any, can be used as general indicators of logging and oil palm disturbance on  
biodiversity, and which taxa respond idiosyncratically to disturbance?

We examine these questions in Southeast Asia, which is one of the world's most threatened  
hotspots of biodiversity (Hoffmann et al. 2010), and consider four alternative land-uses:  
unlogged forest, forest subject to one round of intensive selective logging, forest subject to two  
165 rounds of intensive selective logging, and mature plantations of oil palm. The typical transition  
for unlogged forest is to undergo one or two logging cycles before conversion to oil palm, and so  
these three disturbed habitats represent the gradient of competing land-use types in the study  
region, with logging followed by conversion to oil palm being the most financially productive  
option.

## METHODS

The study was based around the 1 million hectare Yayasan Sabah (YS) logging concession in Sabah, Malaysian Borneo (N4 57.990, E117 48.320). These forests are dominated numerically by large tree species in the family Dipterocarpaceae (Fisher et al. 2011a), which are valuable for timber. Within the YS concession is the 238 000 ha Ulu Segama-Malua Forest Reserve (US-MFR), which was selectively logged between 1987 and 1991 with commercial stems > 0.6 m DBH harvested, yielding  $\approx 113 \text{ m}^3$  of timber per hectare (Fisher et al. 2011b). Between 2001 and 2007, 60% (141 000 ha) of the US-MFR was relogged, with the minimum harvested tree diameter reduced to >0.4 m DBH for commercial species, yielding an additional  $31 \text{ m}^3$  of timber per hectare (Fisher et al. 2011b). Selectively logged forest in the US-MFR is contiguous with 45,200 ha of unlogged (primary) forest in the Danum Valley Conservation Area (DVCA) and Palum Tambun Watershed Reserve. To the north of the US-MFR are oil palm plantations, where sampled sites had mature palms (20-30 years old) at a density of 100 trees per ha (Edwards et al. 2010). Our sampling locations within each habitat were at similar altitudes (mean m a.s.l.  $\pm$  SE: unlogged =  $238 \pm 16$ ; once-logged =  $195 \pm 11$ ; twice-logged =  $230 \pm 11$ ; oil palm =  $229 \pm 22$ ; pairwise comparisons using an ANOVA: all  $P > 0.03$ , with adjusted significance thresholds of  $P < 0.0085$  after Bonferroni Correction) and on similar soils (i.e., ultisols, with no peat, limestone or serpentine soils, Walsh et al. 2011).

### Sampling

Fieldwork was conducted from July to October 2007, May to August 2008, May to October 2009, and April to October 2011. Fourteen widely spaced sites (1–43 km apart) were established within the unlogged, once-logged and twice-logged forests, and in oil palm plantations (Fig. S1).

They comprised four sites >2 km apart within each forest type, and two sites 3.5 km apart in oil palm. Each site had two linear transects (n = 28 transects in total) spaced by 500-800 m  
195 (Edwards et al. 2011b), and study taxa were sampled on each of these transects.

Avifauna.—We used unlimited-radius point counts to sample the bird community in 2008 and 2009 (Lees and Peres 2006, Edwards et al. 2010, Edwards et al. 2011b). Three count stations were established at 250 m intervals (3 stations x 2 transects x 14 sites = 84 stations in total) centered along each transect, and each station was visited for 15 min on three consecutive days  
200 between 05:45 and 10:30 hours. A single experienced observer (D. P. Edwards) noted all birds seen and heard during each sampling period (excluding Apodidae and Hirundinidae, which are difficult to detect and identify within a closed canopy). Unknown vocalizations were recorded and subsequently were checked against known calls (from [www.xeno-canto.org/asia](http://www.xeno-canto.org/asia)). The use of terrestrial-based point counts can undersample certain canopy groups, including secretive  
205 residents and migrants (very few of the latter in Borneo at the sampled times of year; Anderson 2009).

Scavenging mammals.—We deployed two infrared camera traps (Hyperfire™ PC900 and HC600; Reconyx, WI) on each transect, spaced at 250-m intervals from the transect start for a period of 10 days (56 cameras in total). Each camera trap was baited with one chicken carcass  
210 and one rat carcass, which were both tethered to the ground. In addition to motion-triggered shots of scavengers, the camera-traps also took images every 15 min. After positioning the camera-traps and carcasses, we returned to the site on the 4<sup>th</sup> day to check the setup before retrieving the equipment on the 10<sup>th</sup> day. Species are classified as scavengers if they were documented consuming the carcasses on at least one occasion. Animal species that visited the  
215 carcasses but never fed are excluded from the analysis. We also include records of scavenging

water monitor *Varanus salvatori* (Reptilia).

Dung beetles.—We used standardized pitfall traps baited with human dung (Larsen and Forsyth 2005) to sample dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in 2009 and 2011. Five traps were spaced at 100-m intervals (140 traps in total, see Edwards et al. 2011b);  
220 traps were collected every 24 h for four days and were rebaited after two days.

Leaf-litter ants.—We used mini-Winkler extractors to sample ants (Hymenoptera: Formicidae) in 2007–2009 and 2011 (Woodcock et al. 2011). On each transect, seven census points were spaced at 25-m intervals from the transect start, and at each point 1 m<sup>2</sup> of leaf litter and loose topsoil were collected (one site in once-logged forest could not be sampled due to  
225 heavy rainfall, giving 26 transects and 182 points in total, see Woodcock et al. 2011, Ji et al. 2013). Material was sieved to remove larger debris and hung inside the extractors for four days, after which minor workers were removed for identification.

Flying invertebrates.—We used terrestrial Malaise traps to sample flies (Diptera), bees, wasps, and ants (Hymenoptera), beetles (Coleoptera), true bugs (Hemiptera), and Springtails  
230 (Collembola) in 2011 (Ji et al. 2013). On each transect, two traps were spaced 150 m apart and collected after 4 days. The two samples per transect were processed separately, but the samples were pooled within transect (from n = 56 traps to n = 28 samples) for analysis.

#### Taxonomy and DNA metabarcoding

All birds, except Apodidae and Hirundinidae (which are difficult to detect and identify within  
235 a closed canopy), were identified by DPE using sight and sound, scavenging mammals were identified by NTLL, and dung beetles and leaf-litter ants were identified with reference to

collections by THL and FAE, and by PW respectively. Due to the abundance of related workers from a single colony within a Winkler trap, an ant species was scored as being present or absent at each sample point, giving a total potential occurrence (herein abundance) of 7 per transect.

240 Invertebrates sampled with Malaise traps were identified using a metabarcoding pipeline from Yu et al. (2012). Metabarcoding is a rapid and comprehensive method of biodiversity assessment that combines two technologies: DNA taxonomy and high-throughput DNA sequencing. Mass samples of eukaryotes or environmental DNA are amplified and sequenced for one or more taxonomically informative genes, and this method has been shown to yield reliable and  
245 repeatable assessments of species incidences within communities (reviewed by Baird and Hajibabaei 2012, Taberlet et al. 2012, Yu et al. 2012, Ji et al. 2013).

