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Selective-logging and oil palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning

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Abstract. Strong global demand for tropical timber and agricultural products has driven large-scale logging and subsequent conversion 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 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 conversion. However, our knowledge of the impact of logging and conversion 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-use gradient of primary forest, once- and twice-logged forests, and oil palm plantations, we used traditional sampling and DNA metabarcoding to compile an extensive data set in Sabah, Malaysian Borneo for nine vertebrate and invertebrate taxa to quantify the biological impacts of logging and oil palm, develop cost-effective methods of protecting biodiversity, and examine whether there is congruence in response among taxa. Logged forests retained high species richness, including, on average, 70% of species found in primary forest. In contrast, conversion to oil palm dramatically reduces species richness, with significantly fewer primary-forest species than found on logged forest transects for seven taxa. 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 an ecologically and taxonomically diverse range of species, particularly when conservation budgets are limited. Six indicator groups (birds, leaf-litter ants, beetles, aerial hymenopterans, 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. Cross-taxon congruence in responses to disturbance also suggests that the practice of focusing on key indicator taxa yields important information of general biodiversity in studies of logging and oil palm.

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

INTRODUCTION

Tropical rain forests harbor Earth's greatest concentrations of terrestrial biodiversity, yet they are increasingly impacted by selective logging and habitat

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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 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. 2011*b*).

The importance that biodiversity conservation strategies should place on old-growth (primary) 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 biodiversity and conservation value provide only an incomplete assessment of these issues in several key respects.

First, because conducting comprehensive multitaxon 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 rain forest 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 (Kozlowski 2008, Cardoso et al. 2011), with most assessments focusing on a few groups (e.g., ants, dung beetles, butterflies, and moths; Fitzherbert et al. 2008, Foster et al. 2011). While some studies seek to address this bias by considering rarely sampled arthropod taxa, they do so by assessing changes in abundance at higher taxonomic levels rather than by identifying individuals to (morpho-)species level (e.g., Burghouts et al. 1992, Turner and Foster 2009, Edwards et al. 2012*a*). Moreover, many of the commonly censused taxa are wide-ranging 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 data sets 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 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. While such multitaxa 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 Asia, and Africa; Lawton et al. 1998, Schulze et al. 2004, Barlow et al. 2007), for selective logging, standardized 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. 2011*b*, Woodcock et al. 2011) and rarely for the impact of multiple rotations of logging (Edwards et al. 2011*b*, Woodcock et al. 2011). Yet selective logging is amongst the most widespread anthropogenic activities 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, multitaxon information on responses to selective logging is an important constraint on understanding key unresolved questions, such as 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. 2012*c*, 2013, Ramage et al. 2013*a*), and the most appropriate protected area networks to maximize species coverage (Wilson et al. 2010).

Finally, previous research on the effects of logging and forest conversion has generally 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 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. 2011*b*; 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*b*) and Ji et al. (2013) did not incorporate the opportunity 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. 2011*a*, Fisher et al. 2011*a*).

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 data sets 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 determine which management strategies conserve the greatest biodiversity across a range of conservation budgets, of key land-use transitions (Fisher et al. 2011*b*, 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 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? (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 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 (4°57.990′ N, 117°48.320′ E). These forests are dominated numerically by large tree species in the family Dipterocarpaceae (Fisher et al. 2011*a*), 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 ≈ 113 m^3 of timber per hectare (Fisher et al. 2011*b*). 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 m^3/ha of timber (Fisher et al. 2011*b*). 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 yr old) at a density of 100 trees/ha (Edwards et al. 2010). Our sampling locations within each habitat were at similar altitudes (m above sea level [mean ± SE]; unlogged is 238 ± 16, once-logged is 195 ± 11, twice-logged is 230 ± 11, and oil palm is 229 ± 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 (Appendix A). 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 (Edwards et al. 2011*b*), 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, 2011*b*). Three count stations were established at 250-m intervals (3 stations × 2 transects × 14 sites = 84 stations in total) centered along each transect, and each station was visited for 15 minutes on three consecutive days between 05:45 and 10:30. 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 (data *available online*).[17] The use of terrestrial-based point counts can under sample certain canopy groups, including secretive 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, Wisconsin, USA) 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 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 minutes. After positioning the camera traps and carcasses, we returned to the site on the fourth day to check the setup before retrieving the equipment on the 10th day. Species are classified as scavengers if they were documented consuming the carcasses on at least one occasion. Animal species that visited the 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. [2011*b*]); 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^2 of leaf litter and loose topsoil were collected (one site in once-logged forest could not be sampled due to heavy rainfall, giving 26 transects and 182 points in total, see Woodcock et al. [2011] and 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 (BugDorm, Taichung, Taiwan) to sample flies (Diptera), bees, wasps, and ants (Hymenoptera), beetles (Coleoptera), true bugs (Hemiptera), and springtails (Collembola) in 2011 (Ji et al. 2013). On each transect, two traps were spaced 150 m apart and collected after four 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 a closed canopy), were identified by D. P. Edwards using sight and sound, scavenging mammals were identified by N. T.-L. Lim, and dung beetles and leaf-litter ants were identified with reference to collections by T. H. Larsen and F. A. Edwards, and by P. Woodcock, 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 maximum potential occurrence for each species (herein abundance) of seven per transect.

