

# Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia

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## Keywords

Biodiversity conservation; birds; Borneo; cost-effectiveness; dung beetles; forest degradation; logging.

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## Received

20 April 2011

## Accepted

27 July 2011

## Editor

Edward Webb

doi: 10.1111/j.1755-263X.2011.00198.x

## Abstract

The Sundaland Biodiversity Hotspot of Southeast Asia is widely regarded as one of the most imperiled biodiversity hotspots due to high degrees of endemism coupled with extensive logging and forest conversion to oil palm. The large financial returns to these activities have made it difficult to conserve much of the region's lowland primary forest, suggesting a large trade-off between economic interests and biodiversity conservation. Here, we provide an empirical examination of the magnitude of this trade-off in Borneo. By incorporating both financial values and biodiversity responses across logging regimes, we show that selectively logged forests represent a surprisingly low-cost option for conserving high levels of biodiversity. In our study, the standing value of timber dropped from ~\$10,460 ha<sup>-1</sup> to ~\$2,010 ha<sup>-1</sup> after two logging rotations, yet these forests retained over 75% of bird and dung beetle species found in primary unlogged forest. We suggest that the conservation of selectively logged forests represents a highly cost-efficient opportunity to enlarge existing protected areas, improve connectivity between them, and to create new, large protected areas.

## Introduction

Four global biodiversity hotspots encompass Southeast Asia (Myers *et al.* 2000). The Sundaland Hotspot, home to ~5% of the world's endemic plants and ~3% of endemic vertebrates as defined in Myers *et al.* (2000), is widely recognized as one of the most imperiled hotspots in the world due to high levels of endemism coupled with extensive and accelerating deforestation (Myers *et al.* 2000; Brooks *et al.* 2002). Within this hotspot, historic lowland forest cover has been reduced by >70% (Fisher *et al.* 2011), and annual deforestation rates for Malaysia and Indonesia have increased by 8% and 18%, respectively, from the 1990–2000 period to the 2000–2005 period. The major drivers of forest cover

change include the high timber value and yield of the region's forests (Fisher *et al.* 2011), as well as agricultural expansion for lucrative crops, especially oil palm (Sodhi *et al.* 2004; Koh & Wilcove 2008). The large financial returns to logging and oil palm create a sizable trade-off between financial profits and the creation of protected areas in lowland primary forest (Butler *et al.* 2009; Fisher *et al.* 2011). These high opportunity costs have made it difficult to conserve much of the lowland primary forests of Southeast Asia. For example, only 4% and 6% of the primary lowland forests in Malaysia and Indonesia, respectively, are fully protected (IUCN categories I–IV) (ITTO 2005).

Previous studies have shown that selectively logged forests, including those that have been intensively logged,

retain a large fraction of their biodiversity (Africa: Owiunji & Plumptre 1998; Sekercioglu 2002, South America: Mason 1996; Peters *et al.* 2006, and South-east Asia: Cannon *et al.* 1998; Berry *et al.* 2010; Edwards *et al.* 2011). What is needed is an improved understanding of how such production forests fit into conservation agendas both ecologically and financially (Shogren *et al.* 1999; Venter *et al.* 2009; Wilson *et al.* 2010). Understanding the actual trade-offs between biodiversity conservation and financial returns from logging is critical for developing effective conservation strategies. However, in order to quantify this trade-off, one needs accurate, detailed information on both biodiversity and the profitability of forest conversion from the same area.

Here, we look at the financial profits from logging lowland *Dipterocarpaceae* forests in the Sundaland region and relate them to biodiversity losses associated with logging. We calculate the standing timber values for unlogged, once-logged, and twice-logged forests in Sabah, Malaysian Borneo, using data derived from >300,000 ha of logging concessions over the past 40 years, as well as recent cost and auction-price data.