For a detailed protocol see Yu et al. (2012) and Ji et al. (2013), but briefly, we prepared each sample by extracting DNA after homogenizing, and we PCR-amplified each sample for a 658-bp portion near the 5' end of the taxonomically informative mitochondrial gene Cytochrome  
250 Oxidase subunit I (COI), using degenerate primers. The 56 PCR amplicons were sequenced on a Roche GS FLX '454' pyrosequencer, using two 1/4 regions, producing 375,925 raw reads. The sequence dataset was then run through a quality-control (297,171 reads after quality control, at mean read length 445 bp), denoising, and clustering bioinformatic pipeline. Each cluster of sequences is called an Operational Taxonomic Unit (OTU) and represents a set of COI reads that  
255 are more similar to each other than to any other cluster. The goal is for within-cluster similarities to exceed a threshold (here, 97%) so that each cluster is likely to represent a single biological species. For each OTU, we extracted a 'representative sequence,' which in this case was the OTU's 'seed sequence,' as assigned by the clustering pipeline. We then used the program SAP (Munch et al. 2008) to assign a taxonomy to each OTU, keeping only taxonomic levels for which

260 the posterior probability of assignment was >80%.

All non-Arthropoda OTUs and OTUs containing only one read (which tend to be sequencing errors) were discarded. Almost all Arthropoda OTUs could be assigned to ordinal level: of 2 402 OTUs assigned to Arthropoda (1 843 OTUs spanning our five flying invertebrate groups), just 8% were identified simply as being ‘Arthropoda’ (n = 20) or ‘Insecta’ (n = 165). Sequence data are available at datadryad.org (doi: 10.5061/dryad. t3v71) and in GENBANK’s Short Read Archive (accession numbers are available in Ji et al.’s [2013] Supporting Information S6). Finally, separate ‘OTU tables,’ which are the standard site X species tables used in community ecology, were generated for Diptera, Coleoptera, Hemiptera, Hymenoptera, and Collembola for downstream analysis. Read numbers per OTU (cluster ‘size’) are a rough measure of each species’ biomass frequency but are so variable in reliability that Yu et al. (2012) have recommended that these tables be converted to presence-absence datasets, which is the practice that we follow here.

### Data analyses

What are the impacts of land-use change on biodiversity?

275 Species richness.—Patterns of species richness were compared among forest types using sample-based rarefaction curves with 95% CI, constructed in EstimateS v. 8.2.0 (Colwell 2006). Species richness is highly sensitive to sample size, so, in each habitat type, accumulation curves were standardized by the total number of individuals for birds and dung beetles and of incidences (summed from presence-absence data at sample points) for the remaining taxa (Gotelli and 280 Colwell 2001). Species richness is still highly likely to be underestimated in locations where we sampled fewer individuals (given large numbers of rare species) or sampled a smaller area

(particularly important in oil palm where we had fewer sample points) (Colwell et al. 2012). To estimate the probable species pool in each forest type and assess the completeness of our faunal surveys, we thus used two complementary methods. First, we calculated the mean of four  
285 commonly used species richness estimators (JACK1, JACK2, BOOTSTRAP, and Mmean) using EstimateS v. 8.2.0, from which we then calculated the proportion of species sampled, by dividing observed species richness by mean estimated species richness. Second, we extrapolated our sample-based rarefaction curves (this time using the Chao1 species richness estimator), to compare the predicted number of species having sampled the same number of individuals or  
290 presences in each habitat type (Colwell et al. 2012), deriving the target number by doubling the largest number of individuals or presences sampled for that taxon, and constructed in package iNEXT in R 2.15.0 (Hsieh et al. 2013).

We also compared species richness among forest types at the level of individual transects (which is the smallest spatial scale for 6 of our 9 datasets) by fitting a negative binomial error  
295 distribution and log link function, where “site” was included as a random factor, using the glmmadmb function in the glmmADMB package in R 2.15.0 (R Development Core Team 2012). To test whether land-use type successfully explained the spatial structure of species richness, we estimated spatial autocorrelation in our model residuals by means of Moran’s I in software SAM v3.1 (Rangel et al. 2006). We also repeated our analyses for birds and dung beetles having  
300 sampled additional and spatially independent oil palm sites (birds = 2, dung beetles = 1; Fig. S1) to reduce the potential confounding issue of pseudoreplication of study sites.

Species composition and species of conservation concern.—Patterns of species composition were examined at the transect level using species abundance matrices for birds, dung beetles, and leaf litter ants, and presence-absence matrices for scavenging mammals and invertebrate taxa

305 sampled using metabarcoding, in the R packages MASS, vegan and mvabund (Venables and  
Ripley 2002, Wang et al. 2012, Oksanen et al. 2013). Ordination of sites according to species  
similarity based upon total abundance or presence (Bray-Curtis index, Magurran 2004) was then  
achieved using nonmetric multidimensional scaling (MDS, Clarke and Warwick 2001). We  
tested for differences among forest types using a multivariate implementation of a generalized  
310 linear model (Warton et al. 2012), with a negative binomial error distribution and log link  
function in the summary.manyglm function in mvabund. To ensure that differences were not due  
to the use of abundance or presence matrices, we repeated community analyses for birds, leaf-  
litter ants and dung beetles using transect level presence-absence data. To test whether species  
composition results may have been influenced by pseudoreplication of study sites, we used a  
315 Mantel test to compare species composition to geographic distance between pairs of transects  
within a site and between pairs of transects across the entire dataset (Ghazoul 2002, Ramage et  
al. 2013b). Again, we also repeated our analyses for birds and dung beetles including the  
additional oil palm sites.

To obtain an additional measure of the conservation value of anthropogenic land-uses, we  
320 used the number of species from the unlogged forest species pool that were found in logged  
forests and oil palm. Evaluating such 'primary forest species' is particularly important in the  
absence of other objective measures of conservation value (e.g. IUCN Red-listings), for example,  
when individuals are identified to morphospecies or OTU levels (Barlow et al. 2010). We  
focused on primary forest species at two spatial scales: the number of primary forest species  
325 recorded in each of the anthropogenic habitats, expressed as a percentage of the total number of  
primary forest species; and the number of primary forest species at each transect. At the habitat  
level, oil palm is expected to perform poorly, since only half of the sampling effort was used

compared to logged forests. Oil palm could potentially have higher beta-diversity than logged forests and thus might have accrued proportionally more species with additional sample points (e.g., Lee-Cruz et al. 2013), although the high structural and compositional uniformity of plantations probably results in low beta-diversity over large spatial scales. At the transect-level, analysis yields directly comparable results across all habitat types and we tested for differences among forest types using a negative binomial error distribution and log link function, where “site” was included as a random factor, with the `glmmadmb` function in the `glmmADMB` package in R 2.15.0 (R Development Core Team 2012). Again, to test whether transect level models successfully accounted for spatial autocorrelation, we estimated Moran’s I using model residuals in software SAM v3.1 (Rangel et al. 2006), and for birds and dung beetles we repeated these analyses to include additional and independent oil palm sites.

What conservation strategy produces the most effective trade-off between biodiversity protection and cost?