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 repeatable assessments of species incidences within communities (reviewed by Baird and Hajibabaei [2012], Taberlet et al. [2012], Yu et al. [2012], and 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 polymerase chain reaction-amplified each sample for a 658-base-pair portion near the 5′ end of the taxonomically informative mitochondrial gene Cytochrome Oxidase subunit I (COI), using degenerate primers. The 56 PCR amplicons were sequenced on a GS FLX 454 pyrosequencer (Roche, Branford, Connecticut, USA), using two 1/4 regions, producing 375 925 raw reads. The sequence data set was then run through a quality control (297 171 reads after quality control, at mean read length 445 base pairs), denoising, and clustering bioinformatic pipeline. Each cluster of sequences is called an operational taxonomic unit (OTU) and represents a set of COI reads that 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 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 2402 OTUs assigned to Arthropoda (1843 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 online and in GENBANK's Short Read Archive (accession numbers are available in Ji et al.'s [2013] Supporting Information S6; *available online*).[18] Finally, separate OTU tables, which are the standard site

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[17] www.xeno-canto.org/asia

[18] http://datadryad.org/resource/doi:10.5061/dryad.t3v71

× 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 data sets, which is the practice that we follow here.

DATA ANALYSES

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

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 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 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 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 (*available online*).[19]

We also compared species richness among forest types at the level of individual transects (which is the smallest spatial scale for six of our nine data sets) by fitting a negative binomial error 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 evaluated potential 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 sampled additional and spatially independent oil palm sites (birds, $n = 2$; dung beetles, $n = 1$; Appendix A) 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 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 (NMDS; Clarke and Warwick 2001). We tested for differences among forest types using a multivariate implementation of a generalized 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 Mantel test to compare species composition to geographic distance between pairs of transects within a site and between pairs of transects across the entire data set (Ghazoul 2002, Ramage et al. 2013*b*). 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 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 List), 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 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

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[19] http://chao.stat.nthu.edu.tw/blog/software-download/

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 calculated 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 vs. 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, \$4000; twice-logged, \$2010; data from Fisher et al. [2011*b*]) and of oil palm cultivation (\$11 240 per hectare; data from Edwards et al. [2011*a*], Fisher et al. [2011*a*]). 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 data set from which RSW2 can select, not money). We did so under three scenarios. First, a logging only scenario, where 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. (2011*b*) and Ji et al. (2013), but our analysis encompassed a suite of taxa that were not considered in those studies. Second, a logging plus oil palm in all forests scenario, where 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. Lastly, a logging plus oil palm in logged forest scenario, where 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 Roundtable for Sustainable Palm Oil (RSPO) accreditation (Edwards et al. 2012*b*). All three scenarios were run for primary and logged forest transects.

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 one to 10) compared to species that were recorded only in logged forest or oil palm (still scored as one). This is an adaptation of Arponen et al. (2005), which used a weighting of one for common species and four 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 data sets was evaluated at the transect level using four methods (following Barlow et al. [2007]). Spearman's correlations assessed congruence for observed species richness, richness 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 nonparametric 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 had six separate congruence analyses. We used outputs from the three different scenarios described above (logging threat only, logging plus oil palm threat in all forest, and logging plus oil palm threat in logged forest), with both of our metrics of biodiversity (maximizing species richness and richness of primary forest species).

All of these indicator analyses were conducted for logging, and for logging and oil palm combined (except for RSW2, which was not assessed for logging and oil palm transects, see *Data Analyses: What conservation strategy produces the most effective trade-off between biodiversity protection and cost?*).

We scored the number of significant correlations between taxa to determine how each of these four 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 NMDS ordinations of response similarity, from which we were able to identify possible indicator taxa (following Barlow et al. [2007]).

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 springtails (Fig. 1). In contrast, all nine taxa