Our biodiversity data come from these same forests and include birds and dung beetles, which have been identified as two of the most cost-effective taxa to sample, as well as being good indicators of broader biodiversity trends (Gardner *et al.* 2008; Howard *et al.* 1998).

Taken together, these biodiversity and financial datasets give us an opportunity to provide an empirical analysis of the trade-offs between human modification of a landscape and biodiversity (see Daily *et al.* 2003; Polasky *et al.* 2008 for other examples). In doing so, it allows us to explore the role of costs in identifying efficient conservation agendas (Naidoo & Ricketts 2006; Wilson *et al.* 2010). Efficiency is an important goal for conservation, given the increasing isolation of protected areas (Defries *et al.* 2005), increasing habitat loss (Millennium Assessment 2005), and limited conservation funding (Balmford *et al.* 2003). Here, we show that conserving selectively logged forests is a cost-effective way to enlarge or connect existing protected areas in Southeast Asia. Logged forests also provide a large gain/low cost opportunity for creating new conservation areas in their own right. Since production forests (for timber) represent roughly 50% of Malaysian and Indonesian forest cover (ITTO 2005), it is important to understand the financial costs and biodiversity benefits of these lands.

## Methods

We compiled timber data from the Yayasan Sabah Forest Management Area (YSFMA), where detailed prelogging

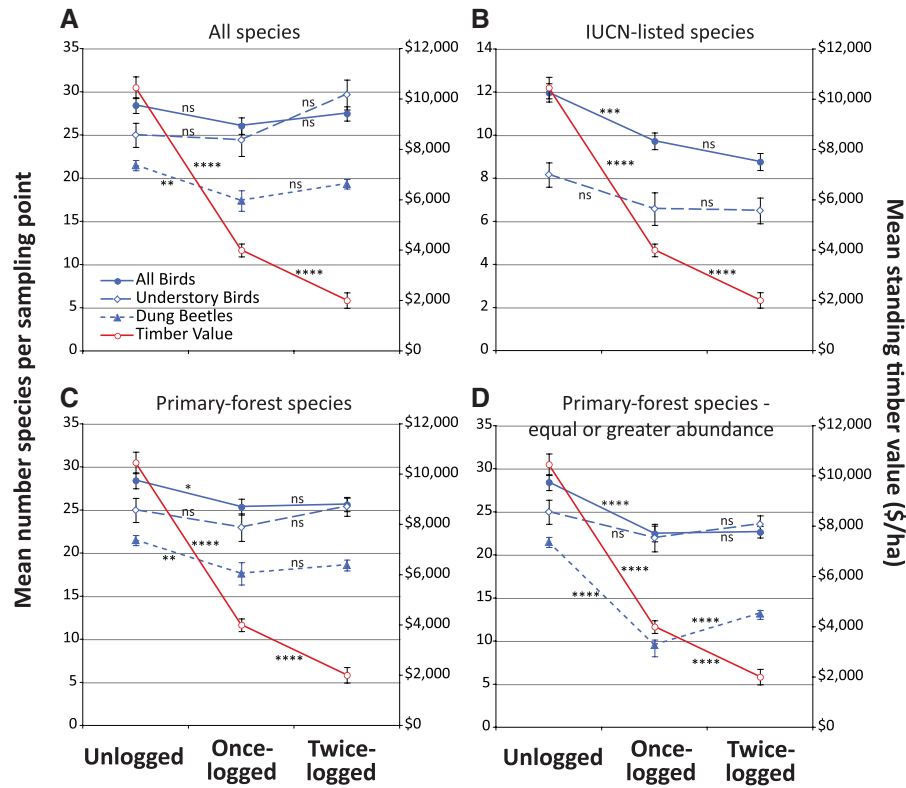
and postlogging censuses were carried out, and all trees marked for removal were noted and measured. The forests in this management area were first logged between 1970 and 1990, and commercially valuable trees >60 cm dbh were removed ("once-logged forests"). Many of these concessions were then logged again between 2000 and 2007, with commercially valuable trees >40 cm dbh removed ("twice-logged forests"). We collapsed the detailed logging records to 12 tree species and a general category (Table S1). Finally, some logging coupes (totaling 58,400 ha) were completely cleared for other uses between 1 and 7 years after a second logging rotation.