To further investigate the conservation value of logged versus primary forests, we used the conservation decision-making software RSW2 (Arponen et al. 2005). We first obtained net profits per hectare of (further) timber extraction from each type of forest (unlogged=\$10,460, once-logged=\$4,000; twice-logged=\$2,010, data from Fisher et al. 2011b) and of oil palm cultivation (\$11,240 per hectare, data from Edwards et al. 2011a, Fisher et al. 2011a). Then, for each taxonomic group, we investigated the number of transects within each of our three forest categories that could be purchased to maximize biodiversity protection with an increasing pool of conservation funds (from \$15,000 to \$90,000 in \$15,000 increments, following Ji et al. 2013). Conservation budgets were limited at \$90,000 to allow RSW2 to select some, but not all, transects (the limiting factor in our analysis is thus the number of transects in our dataset from

which RSW2 can select, not money). We did so under three scenarios: (1) “logging only” – all forest types are threatened by logging (primary forest) or further logging (once-logged and twice-logged forest), but there is no imminent threat from oil palm. This scenario mirrors that applied in Fisher et al. (2011b) and Ji et al. (2013), but our analysis encompassed a suite of taxa that were not considered in those studies; (2) “logging + oil palm in all forests” – all forest types are threatened by (re-)logging and may also be converted to oil palm. By adding the net present value (NPV) of oil palm to timber values, this analysis reduced the proportional difference in opportunity costs between primary and twice-logged forest from 5.2-fold to just 1.6-fold, something that was not considered by previous analyses; and (3) “logging + oil palm in logged forest” – all forest types are threatened by (re-)logging, but only forest that has already been logged is liable to be replaced by oil palm. This is a frequent scenario in Southeast Asia, given that some primary forests are apparently off limits to oil palm conversion, either due to REDD+ obligations (e.g., Sloan et al. 2012) or Round-table for Sustainable Palm Oil (RSPO) accreditation (Edwards et al. 2012b). All three scenarios were run for primary and logged forest transects, and we also repeated the scenarios with the entire pool of transects, permitting conservationists to purchase oil palm (Koh and Wilcove 2007; something which is not normally considered a conservation option, Clements and Posa 2007) and allowing us to assess in a subtly different way the impacts of oil palm.

All analyses were conducted using two different metrics of biodiversity and conservation value: maximizing total species coverage and maximizing the coverage of primary forest species. To maximize total species coverage, all species were weighted equally. To maximize the coverage of species that were found in primary forest, we conservatively increased the ‘local rarity’ weighting of primary forest species by 10-fold (from 1 to 10) compared to species that

were recorded only in logged forest or oil palm (still scored as 1). This is an adaptation of  
375 Arponen et al. (2005), which used a weighting of 1 for common species and 4 for the rarest local  
species, making our analysis conservative.

Which taxa are the best indicators of the impacts of logging and oil palm?

Congruence among our nine datasets was evaluated at the transect level (following Barlow et  
al. 2007). Spearman's correlations assessed congruence for observed species richness, richness  
380 of primary forest species, and transect selections made by RSW2. In addition, the congruence  
among taxonomic groups for species composition was evaluated by means of non-parametric  
Mantel tests in package vegan among the summarized similarity matrices (based on Bray-Curtis  
distances using presence-absence data) for all pairwise combinations of transects within each site  
for each taxon. For RSW2, we used the outputs from the three different scenarios described  
385 above (logging only, logging+oil palm in all forest and logging+oil palm in logged forest), with  
each of our two metrics of biodiversity (maximizing species richness and richness of primary  
forest species). We conducted these six analyses for logging and oil palm combined and, because  
the resulting congruence could be driven primarily by the larger impacts of conversion to oil  
palm versus logging (see **Results**), we then repeated the analyses for logging only. We scored  
390 the number of significant correlations to determine how each of these methods performed. We  
treated those methods with at least one third (12 of 36) of correlations significant as performing  
well, and we used the correlation coefficients from those methods to form the basis of MDS  
ordinations of response similarity, from which we were able to identify possible indicator taxa  
(following Barlow et al. 2007).

395

## RESULTS

What are the impacts of land-use change on biodiversity?

Species richness.—At the habitat level, the conversion of primary or logged forest to oil palm resulted in a heavy loss of species richness for all taxa except scavenging mammals and  
400 springtails (Fig. 1). In contrast, all nine taxa had similar species richness in primary and logged forest. Both types of logged forest had marginally higher observed species richness than primary forest for birds, beetles, springtails, flies, and true bugs, but marginally lower observed species richness for dung beetles (Fig. 1). Extrapolations of sample-based rarefaction curves, which control for the numbers of individuals present (Fig. S2), and estimated total species richness  
405 (Fig. 2a) showed broadly similar patterns to observed species richness, and species richness estimators indicated that we sampled  $\geq 59\%$  (mean  $\pm 1SE = 74.2\% \pm 3.4$ ) of the species present for each taxonomic group, with similar proportions in the different habitats in each case (Fig. 2b).

At the transect level, species richness was significantly lower in oil palm than in primary or  
410 logged forest for most taxa, although scavenging mammals and springtails did not differ across habitat types (Table 1). In contrast, transect-level species richness did not differ significantly between logged and primary forests for most taxa; the only exception to this was true bugs, which had significantly higher species richness in twice-logged forest than in primary forests. There was no spatial autocorrelation of model residuals across transects (Moran's I test: all  $P >$   
415 0.5), except for birds, which showed significant positive spatial autocorrelation at the 0-5 km scale and negative spatial autocorrelation at the 20-25 km scale, but no spatial autocorrelation at the remaining eight scales. Re-analysis with an expanded dataset to include additional and independent sample sites in oil palm for birds and dung beetles revealed very similar results

(Text S1): further evidence that pseudoreplication of sample sites does not confound the negative  
420 impacts of oil palm on species richness.

Species composition and species of conservation concern.— Species composition differed significantly between primary forest and oil palm for seven taxa (except springtails and true bugs) (Fig. 3; statistical tests in Table 2). Species composition was also significantly different between twice-logged forest and oil palm for eight of nine taxa (except scavenging mammals),  
425 and between once-logged forest and oil palm for four of nine taxa (birds, dung beetles, ants and flies) (Fig. 3; statistical tests in Table 2). Conversion of either primary or logged forest to oil palm thus altered species composition for most taxonomic groups. Contrasting logged forest with primary forest, logging resulted in a significant shift in species composition for birds, scavengers, ants, and dung beetles (Fig. 3; Table 2).

430 Changes in species composition based on presence-absence matrices for birds, dung beetles and ants revealed a broadly similar pattern, with the exception of ants, which did not differ between logged and primary forest (statistics in Table S1). Mantel test results showed a significant effect of distance on species composition across habitat types for each taxon (nine tests, all  $P \leq 0.045$ ) but not within habitat types (36 tests, all  $P \geq 0.1$ , except two tests at  $P =$   
435 0.07), indicating that differences across space accounted for species dissimilarities over the entire study area and that distance effects expected from a non-independent sampling regime could be excluded (Ghazoul 2002). We thus found no evidence that pseudoreplication of sampling sites explained the variation in species composition among habitat types for any taxonomic group. Again, re-analysis with an expanded dataset to include additional and independent sample points  
440 in oil palm for birds and dung beetles revealed very similar results on species composition (Text S1).