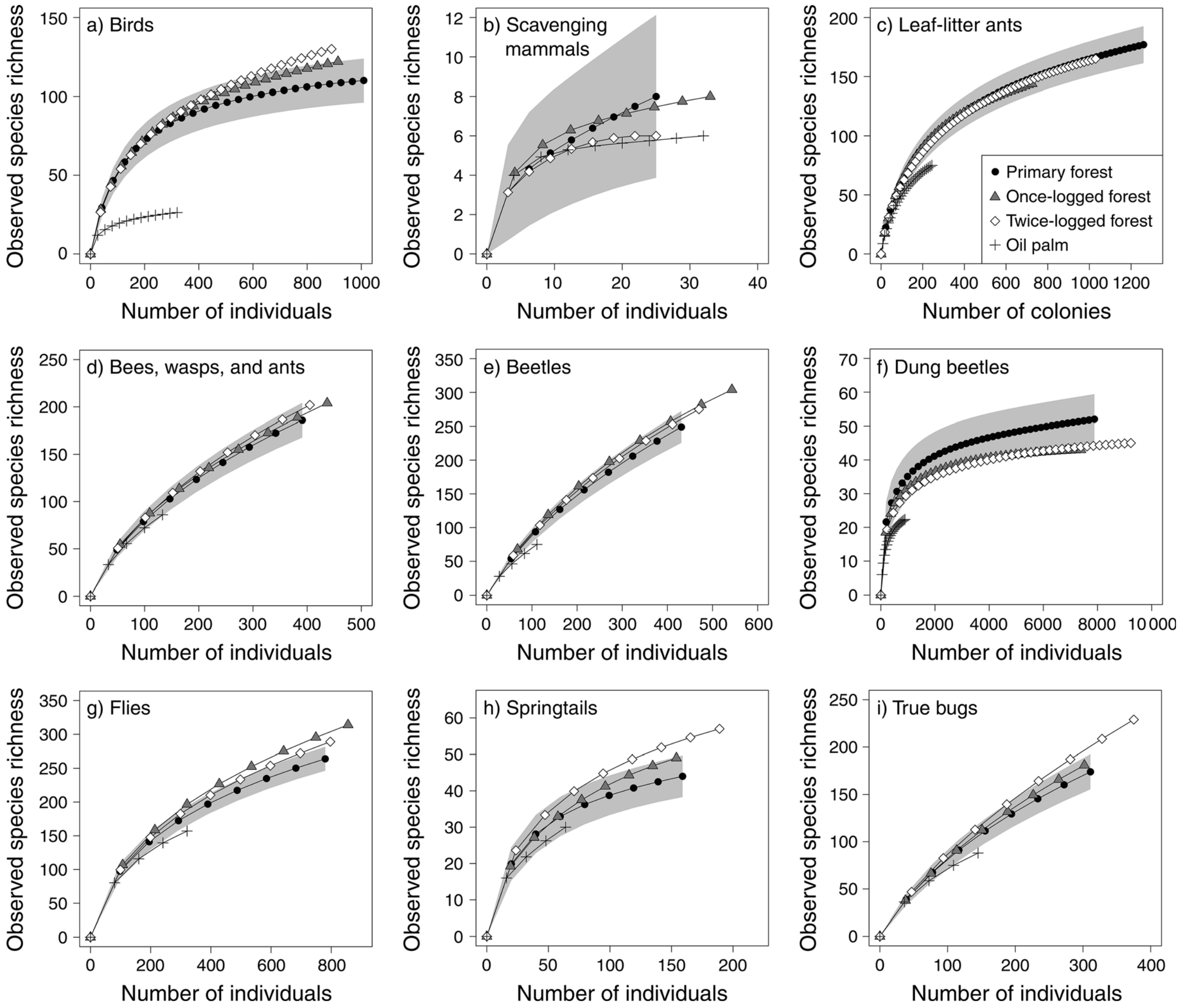

FIG. 1. Observed species richness constructed using sample-based rarefaction curves for primary (unlogged), once-logged, and twice-logged forest, and for oil palm. The *x*-axis is scaled to show the number of individuals, where panels (b), (d), (e), (g), (h), and (i) are number of presences and panel (c) number of colony occurrences. Gray 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 data sets from beetles and bees, wasps, and ants collected using malaise traps and identified with metabarcoding.

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 (Appendix B), and estimated total species richness (Fig. 2a) showed broadly similar patterns to observed species richness. In addition, estimators of species richness indicated that we sampled $\geq$59% (mean $\pm$ SE = 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 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 $P > 0.5$), 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. Reanalysis with an expanded data set to include additional and independent sample sites in oil palm for birds and dung beetles revealed very similar results (Appendix C), providing further evidence that pseudoreplication of sample sites does not confound the negative impacts of oil palm on species richness.

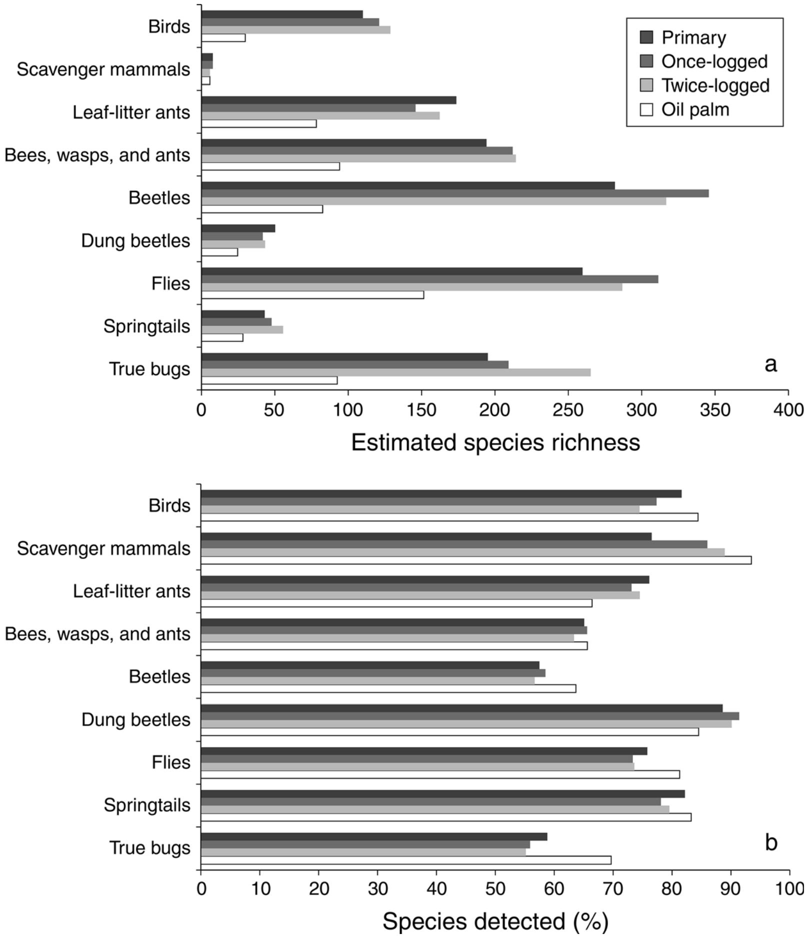

FIG. 2. (a) Estimated species richness (EST) in each habitat. (b) The percentage of species detected, derived by dividing observed species richness (OBS; see Table 1) by estimated species richness. Note that dung beetles and leaf-litter ants were collected using pitfall traps and Winkler sampling, respectively,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

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; see Fig. 3 and 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) and between once-logged forest and oil palm for four of nine taxa (birds, dung beetles, ants, and flies; see Fig. 3 and 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).