For each of our three forest states (unlogged, once-, and twice-logged), we calculated the gross timber values based on the standing stock and government auction prices over 3 years for our 13 species categories (see online methods; Tables S1 and S2). In order to get *net* standing timber values, we subtracted logging costs from the gross timber values, using itemized cost data per cubic meter removed for 16 costing categories based on conventional logging techniques in the area. Costs included prefalling inventories, taxes and royalties, bucking and felling, transporting logs, and other production costs (see Table S3).

Our bird data were divided into two categories based on the method of data collection: understory birds surveyed via mist net transects, and all birds surveyed via point counts.

Birds were sampled between 2007 and 2009 on sites separated by >2 km within each forest type (see Edwards *et al.* 2011 for site locations). All birds were sampled using unlimited-radius point counts. At four sites within each forest type, 12 count stations were established at 250 m intervals (144 stations in total), and each station was visited for 15 minutes on three consecutive days. Understory birds were sampled at six sites within each forest type, with 15 mist nets erected along each of two transects positioned 500–800 m apart at each site. Nets were opened from 06.00–12.00 on three consecutive days (see Edwards *et al.* 2011 for details; 9,720 mist net hours in total), and birds were ringed with a unique number to prevent resampling. We also restricted our analysis to species that are not defined as canopy specialists (14 species removed).

We used standardized pitfall traps baited with human dung to sample dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in 2009 (see Larsen and Forsyth 2005; Edwards *et al.* 2011;). At each of three sites within each forest category, 10 traps were spaced at 100 m intervals (90 traps in total) and traps were collected every 24 hours for 4 days and were rebaited after 2 days.



**Figure 1** Changes in standing timber value and species richness for all birds, understory birds, and dung beetles across unlogged (primary), once-logged, and twice-logged lowland forests. The left-hand y-axis corresponds to mean number of species per sampling unit and the right-hand y-axis corresponds to mean standing timber value per hectare in dollars (in 2009 U.S. dollars). Error bars equal one standard error (ns =  $P > 0.05$ ;

\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; \*\*\*\* =  $P < 0.0001$ ). (a) Changes in timber value and species richness. (b) Changes timber value and Red-Listed species (no dung beetles). (c) Changes in timber value and primary-forest species. (d) Changes in timber value and primary-forest species that remain at similar or greater abundances.

We used General Linear Models in GLMStat v. 5.7.7 (Ken Beath Publisher, <http://www.ozemail.com.au/~kjbeath/glmstat.html>) to compare timber values and biodiversity metrics at our minimum sampling units (coupes, point counts, mist nets and pitfalls) between unlogged and once-logged forest and between once-logged and twice-logged forest. In all cases, residuals were normally distributed and homoscedastic. We also used GLMStat v. 5.7.7 to test the effect that distance from primary forest edge had on richness and abundance across our four biodiversity metrics for each of our species categories (all birds, understory birds and dung beetles) in logged forests.

## Results

After the first logging rotation (mean extraction  $\sim 113 \pm 11 \text{ m}^3 \text{ ha}^{-1}$ ), the net value of the standing timber drops significantly from  $\sim \$10,460 \text{ ha}^{-1}$  to  $\sim \$4,000 \text{ ha}^{-1}$  (Figure 1, red line; GLM:  $F_{1,38} = 139.7, P < 0.0001$ ).

After the second cut, with a mean extraction of  $\sim 31 \pm 5 \text{ m}^3 \text{ ha}^{-1}$ , the standing value of the remaining timber again drops significantly to  $\sim \$2,010 \text{ ha}^{-1}$  (Figure 1;  $F_{1,24} = 23.2, P < 0.0001$ ). Thus, standing value of the twice-logged forest in our sample is 81% lower than unlogged forest. While drastic drops in potential financial returns across logging rotations are expected, they contrast markedly with the responses of birds and dung beetles to logging.