Focusing on species recorded in primary forest ('primary forest species'), both once- and twice-logged forests retained a high percentage of all taxa at the habitat level (Fig. 4; mean  $\pm$  1SE: once-logged =  $72.0 \pm 3.4\%$ ; and twice-logged =  $69.4 \pm 4.2\%$ ). Oil palm consistently  
445 retained a much lower percentage of primary forest species ( $29.0 \pm 4.4\%$ ) than did logged forests (Fig. 4). This was due in part to lower sampling effort in oil palm (see **Methods**), but the magnitude of the difference (>50% fewer primary forest species in oil palm) points to a meaningful reduction. This was supported at the transect level, where the number of primary forest species was significantly higher in logged forests than in oil palm for 7 of 9 taxa (except  
450 scavenging mammals and springtails; Table 3). Again, there was no spatial autocorrelation of model residuals across transects (Moran's I test: all  $P > 0.5$ ) except for birds, which showed a negative spatial autocorrelation at the 20-25 km spatial scale, but no spatial autocorrelation at the remaining nine spatial scales. Finally, re-analysis with the expanded dataset to include additional and independent sample points in oil palm for birds and dung beetles revealed very similar  
455 results (Text S1), and in the case of birds, this additional analysis removed differences in the number of sample points making overall percentages of primary forest species directly comparable between oil palm (11%) versus logged forests ( $83.18 \pm 0.45\%$ ).

What conservation strategy produces the most effective trade-off between biodiversity protection and cost?

460 Selecting only among forested transects (i.e. excluding oil palm, because purchasing oil palm is not normally considered a conservation priority, Clements and Posa 2007) to maximize species richness, when only timber extraction threatens forest, logged forest transects were mainly selected with primary forest transects only selected at higher conservation budgets (Fig. 5a). Contrasting once- with twice-logged forests, twice-logged forests were selected most frequently

465 and especially so at low conservation budgets. Under the scenario of offsetting opportunity costs  
of timber plus oil palm in each forest type, RSW2 selected only logged forests for most taxa, and  
for the remaining taxa only selected primary forest at the highest conservation budgets (Fig. 5c).  
We found the opposite pattern when only logged forests are threatened by conversion to oil  
palm, with more primary forest transects selected at lower conservation budgets but with some  
470 logged forest transects still also selected (Fig. 5e). Under the two scenarios of timber plus oil  
palm threat (Fig. 5c, e), both once-logged and twice-logged forests were selected, with once-  
logged forest dominating for scavenger mammals, beetles and flies and twice-logged forest  
dominating for leaf-litter ants, aerial Hymenoptera, true bugs, and springtails.

Using the alternative conservation metric of maximizing the richness of primary forest  
475 species, across all three scenarios of land-use threat and the majority of taxa, primary forests  
were selected frequently and at lower conservation budgets (Fig. 5b, d, f) than for decisions  
based on maximizing species richness. This was especially so when only logged forests are  
threatened by oil palm conversion (Fig. 5f). Nevertheless, when only accounting for timber threat  
or for timber and oil palm threat across all forest types, logged forests were often selected.  
480 Contrasting once- with twice-logged forests, patterns were largely similar to those for decisions  
based on maximizing species richness, but with a trend towards the selection of more once-  
logged forests at lower conservation budgets. Again, these scenarios underscore that logged  
forests harbor sufficient primary-forest species to warrant frequent selection.

Focusing on selecting from the entire pool of transects, and thus also permitting  
485 conservationists to purchase oil palm (Koh and Wilcove 2007), results were very similar to those  
selecting only between primary and logged forests, with logged forests remaining an important to  
very important component of conservation strategies (Fig. S3). When maximizing species

richness, a small number of oil palm transects were included at higher budgets under each scenario (Fig. S3a, c, e), whereas when maximizing the richness of primary forest species oil palm was very infrequently selected in all three scenarios (Fig. S3b, d, f), underscoring the lack of conservation value of oil palm.

Which taxa are the best indicators of the impacts of logging?

To identify which of our nine taxonomic groups are most effective indicators of the biological impacts of (1) logging plus conversion to oil palm and (2) logging in isolation, we compared levels of congruency among taxa using species richness, species composition, richness of primary forest species and six outputs from the RSW2 conservation planning exercise as response metrics. For species richness and the three RSW2 selections based upon maximizing species richness, there were ten or fewer significant pairwise correlations among taxa, from a maximum total of 36 (Table 4). In contrast, species composition, richness of primary forest species, and RSW2 selections that maximize the richness of primary forest species showed a high number of significant correlations (Table 4). There were more frequent significant correlations in analyses including oil palm transects, probably reflecting the severe impacts of forest conversion to oil palm across taxa.

Focusing on congruence among taxa in their patterns of response to logging and oil palm (Fig. 6a, c, e, g), birds, leaf-litter ants, beetles, dung beetles, aerial Hymenoptera, flies, and true bugs were consistently good predictors of responses in other taxa. However, scavenging mammals always poorly predicted other taxa, and springtails poorly predicted the richness of primary forest species of other taxa (Fig. 6c). Focusing on congruence among taxa in their patterns of response to logging only (Fig. 6b, d, f), most taxa were again good predictors of responses in

510 other taxa. Regardless of metric, birds, leaf-litter ants, beetles, Hymenoptera, flies, and true bugs were strong predictors. Again, scavenging mammals gave little indication of species composition and richness of other primary forest species (Fig. 6b, d), while responses of dung beetles poorly predicted for the former (Fig. 6b) and responses of springtails the latter (Fig. 6d) of these metrics.

515

## DISCUSSION

Understanding the relative effects of different anthropogenic disturbances on biodiversity and integrating this information with the opportunity costs of foregoing more profitable land-uses is essential to identifying conservation strategies that make the best use of limited funding (Polasky  
520 et al. 2008, Wilson et al. 2010, Fisher et al. 2011b). By complementing conventional biodiversity censuses with DNA metabarcoding (Ji et al. 2013), we were able to address this question across >2,300 species, including several rarely censused arthropod orders, and thereby also avoid the taxonomic bias that has limited the generalizability of most previous research on the effects of tropical land-use change (Cardoso et al. 2011).

525 Across an ecologically diverse array of taxa, our results indicate that (1) while logging does have significant negative effects on biodiversity, the conversion of primary or logged forest to oil palm plantations has far greater negative impacts (see also Fitzherbert et al. 2008, Gibson et al. 2011), and (2) the most cost-effective conservation option depends on the metric of conservation used (species richness versus primary forest species) and on the precise make-up of threats, but  
530 in most cases, there is an important role for logged tropical forests (see also Wilson et al. 2010, Fisher et al. 2011b, Ji et al. 2013). We also found high levels of cross-taxon congruence in

responses to logging and agricultural conversion, suggesting that the effects of disturbance on most groups can be reliably approximated by censusing a small number of focal taxa. This mirrors research on cross-taxon congruence after different forms of land-use disturbance in the  
535 tropics (Lawton et al. 1998, Schulze et al. 2004, Barlow et al. 2007). Our results provide comprehensive evidence that across a range of conservation priorities and budgets, and spanning vertebrates and invertebrates, protecting logged forest represents a cost-effective option in Southeast Asia. Action is urgently required, however, because logged forests are highly vulnerable to conversion to agricultural plantations (e.g., Asner et al. 2006, Gaveau et al. 2012),  
540 which we have shown here support very few species of conservation value (see also Edwards et al. 2010, Gibson et al. 2011).