Changes in species composition based on presence–absence matrices for birds, dung beetles, and ants revealed a broadly similar pattern, with the exception of no difference between logged and primary forest for ants (statistics in Appendix D). 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 $P = 0.07$). The lack of relationship between distance and composition within habitat types (some of which included sites separated by 25–40 km; see Appendix A) strongly suggests that dissimilarities among habitat types are driven by disturbance regime rather than by spatial autocorrelation, and thus that distance effects expected from a nonindependent 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. Reanalysis with an expanded data set to include additional and independent sample points in oil palm for birds and dung beetles again revealed big impacts on species composition, but again Mantel test results suggest that disturbance not spatial autocorrelation of sample points explained differences (Appendix C).

TABLE 1. Total abundance, observed species richness (OBS) at the habitat level, and species richness (mean ± SE) per transect of nine study taxa.

Taxonomic group and habitats	Total abundance	Observed species richness	Species richness per transect	χ^2	P
Birds				51.42	<0.001
UL	1009	110	56.4^{a} ± 2.4		
1L	914	122	51.9^{a} ± 3.5		
2L	890	130	50.0^{a} ± 3.8		
OP	640	31	16.3^{b} ± 1.0		
Scavenging mammals				0.55	0.9
UL	25	8	3.3 ± 0.2		
1L	33	8	4.1 ± 0.2		
2L	25	6	3.1 ± 0.3		
OP	32	6	3.8 ± 0.4		
Leaf-litter ants				42.88	<0.001
UL	1260	180	72.3^{a} ± 2.7		
1L	725	144	64.0^{a} ± 2.5		
2L	1030	165	60.6^{a} ± 2.2		
OP	244	75	35.5^{b} ± 1. 8		
Bees, wasps, and ants				14.07	0.003
UL	391	186	48.9^{a} ± 2.1		
1L	437	204	54.6^{a} ± 3.3		
2L	405	202	50.6^{a} ± 3.4		
OP	133	86	33.3^{b} ± 3.5		
Beetles				33.92	<0.001
UL	431	249	53.9^{a} ± 5.6		
1L	543	304	67.9^{a} ± 8.4		
2L	470	275	58.8^{a} ± 3.4		
OP	111	75	27.8^{b} ± 2.3		
Dung beetles				26.9	<0.001
UL	7885	52	32.1^{ab} ± 1.0		
1L	7386	43	27.3^{b} ± 2.3		
2L	9231	45	32.5^{a} ± 0.6		
OP	1783	25	13.0^{c} ± 1.5		
Flies				7.25	0.06
UL	780	264	97.5^{a} ± 4.2		
1L	856	314	107.0^{a} ± 6.7		
2L	797	289	99.6^{a} ± 3.3		
OP	321	157	80.3^{b} ± 7.4		
Springtails				2.32	0.5
UL	159	44	19.9 ± 1.7		
1L	154	49	19.3 ± 1.0		
2L	189	57	23.6 ± 1.2		
OP	64	30	16.0 ± 0.4		
True bugs				5.8	0.1
UL	311	174	38.9^{b} ± 4.7		
1L	302	181	37.8^{b} ± 3.3		
2L	375	229	46.9^{a} ± 3.0		
OP	145	88	36.3^{b} ± 4.3		

Notes: Superscripts reveal pairwise differences at $P < 0.05$, with 3 degrees of freedom in all cases. Key to abbreviations: UL, primary (unlogged) forest; 1L, once-logged forest; 2L, twice-logged forest; and OP, oil palm.

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 ± SE, once-logged is 72.0% ± 3.4%, and twice-logged is 69.4% ± 4.2%). Oil palm consistently retained a much lower percentage of primary forest species (29.0% ± 4.4%) than did logged forests (Fig. 4). This was due in part to lower sampling effort in oil palm (see *Methods: Data analyses: Species composition and species of conservation concern*), 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 seven of nine taxa (except scavenging mammals and springtails; see 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-