Logged forests retained much of their biodiversity, as illustrated in four related ways. First, the mean number of bird species recorded per sampling unit shows no significant changes across unlogged, once-logged, and twice-logged forests (Figure 1a; all  $P > 0.05$ ). The mean number of dung beetles recorded per sampling unit does show a significant decline between the unlogged and once-logged forests ( $F_{1,58} = 9.6, P = 0.003$ ), but no further decline between once-logged and twice-logged forests ( $P > 0.1$ ).

Second, focusing on the total number of bird species on the IUCN Red List of endangered species that were

recorded in our unlogged, once-logged, and twice-logged forests, we find a statistically significant drop in species richness of Red-listed birds from unlogged forests to once-logged forests for “all birds” ( $F_{1,94} = 15.3, P = 0.0002$ ), but no further change from once- to twice-logged forest ( $P = 0.09$ ; Figure 1b). Also there was no significant change in Red-listed understory birds across logging regimes (both  $P > 0.1$ ). (Dung beetles have yet to be assessed by the IUCN.) See Table 1 for a list of Red-listed birds found in each forest category.

Third, we looked at which species present in unlogged forest (herein termed “primary-forest species”) remain in the once- and twice-logged forests, since primary-forest species are the ones most likely to be imperiled by ongoing logging. (Using only total species richness for logged forests could mask losses of sensitive species due to an influx of species associated with degraded or early successional habitats). We see a statistically significant decline in primary-forest species between unlogged and once-logged forests for “all birds” sampled via point counts ( $F_{1,94} = 5.6, P = 0.02$ ) and for dung beetles ( $F_{1,58} = 7.4, P = 0.009$ ), but no significant decline for understory birds sampled via mist nets ( $P > 0.3$ ; Figure 1c). Further, there are no significant differences for primary-forest birds or dung beetles between once- and twice-logged forests (all  $P > 0.2$ ).

Fourth, because simple presence/absence measures can mask declines in abundance of primary-forest species within the logged forests, we also looked at primary-forest species that are found in equal or greater densities in logged forests (Figure 1d). This revealed a significant decline after a first logging rotation for “all birds” ( $F_{1,94} = 21.7, P < 0.0001$ ), but no further loss with a second logging rotation ( $P > 0.8$ ). There was no significant change in understory birds across logging rotations (both  $P > 0.1$ ). For dung beetles, there was a significant decline between the unlogged and once-logged forest ( $F_{1,58} = 189.6, P < 0.0001$ ), but then a significant increase in the number of species found at greater or equal abundances after a second logging rotation ( $F_{1,58} = 23.8, P < 0.0001$ ).

We tested to see if the high level of species retention in these logged forests was a function of distance from the primary unlogged forest, which would be indicative of either a rescue effect (populations in logged forest sustained by emigration from unlogged forest) or a spillover effect (individual birds and beetles wandering out of the unlogged forest). Even though our logged sites were at varying distances from unlogged forests (1.1–21.3 km), we found no statistically significant effect of distance on species richness or abundance of individuals in any of our four metrics (Table S4, Figure S1). Moreover, many bird species in the logged forests showed evidence of lo-

**Table 1** Total number of individuals of IUCN Red-listed bird species recorded in each forest type—unlogged (UL), once-logged (1L), and twice-logged (2L)—using point counts and mist netting. Species in **bold** are endemic to Borneo