Impacts of logging and forest conversion to oil palm on biodiversity.—Selective logging is a pan-tropical disturbance that can cause severe residual damage to forest structure as falling  
lumber crushes remaining trees and logging roads and skid trails bisect the forest (Pinard and  
545 Putz 1996, Pinard et al. 2000), especially after multiple logging rotations. Our results highlight a range of implications of logging for conservation. On the negative side, while total species richness was relatively insensitive to logging, most taxa underwent a shift in species composition. High species richness in both once- and twice-logged forest was likely maintained by an influx of generalist species of low conservation importance and a concomitant reduction in  
550 primary forest specialists (Hamer et al. 2003). While improved forest management practices may help to alleviate these changes (Lindenmayer et al. 2012, Putz et al. 2012, but see Edwards et al. 2012c), protecting areas of unlogged forest is therefore vital for the persistence of forest specialists (Gibson et al. 2011, Edwards et al. 2013), underscoring the importance of defining

conservation objectives to protect primary forest species rather than to maximize overall species  
555 richness.

More positively, over 70% of bird, scavenging mammal, dung beetle, leaf-litter ant, fly, and  
springtail species found in primary forest were also present in once- and twice-logged forests  
(with >55% of aerial Hymenoptera, true bugs and beetles being detected), albeit sometimes at  
lower densities. Further, because shared species can go undetected in one or other habitat, the  
560 percentage of primary forest species we documented in logged forest is likely an underestimate.  
Across a diverse array of taxa, therefore, even heavily logged forests in Southeast Asia support  
valuable biodiversity, as found by Edwards et al. (2011b) and Woodcock et al. (2011) for a more  
restricted range of taxa. Because the volume of timber removed in Southeast Asia is the most  
intensive globally, often several fold that of other regions (Putz et al. 2001, Fisher et al. 2013) it  
565 seems likely that logged forests elsewhere are also likely to retain high levels of biodiversity, as  
has already been shown for a few taxonomic groups (e.g., birds: Thiollay 1992, Mason 1996,  
Aleixo 1999, Wunderle et al. 2006, Felton et al. 2008; bats: Peters et al. 2006, Castro-Arellano et  
al. 2007; amphibians: Adum et al. 2013). Given that selective logging occurs across millions of  
square kilometers of tropical forest (Asner et al. 2009), these results suggest that timber  
570 concessions can play an important role in global conservation strategies for a wide range of taxa.

Our results also reveal the impact of early re-entry logging, which is increasing across the  
tropics (e.g., Edwards et al. 2011b). For the majority of taxa, impacts of the second rotation of  
logging were minimal, such that communities in once- and twice-logged forests were  
indistinguishable. Dung beetles and true bugs had higher transect-level species richness in twice-  
575 logged forest, while dung beetles had different species composition in twice-logged forest (birds,  
springtails and bees, wasps, and ants also differed marginally significantly). While there are

negative impacts of the second logging rotation in terms of long-term sustainability, biologically speaking, the impacts are comparatively minimal across multiple taxa.

Oil palm plantations continue to expand rapidly in Southeast Asia and increasingly across the  
580 tropics (Fitzherbert et al. 2008). Conversion of primary and logged forest to oil palm creates a  
homogeneous canopy structure, open understorey, and markedly altered microclimate (Luskin &  
Potts 2011) that drive a substantial reduction in species richness and significant shifts in species  
composition. This finding is consistent across several hyperdiverse but rarely considered  
arthropod orders, such as Diptera (n = 469 species censused) and Hemiptera (n = 401), plus more  
585 frequently censused taxa (e.g., birds, ants and dung beetles). We are thus confident that oil palm  
plantations currently have very limited biodiversity value and that the conversion of unlogged or  
logged forest to oil palm results in major losses to conservation (Fitzherbert et al. 2008, Foster et  
al. 2011).

Use of meta-barcoding in conservation research.—Arthropods may represent over 90% of  
590 rainforest fauna (May 2010, Basset et al. 2012), but how many arthropod taxa are affected by  
land-use change and different forest management strategies are major knowledge gaps (Gardner  
et al. 2009, Cardoso et al. 2011). For example, an exhaustive meta-analysis of 138 studies on the  
impacts of land-use change in the tropics (Gibson et al. 2011) located just one study on true bugs  
and none on springtails. Together, these taxa accounted for >470 species in our dataset –  
595 approximately equal to birds, dung beetles and leaf-litter ants combined. This discrepancy partly  
reflects the difficulties and cost associated with identification of many tropical arthropod taxa,  
and is an important constraint on our understanding of how anthropogenic disturbance affects  
biodiversity.

By using DNA metabarcoding we were able to address this shortcoming and evaluate the  
600 effects of land-use change on the richness and diversity of five hyperdiverse and rarely studied  
arthropod assemblages (see also Ji et al. 2013). Because metabarcoding detects most arthropod  
orders and because the costs of sample processing scale with the number of samples (not the  
number of individuals or species as in conventional biodiversity assessments), it is feasible to  
assess changes simultaneously across several taxa. This circumvents the problems associated  
605 with differing sampling methodologies and logging histories that limit the reliability of meta-  
analyses. It also means that metabarcoding is both time- and cost-effective compared to standard  
sampling techniques for invertebrates, but not necessarily for birds (see Table 1 and Discussion  
in Ji et al. [2013] for further elaboration). We therefore argue that metabarcoding represents a  
major opportunity to advance our understanding of anthropogenic impacts on poorly understood  
610 arthropod biodiversity and to do so in a standardized and cost-effective manner.

Sampling limitations.—The value of logged forests could be exaggerated by spillover effects  
from adjacent primary forests or because species extinction debts are repaid over longer  
timescales than those typically studied (Gibson et al. 2011). Whilst we did not investigate these  
615 suggestions directly, several of the invertebrate groups considered have limited dispersal  
distances and short generation times (e.g. springtails). Since study sites in logged forest spanned  
1.1-21.3 km from primary forest edge (Fisher et al. 2011b) and up to 23 years since logging, for  
these taxa, spillover effects are unlikely and there should have been ample time for the majority  
of extinctions to occur (see also Adum et al. 2013). Our study has focused on nine vertebrate and  
invertebrate groups, but we have not sampled plants. Although two previous studies have  
620 revealed limited negative impacts of logging on trees in Borneo (Cannon et al. 1998, Berry et al.  
2008), these remain an important group with which to identify the impacts of twice-logging and

for understanding potential longer-term consequences of logging, especially given that mature, seed producing trees are those that are harvested.

Conversely, it has been argued that the value of logged forest may be underestimated relative to primary forest, because pseudoreplication of sample sites could explain variation in communities between logged and primary forest due to the turnover of species over space, rather than logging treatment effects per se (Ramage et al. 2013b). There was pseudoreplication of some sample sites in our study, in that some sites impacted by the same disturbance type were grouped together relative to other disturbance types, and this was particularly so with respect to primary forest. There was, however, no evidence that turnover with space explained changes in species composition after logging or conversion in our study, suggesting that pseudoreplication of sample sites does not explain our results. We also found similar results with an expanded dataset of spatially separated oil palm sites for birds and dung beetles (Text S1). We are thus confident that forest conversion to oil palm has substantial negative impacts on biodiversity, and that logging also has some negative impacts on fauna. We suggest that conservation strategies relying solely on logged forest will not effectively conserve all of the species found in undisturbed habitat (Edwards et al. 2013).