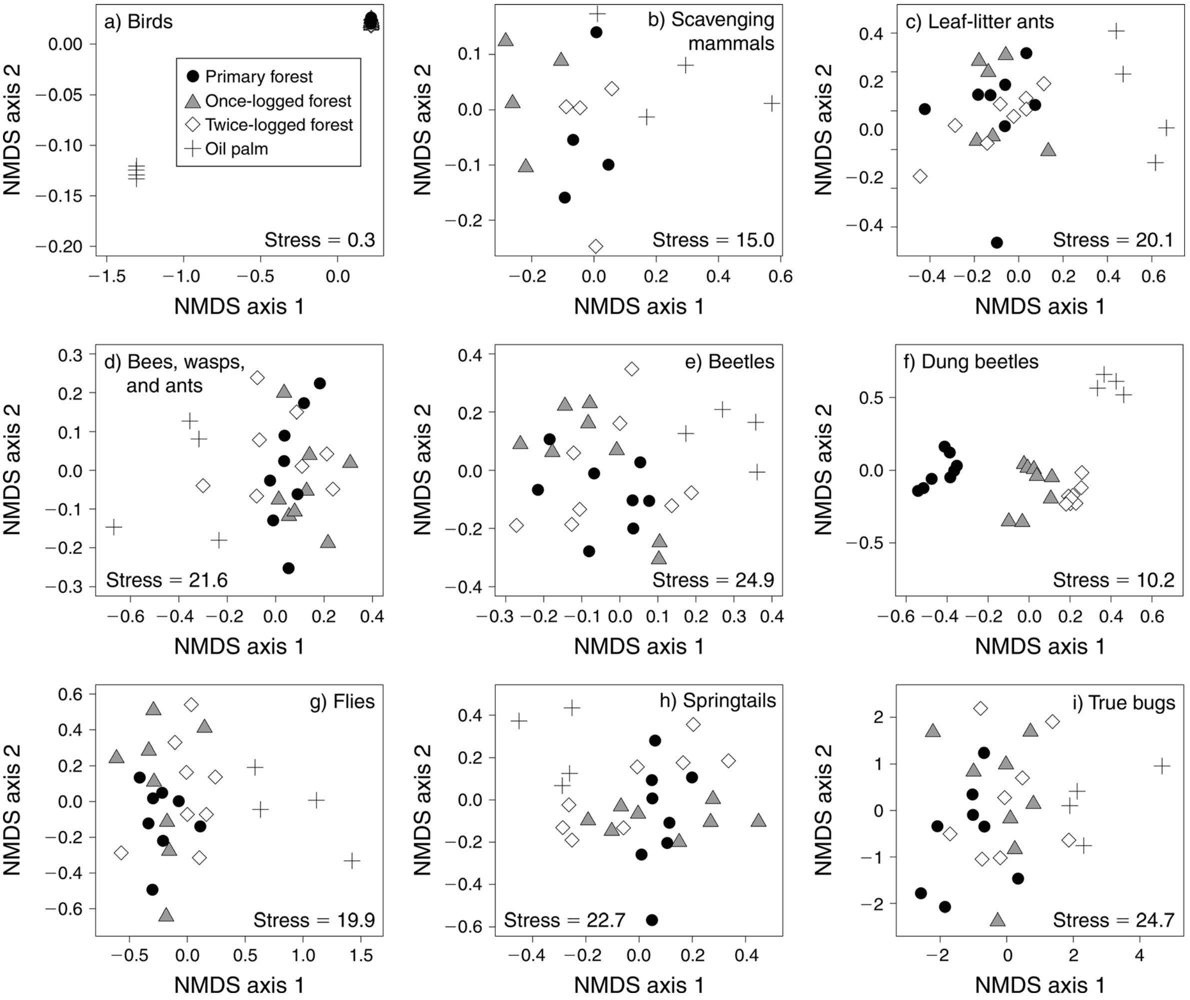

FIG. 3. Nonmetric multidimensional scaling (NMDS) ordination of species composition among primary, once-logged, and twice-logged forests, and oil palm.

km spatial scale, but no spatial autocorrelation at the remaining nine spatial scales. Finally, reanalysis with the expanded data set to include additional and independent sample points in oil palm for birds and dung beetles revealed very similar results (Appendix C), and in the case of birds, this additional analysis removed differences in the number of sample points making overall percentages of primary forest bird

TABLE 2. Variation in species composition among habitats using transect-level abundance (birds, dung beetles, leaf-litter ants) and presence–absence (other taxa) matrices.

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

Notes: Results show deviance and *P* value for overall comparisons, and Wald statistic and *P* values for pairwise comparisons. See Table 1 for abbreviations. *P* value calculated using 999 resampling iterations via pit trap sampling to account for correlation in testing.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

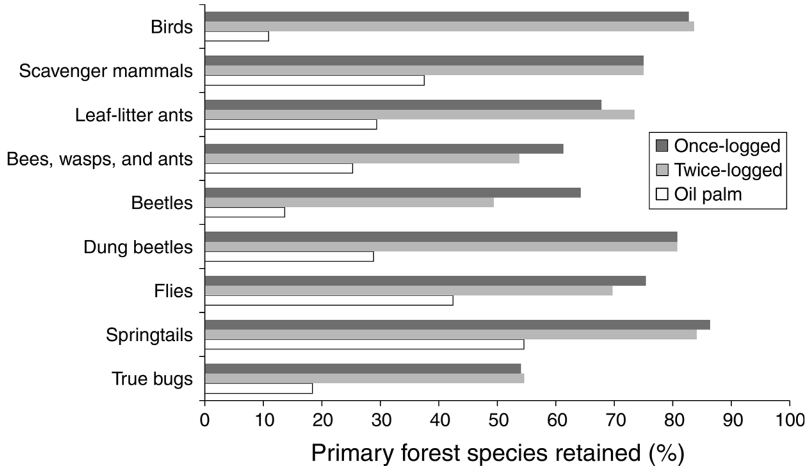

FIG. 4. The percentage of primary forest species that remain after logging or conversion to oil palm. For species totals in primary forest see Table 2. Note that sampling effort for oil palm was one-half that in forest types.

species directly comparable between oil palm (11%) vs. once- and twice-logged forests (83% ± 0.5%).

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

Selecting among forested transects 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 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 logged forest transects still also selected (Fig. 5e). Finally, contrasting whether once- or twice-logged forests were most commonly selected under the two scenarios of timber plus oil palm threat (Fig. 5c, e), once-logged was more frequently selected than twice-logged forest for scavenger mammals, beetles, and flies, whereas twice-logged forest was more commonly selected for leaf-litter ants, aerial Hymenoptera, true bugs, and springtails.

Using the alternative conservation metric of maximizing the richness of primary forest 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 (Fig. 5b) or for timber and oil palm threat across all forest types (Fig. 5d), logged forests were still an important component of the optimal conservation strategy, being frequently selected in both cases. 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

TABLE 3. Total species richness in primary forest and the richness (mean ± SE) of primary forest species per transect in once-logged forest, twice-logged forest, and oil palm.