Species	IUCN <sup>a</sup>	Point counts			Mist nets		
		UL	1L	2L	UL	1L	2L
<i>Arborophila charltonii</i>	NT	10	14	21			
<i>Rollulus roulroul</i>	NT	1	0	0			
<i>Lophura ignita</i>	NT	0	2	3			
<i>Argusianus argus</i>	NT	36	13	6			
<i>Ichthyophaga humilis</i>	NT	1	0	0			
<i>Spizaetus nanus</i>	VU	1	1	1			
<i>Treron capellei</i>	VU	3	0	0			
<i>Psittinus cyanurus</i>	NT	2	0	13			
<i>Psittacula longicauda</i>	NT	1	0	0			
<i>Cuculus vagans</i>	NT	4	5	0	1	0	0
<b><i>Carpococcyx radiatus</i></b>	<b>NT</b>	<b>2</b>	<b>2</b>	<b>0</b>			
<i>Centropus rectunguis</i>	VU	15	9	15			
<i>Batrachostomus auritus</i>	NT	1	0	0			
<i>Harpactes kasumba</i>	NT	10	5	0			
<i>Harpactes diardii</i>	NT	22	17	6	0	1	2
<i>Harpactes orrhophaeus</i>	NT	1	0	0			
<i>Harpactes duvaucelii</i>	NT	13	3	12	0	0	3
<i>Actenoides concretus</i>	NT				5	0	1
<i>Alcedo euryzona</i>	VU				0	6	0
<i>Anthraceros malayanus</i>	NT	14	7	16			
<i>Buceros rhinoceros</i>	NT	42	24	11			
<i>Rhinoplax vigil</i>	NT	24	8	3			
<i>Aceros comatus</i>	NT	7	2	0			
<i>Megalaima mystacophanos</i>	NT	19	17	31			
<i>Megalaima henrici</i>	NT	18	2	1			
<i>Indicator archipelagicus</i>	NT				1	0	0
<i>Dinopium rafflesii</i>	NT	0	0	1			
<i>Meiglyptes tukki</i>	NT	16	10	9	1	2	3
<i>Calyptomena viridis</i>	NT	3	4	3	5	0	1
<i>Eurylaimus ochromalus</i>	NT	54	45	42			
<i>Pitta caerulea</i>	NT	4	1	0			
<b><i>Pitta baudi</i></b>	<b>VU</b>	<b>16</b>	<b>11</b>	<b>7</b>	<b>5</b>	<b>3</b>	<b>2</b>
<b><i>Pitta ussheri</i></b>	<b>NT</b>	<b>21</b>	<b>19</b>	<b>29</b>	<b>2</b>	<b>2</b>	<b>3</b>
<i>Aegithina viridissima</i>	NT	25	43	38			
<b><i>Pityriasis gymnocephala</i></b>	<b>NT</b>	<b>7</b>	<b>9</b>	<b>1</b>			
<i>Pericrocotus igneus</i>	NT	7	2	1			
<i>Oriolus xanthonotus</i>	NT	17	37	35			
<i>Platylophus galericulatus</i>	NT	19	12	1			
<i>Platysmurus leucopterus</i>	NT	22	9	10			

<sup>a</sup>IUCN status.  
 NT = near threatened.  
 VU = vulnerable.

cal breeding, such as territory holding and forming family parties with juveniles (Edwards *et al.* 2011, see also Yap *et al.* 2007).

Our four metrics thus show that despite large-scale conventional logging, these forests provide an important habitat for forest-dwelling birds and dung beetles and for imperiled birds. At the same time, if we view financial

returns from logging as *indicative* of the opportunity cost of conservation for these forests, it is 60–80% cheaper to offset the financial gains from logged forests compared to unlogged forests. As a result, the cost of offsetting a single hectare of unlogged forest is equal to the cost of offsetting 2.5 and 5 ha of once-logged and twice-logged forest, respectively, while still retaining high levels of forest-dwelling and imperiled species (Figure 1).