Identifying options for cost-effective conservation.—The ideal approach to saving forest species is to save all remaining primary forest from logging and conversion. However, there are strict financial limitations that preclude such a conservation strategy, meaning that we must consider the best way to cost-effectively conserve biodiversity. To avoid allocating conservation budgets inefficiently (Polasky et al. 2008), it is vital to assess how the opportunity costs of foregoing logging and conversion to oil palm change the apparent importance of primary forest over logged forests.

645 In this study we show that with logging but no threat from oil palm (scenario 1, see also  
Fisher et al. 2011b, Ji et al. 2013), logged forest provides the best coverage of species where  
conservation budgets are limited. This is because the difference in the opportunity costs of  
foregoing logging in primary forest versus previously logged forest is high, but the difference in  
biodiversity retained between the two habitats is relatively low. As a result, larger areas of  
650 logged forest – and therefore greater species coverage – can be purchased for the same price.  
Indeed, the high timber value of unlogged forest means that this habitat only begins to be  
selected after most of the logged forest sites have been purchased. Protecting primary forest  
specialists (i.e., species that occur only in primary forests) in this scenario would therefore  
require substantial additional investment.

655 The situation becomes more complex when the potential for conversion to oil palm is  
considered. With logging plus the threat of oil palm development across all habitats (scenario 2),  
the purchase of logged forest still provides the best coverage of species where funding is low  
(particularly where the focus is on maximizing total species richness). However, as conservation  
budgets increase, purchasing unlogged forest becomes an important component of strategies to  
660 maximize the number of primary forest species (which we argue is a more appropriate  
conservation objective than maximizing species richness). This shows that the size of  
conservation budgets is integral in determining the most effective option (Wilson et al. 2007). In  
contrast, when the threat from oil palm development is concentrated on previously logged forest  
(scenario 3), primary forest is more frequently selected even with low conservation budgets. By  
665 excluding the possibility of converting primary forest to oil palm (e.g., as per RSPO rules for oil  
palm expansion, Edwards et al. 2012b), the opportunity costs of conserving primary forest are  
reduced such that they are cheaper to purchase than logged forest. Importantly, the endpoint

without conservation investment is different for primary and logged forest in this scenario: while protecting primary forest would stop logging, protecting logged forest would prevent conversion to oil palm. Whilst purchasing primary forest may thus appear the most cost-effective option in scenario 3, this interpretation should only be applied with appropriate consideration for the overall biodiversity consequences across the competing land-uses and issues such as landscape connectivity.

Three more general points arise from the conservation planning exercise. Firstly, while the profitability of palm oil has previously been highlighted as a major obstacle to forest conservation in Southeast Asia (Fisher et al. 2011a), we show that considering the opportunity costs of oil palm in a conservation-planning context can substantially alter interpretations of land-use change impacts relative to scenarios involving logging alone (Fisher et al. 2011b). Secondly, although there are similarities in the most cost-effective strategies among scenarios, there are also important differences – the best option is therefore likely to be influenced by both the suitability of forest for logging and for conversion, and by national governance and international land-use policies (e.g., REDD+, Sloan et al. 2012). This suggests an important policy focus of lobbying for primary forests to be formally protected from conversion to oil palm, because in doing so, only the opportunity costs of logging then need to be offset to effect conservation of primary forest (set against the more expensive alternative of covering the opportunity costs of both logging plus oil palm when there is no legal prevention of primary forest clearance to agriculture). Finally, differing conservation priorities can produce subtly different outcomes – focusing on conserving primary forest species may not necessarily yield the same decisions as focusing on maximizing total species richness. This emphasizes the

690 importance of clearly outlining conservation objectives when evaluating land-use change  
impacts.

Our planning analyses ignore the element of scale in species' extinction risks: thus the  
conservation planning exercise could yield different results if only a small patch of primary  
forest could be conserved in isolation that would ultimately lose species due to fragmentation  
695 and edge effects (Didham et al. 1998, Laurance et al. 2002, Benedick et al. 2006, Laurance et al.  
2011, Rybicki and Hanski 2013). The focus was also solely on maximizing species coverage,  
with complementary research needed for other priorities, such as maintaining ecosystem services  
or aesthetic value. Our planning exercise could have over-valued the potential for logged forests  
to conserve biodiversity if the large network of logging roads and skid trails created to remove  
700 timber (Laporte et al. 2007; Laurance et al. 2009) ultimately facilitates the hunting of large-  
bodied vertebrates (Poulsen et al. 2009, 2011) and perhaps the illegal clearance of logged forests  
(Asner et al. 2006). In Indonesian Borneo, there is no evidence that logged forests are illegally  
cleared more frequently than are protected areas, with both experiencing equal levels of  
deforestation (Gaveau et al. 2013).

705 Previous applications of conservation planning software have generally focused on  
identifying specific priority areas for conservation and cost-effective protected area networks  
(e.g. Naidoo et al. 2006, Kremen et al. 2008, Polasky et al. 2008, Egoh et al. 2010, Di Minin et  
al. 2013, Faleiro and Loyola 2013). While such applications provide valuable information, they  
are also constrained by the need for accurate data on current and predicted species distributions,  
710 ecology and vulnerability to different forms of disturbance (Fiorella et al. 2010, Wilson et al.  
2010, Di Minin et al. 2013). These data are very limited for most invertebrate and plant taxa (as  
well as for many vertebrates), particularly in the tropics (Jetz et al. 2008, Cardoso et al. 2011,

Feeley and Silman 2011). Importantly, our results illustrate that in the absence of such location- and species-specific information, the application of non-spatial conservation planning tools that explicitly consider the profits returned by different land-uses can be highly informative in developing broad scale, cost-effective conservation strategies. This approach would be particularly valuable in extending studies that focus simply on quantifying impacts of land-use change on biodiversity metrics (e.g., Edwards et al. 2011b; Woodcock et al. 2011), potentially providing an important bridge between this extensive body of research and conservation decisions that must also consider the costs and benefits of different actions.

Indicator Taxa.—Understanding the extent to which different taxa respond consistently to anthropogenic disturbance is necessary to evaluate whether or not findings from previous research are generalisable. Moreover, where different taxa share similar responses, future survey and research costs can be significantly reduced without compromising data quality. Equally, identifying taxa that respond idiosyncratically is important: whilst findings from such taxa may have limited general applicability, conservation strategies that over-emphasize indicators may place more atypical groups at greater risk.

Our results illustrate firstly that the choice of metric is important when assessing indicator potential. There was little cross-taxon congruence in the effects of disturbance on species richness and conservation planning exercises based upon maximizing species richness. This presumably reflects the limited biological information retained by species richness, which neither captures changes in species abundance nor species identity. In contrast, most taxa responded similarly to the effects of logging and conversion on community composition, richness of primary forest species, and conservation planning exercises that maximize the coverage of primary forest species. Findings extrapolated to other taxa are therefore more likely to be reliable

if based on these metrics. This also suggests that by narrowing conservation focus, a greater efficiency is achieved in terms of using one taxon to represent others.