Taxonomic group	Primary total	Species richness of primary forest species			χ^2	*P*
		Once-logged	Twice-logged	Oil palm		
Birds	110	46.5^a ± 2.8	41.5^a ± 2.9	6.0^b ± 0.8	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^a ± 2.3	53.1^a ± 1.9	26.5^b ± 1.0	39.46	<0.001
Bees, wasps, and ants	186	40.1^a ± 2.0	34.9^a ± 2.7	21.0^b ± 2.3	25.27	<0.001
Beetles	431	45.4^a ± 6.6	34.0^a ± 1.6	27.8^b ± 3.2	12.72	0.002
Dung beetles	52	26.9^a ± 2.2	29.9^a ± 0.5	9.3^b ± 0.7	31.61	<0.001
Flies	264	88.0^a ± 5.3	82.1^a ± 2.7	63.8^b ± 9.3	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^a ± 3.0	25.8^a ± 2.5	14.5^b ± 2.5	12.33	0.002

Note: Superscripted lowercase letters reveal pairwise differences between logged forests and oil palm at $P < 0.05$.

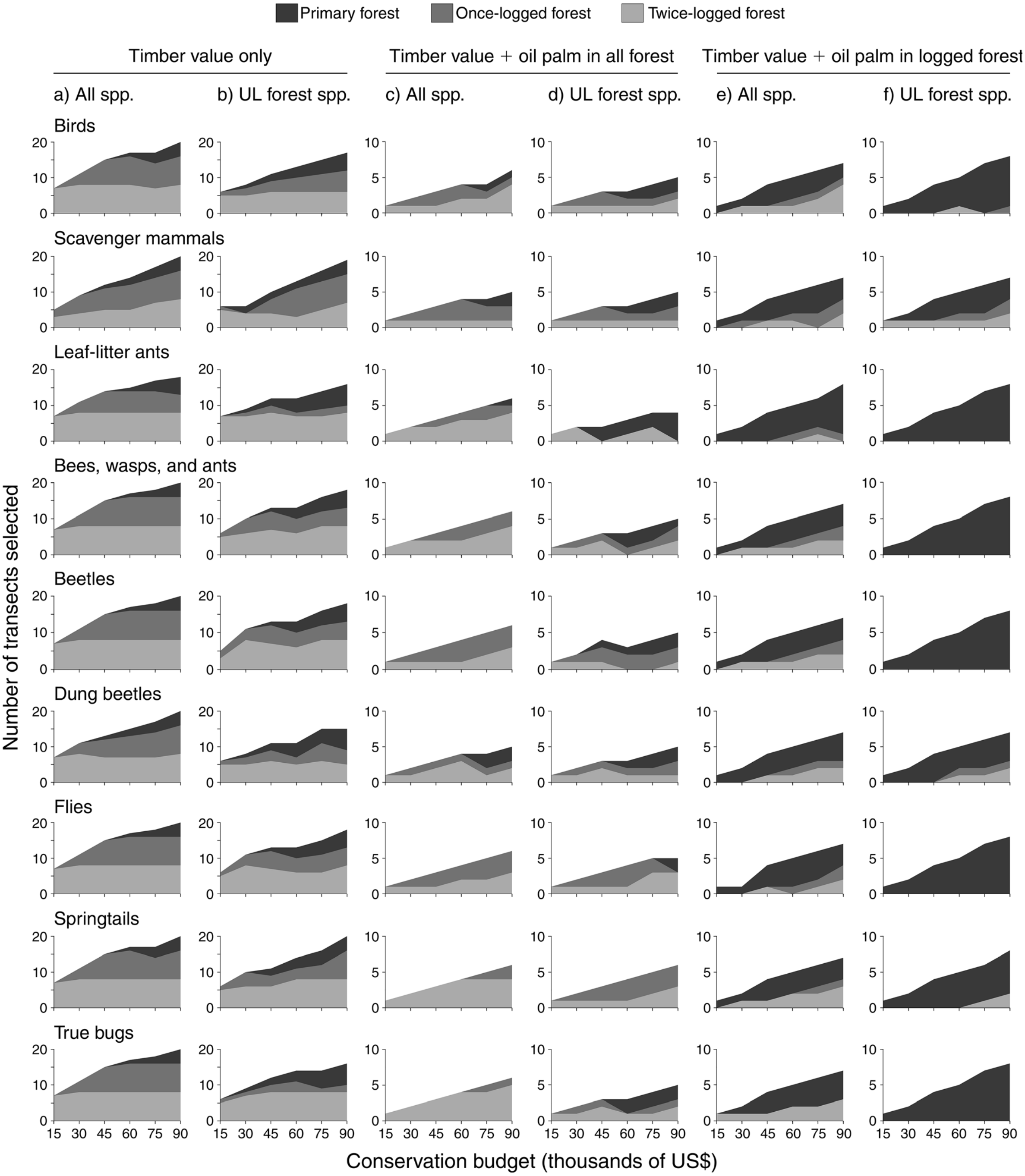

FIG. 5. For nine study taxa, the number of primary, once-logged, and twice-logged transects selected by RSW2 (conservation decision-making software [Arponen et al. 2005]) at conservation budgets rising in US$15 000 increments from US$15 000 to US$90 000. Selections are made under three scenarios of land-use 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; 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, US$10 460; once-logged, US$4000; twice-logged, US$2010; and oil palm, US$11 240 (values are in 2009 US$ and extracted from Fisher et al. [2011*a, b*]). Under each land-use scenario there are two metrics of biodiversity output: panels (a, c, e) maximizing total species coverage (all spp.; i.e., all species are weighted equally in their conservation importance) and panels (b, d, f) maximizing the coverage of species that were found in primary forest (unlogged [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).