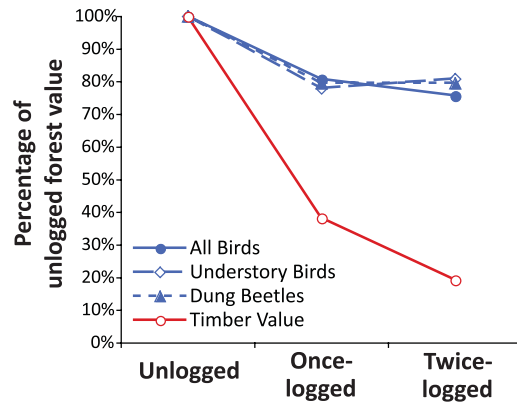
## Discussion

While previous research has explored the biodiversity impacts of logging in Southeast Asia, none has examined the financial gains of logging in relation to biodiversity losses within the same forests. This is primarily due to the difficulty in obtaining accurate and detailed logging records and biodiversity surveys from the same sites. The logging profits reported here for Borneo might be biased upwards due to the potential of declining marginal value of subsequently logged lands (e.g., timber companies may log the best lands first), as well as incremental cost increases as logging continues (e.g., transportation costs). However, the logging regime and the volume of wood extracted seem to be typical for lowland forests in Borneo (Marsh & Greer 1992; Curran *et al.* 2004), as well as across Southeast Asia in *Dipterocarpaceae*-dominated forests (Putz *et al.* 2001; Sist *et al.* 2003), and there is evidence to suggest a wider applicability of our financial analysis to other parts of Southeast Asia (Sheeran 2006).

Previous studies confirm that numerous species across diverse taxa persist in logged forests in Southeast Asia, including mammals, amphibians, ants, trees, and herbaceous plants (Cannon *et al.* 1998; Berry *et al.* 2010). Paralleling these studies is a suite of additional studies noting the critical importance of assessing the costs of conservation (Ando *et al.* 1998; Shogren *et al.* 1999; Balmford *et al.* 2003; Naidoo & Ricketts 2006).

By incorporating both financial values and biodiversity responses across logging rotations, we are able to show that the costs of conservation across unlogged, once-, and twice-logged forests vary more than the biodiversity benefits—that is, even twice-logged forests retain over 75% of species of understory birds ( $n = 68$  species), all birds ( $n = 140$  species), and dung beetles ( $n = 49$  species), while the standing value of timber drops by 81% (Figure 2). Due to this larger variation in costs compared to benefits, incorporating costs in a conservation agenda for this landscape is critical in order to efficiently allocate limited conservation funding (Ando *et al.* 1998).

Given their potential cost-effectiveness, logged forests represent an opportunity to increase connectivity between protected areas and to enlarge existing parks, two goals that are becoming increasingly urgent in Southeast



**Figure 2** Percentage changes in number of species from unlogged (primary) forests and standing timber values across unlogged, once-, and twice-logged forests. Values from unlogged (primary) forests are taken as the baseline, i.e., 100%.

Asia as existing parks are illegally degraded or become increasingly isolated by conversion of adjacent areas to oil palm plantations and other agricultural lands (Defries *et al.* 2005; Sodhi *et al.* 2010). Logged forests also represent important targets for conservation in their own right given the large biodiversity benefits potentially delivered at much lower cost.

We studied how a change in the “state” of the forest affects biodiversity, but we did not address how the area of extent of these states affects our results. In our study area, ~90% of the primary forests have been logged. Our analysis of distance effects suggests that for forest bird and dung beetle communities at the scale of our study, the biological value of logged forests is not simply due to rescue effects or spillover effects (Table S4). However, this does not eliminate the possibility that source-sink dynamics could be important for particular species.