Using these better performing metrics, birds, leaf-litter ants, beetles, dung beetles, Hymenoptera, flies, and true bugs tend to be affected similarly by land-use change, making this  
740 the first study to identify indicator taxonomic groups for the impacts of logging. Extrapolations based on existing findings from the those commonly sampled taxonomic groups amongst this list (i.e., birds, ants, and dung beetles) might therefore provide reliable approximations of overall effects of logging and forest conversion where data on other taxa are lacking (see also Barlow et al. (2007) for similar results for forest conversion to plantations). However, scavenging  
745 mammals and, to a lesser extent, springtails poorly predicted patterns in other taxonomic groups. This could reflect differences in taxon-specific traits (e.g. high dispersal ability and generalist habitat requirements of scavenging mammals), and in the case of scavenging mammals, the attractiveness of sampling methods and so few species, resulting in a lack of significant variation between logged forest and oil palm for species composition and primary forest species metrics.  
750 They also underscore the importance of ensuring sufficient taxonomic coverage, lest conservation conclusions be inappropriately extrapolated from indicator taxa to all groups. Finally, because we have focused on Southeast Asia, indicator taxa from this region might not apply elsewhere in the tropics, although a priori we would expect similar responses for frequently sampled taxa, such as birds, which have already revealed similar patterns to logging.

755 **Conclusions.**— Primary forests within protected areas are vital to global conservation (Gibson et al. 2011, Laurance et al. 2012), but protected areas are increasingly being isolated (DeFries et al. 2005, Newmark 2008) and encroached upon (Laurance et al. 2012). While our results underscore that taxonomically comprehensive conservation strategies will require the protection

of unlogged forest, they also illustrate that conservation can valuably incorporate timber  
760 concessions. Where conservation budgets are low, or where the only threat is from timber  
harvesting, protecting production forests represents a comparatively cheap option for protecting  
large numbers of species, with substantial additional funds needed to prevent the loss of a  
smaller number of primary forest specialists. However, the situation becomes more nuanced  
where there is a threat from conversion to oil palm plantations. Here, the most cost-effective  
765 conservation strategies will combine unlogged and logged forest – although because of the high  
returns from oil palm, even the most cost-effective strategies may severely stretch budgets.  
These findings illustrate that explicitly incorporating information on land-use policy,  
conservation resources, and the relative biodiversity and financial values of competing land-uses  
provides a more complete picture than studies focusing on changes in biodiversity metrics alone.  
770 We therefore conclude by arguing that regional conservation strategies should move beyond the  
question of whether or not logged forest can contribute to conservation (they can) to examining  
the most efficient approaches for combining logged and unlogged forest in a holistic strategy.

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## Ecological Archives material

TABLE S1. Variation in species composition among habitats with presence-absence matrices.

TABLE S2. Correlations among taxa using 9 metrics to quantify land-use impacts

TABLE 1. Total abundance, observed species richness (OBS) at the habitat level, and mean species richness per transect of nine study taxa. Superscripts reveal pairwise differences at  $P < 0.05$ , with 3 degrees of freedom in all cases. UL = primary (unlogged) forest, 1L = once-logged forest, 2L = twice-logged forest, OP = oil palm.

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Taxonomic group	Habitat	Total abundance	Observed Species		$\chi^2$	P
			Species richness	richness per transect		
Birds	UL	1009	110	$56.4 \pm 2.4^a$	51.42	<0.001
	1L	914	122	$51.9 \pm 3.5^a$		
	2L	890	130	$50.0 \pm 3.8^a$		
	OP	640	31	$16.3 \pm 1.0^b$		
Scavenging						
mammals	UL	25	8	$3.3 \pm 0.2$	0.55	0.9
	1L	33	8	$4.1 \pm 0.2$		
	2L	25	6	$3.1 \pm 0.3$		
	OP	32	6	$3.8 \pm 0.4$		
Leaf-litter						
ants	UL	1260	180	$72.3 \pm 2.7^a$	42.88	<0.001
	1L	725	144	$64.0 \pm 2.5^a$		
	2L	1030	165	$60.6 \pm 2.2^a$		
	OP	244	75	$35.5 \pm 1.8^b$		

Bees, wasps, & ants	UL	391	186	$48.9 \pm 2.1^a$	14.07	0.003
	1L	437	204	$54.6 \pm 3.3^a$		
	2L	405	202	$50.6 \pm 3.4^a$		
	OP	133	86	$33.3 \pm 3.5^b$		
Beetles	UL	431	249	$53.9 \pm 5.6^a$	33.92	<0.001
	1L	543	304	$67.9 \pm 8.4^a$		
	2L	470	275	$58.8 \pm 3.4^a$		
	OP	111	75	$27.8 \pm 2.3^b$		
Dung beetles	UL	7885	52	$32.1 \pm 1.0^{ab}$	26.9	<0.001
	1L	7386	43	$27.3 \pm 2.3^b$		
	2L	9231	45	$32.5 \pm 0.6^a$		
	OP	1783	25	$13.0 \pm 1.5^c$		
Flies	UL	780	264	$97.5 \pm 4.2^a$	7.25	0.06
	1L	856	314	$107.0 \pm 6.7^a$		
	2L	797	289	$99.6 \pm 3.3^a$		
	OP	321	157	$80.3 \pm 7.4^b$		
Springtails	UL	159	44	$19.9 \pm 1.7$	2.32	0.5
	1L	154	49	$19.3 \pm 1.0$		
	2L	189	57	$23.6 \pm 1.2$		
	OP	64	30	$16.0 \pm 0.4$		
True bugs	UL	311	174	$38.9 \pm 4.7^b$	5.8	0.1
	1L	302	181	$37.8 \pm 3.3^b$		

2L	375	229	$46.9 \pm 3.0^a$
OP	145	88	$36.3 \pm 4.3^b$

TABLE 2. Variation in species composition among habitats using transect level abundance (birds, dung beetles, leaf-litter ants) and presence-absence (other taxa) matrices. Results show deviance and p-value for overall comparisons, and Wald statistic and p-values for pairwise comparisons. § P < 0.1; \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001, with significant results shown in bold. P-value calculated using 999 resampling iterations via pit.trap sampling to account for correlation in testing. UL = primary (unlogged) forest, 1L = once-logged forest, 2L = twice-logged forest, OP = oil palm.