Table 4. Number of significant correlations among nine taxa using four methods of determining biodiversity value.

Method of determining biodiversity value	Forest only	Forest and oil palm
Species richness	4	10
Species composition	**14**	**32**
Primary forest species richness	**13**	**23**
RSW2		
Maximizing species richness		
Timber only	9	-
Timber and oil palm	4	-
Timber and oil palm in logged forest	1	-
Maximizing primary forest species richness		
Timber only	6	-
Timber and oil palm	4	-
Timber and oil palm in logged forest	**22**	-

Notes: RSW2 (conservation decision-making software [Arponen et al. 2005]) 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 logging and for the combined impacts of logging and oil palm. 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.

scenarios underscore that logged forests harbor sufficient primary-forest species to warrant frequent selection.

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

To identify which of our nine taxonomic groups are the most effective indicators of the biological impacts of logging in isolation (Appendix E) and logging plus conversion to oil palm (Appendix F), 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 (logging only) 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 the RSW2 selection to maximize the richness of primary forest species when landscapes are threatened by timber extraction plus oil palm in logged forest showed a high number of significant correlations (Table 4). Overall, significant correlations were more frequent in analyses including oil palm transects (Table 4), probably reflecting the consistently severe impacts of forest conversion to oil palm across taxa.

Focusing on congruence among taxa in their patterns of response to logging (Fig. 6a, c, e), most taxa were good predictors of responses in other taxa. Regardless of metric, birds, leaf-litter ants, beetles, Hymenoptera, flies, and true bugs were strong predictors. However, scavenging mammals gave little indication of species composition and richness of other primary forest species (Fig. 6a, c), while responses of dung beetles poorly predicted for the former (Fig. 6a) and responses of springtails the latter (Fig. 6c) of these metrics. Focusing on congruence among taxa in their patterns of response to logging and oil palm (Fig. 6b, d), birds, leaf-litter ants, beetles, dung beetles, aerial Hymenoptera, flies, and true bugs were consistently good predictors of responses in other taxa. Again, scavenging mammals always poorly predicted other taxa, and springtails poorly predicted the richness of primary forest species of other taxa (Fig. 6d).

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 et al. 2008, Wilson et al. 2010, Fisher et al. 2011*b*). By complementing conventional biodiversity censuses with DNA metabarcoding (Ji et al. 2013), we were able to address this question across >2300 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).

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 vs. primary forest species) and on the precise make-up of threats, but in most cases, there is an important role for logged tropical forests (see also Wilson et al. 2010, Fisher et al. 2011*b*, Ji et al. 2013). We also found high levels of cross-taxon congruence in responses to logging and agricultural