Species that are either restricted to unlogged forest or decline markedly in abundance following logging pose an especially difficult challenge for conservationists in Southeast Asia. At our level of sampling effort, four bird species (*Treron capellei*, *Harpactes oreskios*, *Pitta guajana*, and *Aethopyga temminckii*) and one dung beetle (*Onthophagus sarawacus*) showed statistically significant declines following logging (Edwards *et al.* 2011). In the case of birds, there were a number of other species that were absent in logged forest; these were either species that are inherently rare but typically restricted to unlogged forests (e.g., *Indicator archipelagicus*; Lambert 1992), or species that preferred agricultural landscapes and are therefore rare in any forest type (e.g., *Copsychus saularis*). Additionally, all three of our metrics involving dung beetles (Figures 1a, c, and d) show significant declines after a first logging rotation, although these declines do not continue into the

second rotation. Protecting such species must be a priority; however, the opportunity costs of conserving them, especially if they require large tracts of unlogged forest, could be enormous (Fisher *et al.* 2011).

Enlarging existing protected areas by acquiring logged forests can ensure larger, more viable populations of forest-dwelling species and reduce deleterious edge effects. Moreover, well-protected logged forests are likely to recover over time and therefore represent not only important current habitat for species, but also future habitat for species that require mature forests and cannot tolerate logged forests. For such species, maintaining connectivity between logged forests and unlogged forests is likely to be important in order to permit eventual dispersal into the recovering logged forest.

Our analysis ignores a critical driver of forest cover change in Southeast Asia: the expansion of oil palm plantations (Koh & Wilcove 2008; Koh & Ghazoul 2010). Recent analysis suggests that over 55% of oil palm expansion in Malaysia and Indonesia between 1990–2005 came at the expense of forests (Koh & Wilcove 2008), and over 90% of the total agricultural expansion in the 1980s and 1990s in this region came at the expense of forests (Gibbs *et al.* 2010). Oil palm alone is a remarkably lucrative crop, with plantations showing net profits over the lifetime of a plantation up to \$10,000 ha<sup>-1</sup> (Butler *et al.* 2009).

The threat of oil palm plantations to forested land affects conservation planning in complicated ways. First, if both selectively logged and unlogged forests are equally suitable for oil palm plantations then the inclusion of their foregone oil palm profits changes only the magnitude of opportunity costs, not the relative difference between returns to conversion of unlogged, once-, and twice-logged forests. This is because the opportunity cost of foregoing oil palm agriculture for conservation can be equally applied across unlogged, once-logged, and twice-logged forests due to the equal suitability of the land for plantations. However, the biodiversity metrics would change drastically with the inclusion of oil palm landscapes as several studies have shown catastrophic losses of species across multiple taxa when forests are converted to oil palm (Fitzherbert *et al.* 2008; Edwards *et al.* 2010). Thus, while conserving unlogged forests is critically important, protecting logged forests from becoming oil-palm plantations emerges as a critical and cost-effective conservation strategy for stemming large losses of biodiversity.

In cases where both logged and unlogged forests are unlikely candidates for agricultural expansion, one could make the argument that conservation funds need not be spent on these lands, because they are already delivering biodiversity benefits. However, if the lack of threat is a function of the sociopolitical system, rather than biophysical factors (e.g., zoning restrictions or the price point

for crude palm oil as opposed to slope or soil conditions), then the threat may be only temporarily abated. In such cases, the call for actively pursuing the protection of logged forests is warranted. The difficult choice materializes when, in light of limited conservation funds, one must decide between protecting unlogged forests without agricultural opportunity costs and twice-logged forests with agricultural opportunity costs. In such cases, the financial cost (per hectare) of protection could be similar for both landscapes (see Fisher *et al.* 2011), but the biodiversity benefits would favor unlogged forests (assuming no fundamental differences in the matrices surrounding these areas). This is a situation in which spatial modeling of the full opportunity costs of conservation is critical, and also one in which an understanding of the carbon profiles is necessary, especially in the context of deploying funds like REDD+.