Taxonomic group	Overall	Pairwise comparisons					
		UL-1L	UL-2L	1L-2L	UL-OP	1L-OP	2L-OP
Birds	<b>1354***</b>	<b>10.98**</b>	<b>12.18**</b>	9.68 <sup>§</sup>	<b>6.92**</b>	<b>9.98***</b>	<b>13.47**</b>
Scavenging mammals	<b>41.59**</b>	1.80 <sup>§</sup>	<b>1.86*</b>	1.44	<b>1.31*</b>	0.73	0.58
Leaf-litter ants	<b>1585***</b>	<b>13.95**</b>	<b>13.75*</b>	10.75	<b>13.69**</b>	<b>12.31**</b>	<b>13.04**</b>
Bees, wasps, ants	<b>1312*</b>	7.01	6.26	8.08 <sup>§</sup>	4.47 <sup>§</sup>	4.11	<b>5.42*</b>
Beetles	<b>1824*</b>	9.15	8.18	8.77	4.72 <sup>§</sup>	4.20	4.95 <sup>§</sup>
Dung beetles	<b>1577***</b>	<b>30.87**</b>	<b>35.46**</b>	<b>17.59**</b>	<b>15.19**</b>	<b>12.36**</b>	<b>13.21**</b>
Flies	<b>263.9*</b>	4.19	4.03	3.97	<b>3.24*</b>	2.63 <sup>§</sup>	<b>3.51*</b>
Springtails	<b>329.9**</b>	4.21	4.86	5.00 <sup>§</sup>	3.02	2.89	<b>4.14**</b>
True bugs	<b>217.7**</b>	1.69	2.45	2.07	1.63	1.83	<b>2.68*</b>

Table 3: Total species richness in primary forest and the mean richness of primary forest species per transect in once-logged forest, twice-logged forest and oil palm. Superscripts reveal pairwise differences between logged forests and oil palm at  $P < 0.05$ .

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Taxonomic group	Species richness of primary forest				$\chi^2$	P
	Primary total	Once-logged	Twice-logged	Oil palm		
Birds	110	46.5 ± 2.8 <sup>a</sup>	41.5 ± 2.9 <sup>a</sup>	6.0 ± 0.8 <sup>b</sup>	74.58	< 0.001
Scavenging mammals	8	3.9 ± 0.1	3.1 ± 0.33	2.5 ± 0.31	1.91	0.38
Leaf-litter ants	180	54.7 ± 2.3 <sup>a</sup>	53.1 ± 1.9 <sup>a</sup>	26.5 ± 1.0 <sup>b</sup>	39.46	< 0.001
Bees, wasps, & ants	186	40.1 ± 2.0 <sup>a</sup>	34.9 ± 2.7 <sup>a</sup>	21.0 ± 2.3 <sup>b</sup>	25.27	< 0.001
Beetles	431	45.4 ± 6.6 <sup>a</sup>	34.0 ± 1.6 <sup>a</sup>	27.8 ± 3.2 <sup>b</sup>	12.72	0.002
Dung beetles	52	26.9 ± 2.2 <sup>a</sup>	29.9 ± 0.5 <sup>a</sup>	9.3 ± 0.7 <sup>b</sup>	31.61	< 0.001
Flies	264	88.0 ± 5.3 <sup>a</sup>	82.1 ± 2.7 <sup>a</sup>	63.8 ± 9.3 <sup>b</sup>	8.68	0.01
Springtails	44	17.6 ± 1.1	19.4 ± 0.9	13.8 ± 0.4	1.66	0.44
True bugs	174	25.1 ± 3.0 <sup>a</sup>	25.8 ± 2.5 <sup>a</sup>	14.5 ± 2.5 <sup>b</sup>	12.33	0.002

TABLE 4: Number of significant correlations among nine taxa using four methods of determining biodiversity value. RSW2 method is subdivided by two metrics—maximizing species richness or primary forest species richness across selected sites—with three scenarios of land-use threat against which the costs of conservation selections must compete. Congruences are given for the combined impacts of logging and oil palm, and only for logging. There was a maximum of 36 combinations among taxa, and numbers in bold represent those metrics for which over one third of correlations were significant.

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Method of determining biodiversity value	Forest & oil palm	Forest only
Species richness	10	4
Species composition	<b>32</b>	<b>14</b>
Primary forest species richness	<b>23</b>	<b>13</b>
RSW2		
- Maximizing species richness		
Timber only	4	9
Timber & oil palm	1	4
Timber & oil palm in logged forest	2	1
- Maximizing primary forest species richness		
Timber only	<b>16</b>	6
Timber & oil palm	2	4
Timber & oil palm in logged forest	<b>27</b>	<b>22</b>

## Figure legends

FIG. 1. Observed species richness, constructed using sample-based rarefaction curves for primary  
1130 (unlogged), once-logged and twice-logged forest, and for oil palm. The x-axis is scaled to show  
the number of individuals, where (b), (d), (e), (g), (h) and (i) are number of presences and (c)  
number of colony occurrences. Grey shading represents the 95% CI for primary forest. Note that  
'dung beetles' and 'leaf-litter ants' were collected using pitfall traps and Winkler sampling  
respectively, and represent distinct datasets from 'beetles' and 'bees, wasps and ants' collected  
1135 using malaise traps and identified with metabarcoding.

FIG. 2. (a) Estimated species richness (EST) in each habitat. (b) The percentage of species  
detected, derived by dividing observed species richness (OBS, Table 1) by estimated species  
richness (EST). Note that 'dung beetles' and 'leaf-litter ants' were collected using pitfall traps  
and Winkler sampling respectively, and represent distinct datasets from 'beetles' and 'bees,  
1140 wasps and ants' collected using malaise traps and identified with metabarcoding.

FIG. 3. Non-metric multidimensional scaling (MDS) ordination of species composition among  
primary, once-logged, twice-logged forests and oil palm.

FIG. 4. The percentage of primary forest species that remain after logging or conversion to oil  
palm. For species totals in primary forest see Table 2. Note that sampling effort for oil palm was  
1145 half that in forest types.

FIG. 5. For nine study taxa, the number of primary, once-logged and twice-logged transects  
selected by RSW2 at conservation budgets rising in \$15,000 increments from \$15,000 to \$90,000  
Selections are made under three scenarios of land-use threat: (a, b) that forests are threatened by  
logging, but not conversion to oil palm; (c, d) that all land is suitable for logging and oil palm;

1150 and (e, f) that all land is suitable for logging, but that only logged areas are suitable for  
conversion to oil palm. Per hectare values are: primary forest=\$10,460; once-logged=\$4,000;  
twice-logged=\$2,010; and oil palm=\$11,240 (values are in 2009 US\$ and extracted from Fisher  
et al. 2011a,b). Under each land-use scenario there are two metrics of biodiversity output: (a, c,  
1155 e) maximizing total species coverage (All spp; i.e., all species are weighted equally in their  
conservation importance) and (b, d, f) maximizing the coverage of species that were found in  
primary forest (UL forest spp; i.e., primary forest species are weighted 10-fold more important  
than those species only recorded in logged forest or oil palm).

FIG. 6. MDS plots of congruence in responses among taxa for methods of determining the  
biological impacts of land-use change that yielded significant correlations in over a third (>12 of  
1160 36) of comparisons (see **Methods**, Table 4). Congruence is shown for analyses that incorporate  
both logging and oil palm impacts, and for logging impacts only. Species composition (a, b),  
richness of primary forest species (c, d), RSW2 selection to maximize richness of primary forest  
species when all forest is threatened with timber extraction, but only logged forest is threatened  
with oil palm conversion (e, f), and RSW2 selection to maximize richness of primary forest  
1165 species when all forest sites are threatened by timber extraction, but not conversion to oil palm  
(g). Taxa with similar responses concentrate toward the center of the MDS plot, whereas taxa  
that exhibit unique responses appear as outliers. In some instances, taxa have such similar  
responses that their points overlay each other and are indistinguishable graphically.