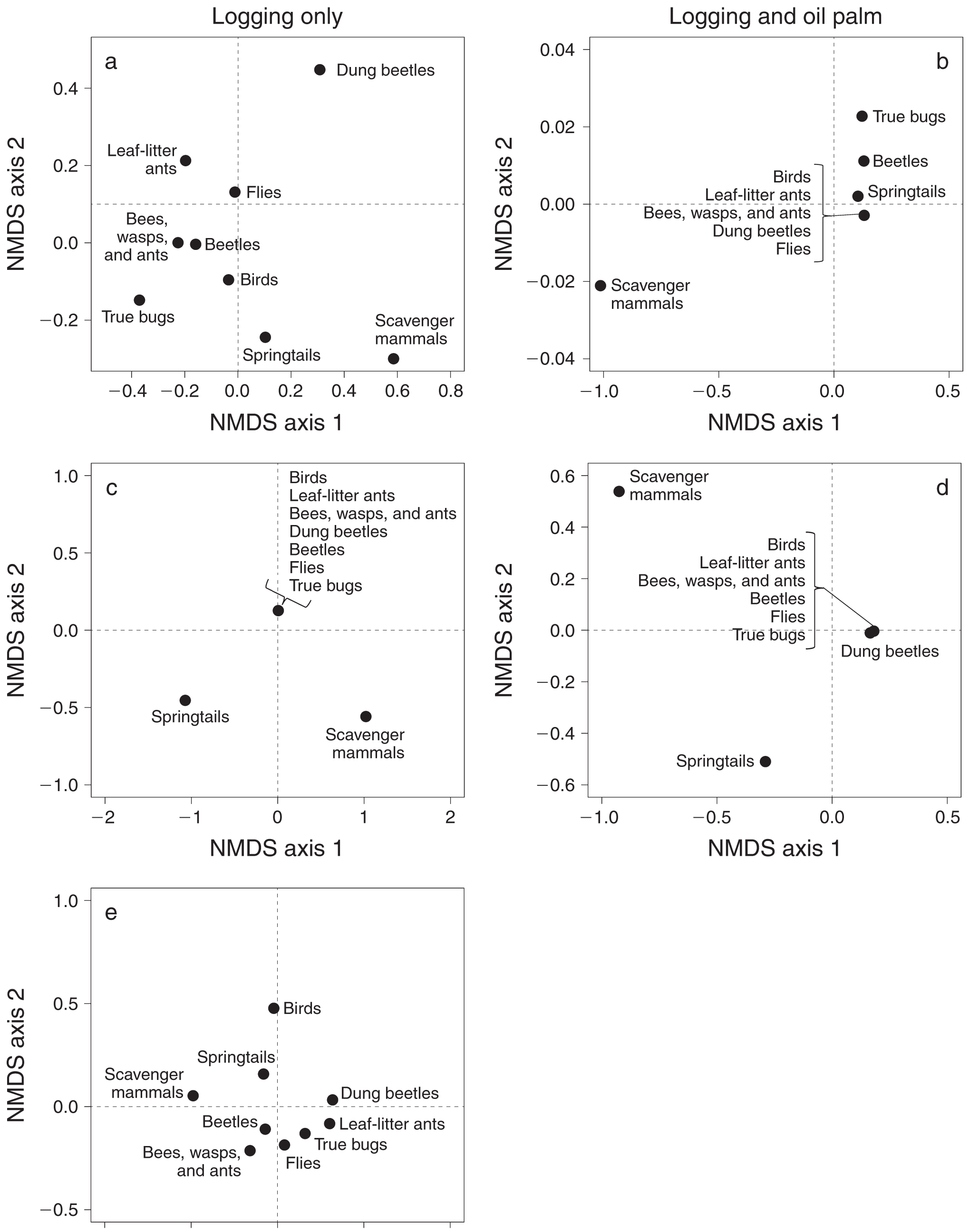

FIG. 6. NMDS plots of congruence in responses among taxa for methods of determining the biological impacts of land-use change that yielded significant correlations in over a third (>12 of 36) of comparisons (see Table 4). Congruence is shown for analyses that incorporate both logging and oil palm impacts, and for logging impacts only. (a, b) Species composition, (c, d) richness of primary forest species, (e) 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. Taxa with similar responses concentrate toward the center of the NMDS 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. See Fig. 5 for description of RSW2.

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 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), 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 pantropical disturbance that can cause severe residual damage to forest structure as falling trunks and canopies crush remaining trees and logging roads and skid trails bisect the forest (Pinard and 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 thus likely maintained by an influx of generalist species of low conservation importance and a concomitant reduction in 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. [2012*c*]), 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 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 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. (2011*b*) 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 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 concessions can play an important role in global conservation strategies for a wide range of taxa.

Our results also reveal the impact of early reentry logging, which is increasing across the tropics (e.g., Edwards et al. 2011*b*). 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-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 appear comparatively minimal across multiple taxa.

Oil palm plantations continue to expand rapidly in Southeast Asia and increasingly across the tropics (Fitzherbert et al. 2008). Conversion of primary and logged forest to oil palm creates a homogeneous canopy structure, open understory, and markedly altered microclimate (Luskin and Potts 2011), and drives 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 commonly 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 metabarcoding in conservation research

Arthropods may represent over 90% of rain forest fauna (May 2010, Basset et al. 2012), but the effects of land-use change and different forest management strategies on many arthropod taxa represent 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 data set, 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 across the tropics.

By using DNA metabarcoding we were able to address this shortcoming and evaluate the 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 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 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 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). While we did not investigate these 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. 2011*b*) 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 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. 2013*b*). 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. 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 data set of spatially separated oil palm sites for birds and dung beetles (Appendix C). 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 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.

We show that with logging but no threat from oil palm (scenario one; see also Fisher et al. [2011*b*] and 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 vs. previously logged forest is high, but the difference in biodiversity retained between the two habitats is relatively low. As a result, larger areas of 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.

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 two), 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 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 three), primary forest is more frequently selected even with low conservation budgets. By excluding the possibility of converting primary forest to oil palm (e.g., as per RSPO rules for oil palm expansion; see Edwards et al. [2012*b*]), 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: protecting primary forest would stop logging, whereas protecting logged forest would prevent conversion to oil palm. Whilst purchasing primary forest may thus appear the most cost-effective option in scenario three, 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. 2011*a*), 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. 2011*b*). 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+, see 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 importance of clearly outlining conservation objectives when evaluating land-use change impacts.

Our planning analyses ignore the element of scale in species' extinction risks. Consequently, our result might change if only a small, isolated patch of primary forest could be conserved, which would ultimately lose species due to fragmentation and edge effects (Didham et al. 1998, Laurance et al. 2002, 2011, Benedick et al. 2006, 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 overvalued the potential for logged forests to conserve biodiversity if the large network of logging roads and skid trails created to remove 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). Although there is no evidence that logged forests in Indonesian Borneo are illegally cleared more frequently than are protected areas (Gaveau et al. 2013), the possibility of clearance or increased hunting pressure represent important considerations in the design and governance of conservation networks, and appropriate mitigation measures should be identified during the reserve planning phase.

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, 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 nonspatial 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. 2011*b*, 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 generalizable. Moreover, where different taxa share similar responses, future survey and research costs can by 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 overemphasize 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 the first study to identify indicator taxonomic groups for the impacts of logging. Extrapolations based on existing findings from the 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).

Scavenging 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). Patterns for scavenging mammals might also be expected to differ from those for other taxa because (1) the sampling method may attract individuals over a very large area, hence trap location is a less accurate predictor of habitat preference than for other taxa (particularly those sampled passively), and (2) the comparatively low species richness of scavenger mammals reduces the potential for significant variation between logged forest and oil palm for species composition and primary forest species metrics. The identification of taxa that respond idiosyncratically to disturbance underscores 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 for logging impacts from this region might not apply elsewhere in the tropics, although a priori we would expect frequently sampled taxa, such as birds and dung beetles, to be important given that they have already revealed similar patterns to logging in other regions.

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 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 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. 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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Supplemental Material

Ecological Archives

Appendices A–F are available online: http://dx.doi.org/10.1890/14-0010.1.sm