Despite the significant obstacle to conservation that oil palm plantations represent, the area under logging concessions still dwarfs that under oil palm. For example, Indonesia, the world's biggest oil palm producer, has ~9.7 million ha under oil palm but ~46 million ha of natural forest in logging concessions (ITTO 2005; Koh & Ghazoul 2010), suggesting there are many opportunities for conservation efforts directed at logged forests that are not currently under threat of conversion to oil palm. However, given the potential future expansion of oil palm plantations and other land developments onto selectively logged lands, the fate of much of Southeast Asia's biodiversity may ultimately hinge on whether the conservation community can overcome the opportunity cost of oil palm (Butler *et al.* 2009) or can encourage the implementation of large-scale landscape planning in order to reliably protect areas critical for biodiversity (Venter *et al.* 2009).

The bird and dung beetle losses that occur during logging are not trivial, and our results should not be used to suggest that, by logging primary forests, governments could gain huge financial profits at little cost to biodiversity. The logging of primary forests precipitates a significant loss of biodiversity, as shown in all four of our indicators. Beyond biodiversity, Southeast Asia's lowland *dipterocarp* forests provide numerous ecosystem services, including carbon storage, regulation of river flows and sedimentation, and a variety of aesthetic and cultural benefits. In some cases, these ecosystem services have quantifiable economic values, such that the logging of primary forests will predicate (sometimes large) social costs. We did not calculate the trade-off curves for these wider ecosystem services with respect to logging. However, new and future regulation and market-based incentives for forest conservation (e.g., payments for ecosystem services and REDD+) will have to incorporate these

wider social values (including foregone benefits to local, forest-dependent communities) for a fuller understanding of conservation trade-offs (Ghazoul *et al.* 2010). Finally, we did not assess the consequences for ecosystem processes stemming from species loss and population declines due to logging which, in turn, could affect some of these wider ecosystem service values.

Notwithstanding these caveats, our results clearly show that under a typical logging regime in Borneo—and probably across wider areas of Sundaland—there is a non-linear relationship between biodiversity and financial returns, such that there is not a direct trade-off between the two. Therefore, where economic constraints make it difficult to protect more unlogged forests, the protection of selectively logged forests to connect or expand existing protected areas or as stand-alone reserves, provides a cost-effective way to conserve much of the biodiversity of Southeast Asia's rapidly disappearing lowland forests.

## Acknowledgments

We would like to thank Ian Bateman, Brett Day, Lyndon Estes, Xingli Giam, Lian Pin Koh, Sian Morse-Jones, Kenneth Mulder, Navjot Sodhi, and the Dronogos Group at Princeton University for valuable discussions related to this manuscript. We also thank Yayasan Sabah, Danum Valley Management Committee, Sabah Parks, the State Secretary, Sabah Chief Minister's Departments and the Economic Planning Unit of the Prime Minister's Department for permission to conduct research. B.F. was supported by a STEP fellowship at Princeton University, D.P.E. by a Leverhulme Trust research grant, and T.H.L. by a fellowship from Kathryn Fuller Science for Nature Fund, WWF-US. Additional support was provided by a grant from the High Meadows Foundation to D.S.W.

## Supporting Information

Additional Supporting Information may be found in the online version of this article, including Supplementary Methods and References. Methods and References.

**Table S1:** Timber species and volumes extracted from ~310,000 ha of *Dipt.* dominated lowland rainforest in Sabah, Malaysia

**Table S2:** Auction prices for species felled in logging records

**Table S3:** Cost estimates for conventional logging practices in *Dipt.* dominated lowland rainforests—Malaysia

**Table S4:** Results for testing the role of distance from primary forests for our biodiversity results

**Figure S1:** The only model for testing distance effect with  $P$ -value  $< 0.1$  was understory birds for total species

richness ( $R^2 = 0.26$ ,  $F_{1,10} = 3.6$ ,  $P = 0.87$ ). This suggested a positive relationship with distance, i.e., not supportive of rescue effects.  $Y$ -axis is total abundance of understory birds. Filled markers represent once-logged forests, and open markers represent twice-logged forests.

### Supplementary References

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