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Biofuel Plantations on Forested Lands: Double Jeopardy for Biodiversity and Climate

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Abstract: *The growing demand for biofuels is promoting the expansion of a number of agricultural commodities, including oil palm (*Elaeis guineensis*). Oil-palm plantations cover over 13 million ha, primarily in Southeast Asia, where they have directly or indirectly replaced tropical rainforest. We explored the impact of the spread of oil-palm plantations on greenhouse gas emission and biodiversity. We assessed changes in carbon stocks with changing land use and compared this with the amount of fossil-fuel carbon emission avoided through its replacement by biofuel carbon. We estimated it would take between 75 and 93 years for the carbon emissions saved through use of biofuel to compensate for the carbon lost through forest conversion, depending on how the forest was cleared. If the original habitat was peatland, carbon balance would take more than 600 years. Conversely, planting oil palms on degraded grassland would lead to a net removal of carbon within 10 years. These estimates have associated uncertainty, but their magnitude and relative proportions seem credible. We carried out a meta-analysis of published faunal studies that compared forest with oil palm. We found that plantations supported species-poor communities containing few forest species. Because no published data on flora were available, we present results from our sampling of plants in oil palm and forest plots in Indonesia. Although the species richness of pteridophytes was higher in plantations, they held few forest species. Trees, lianas, epiphytic orchids, and indigenous palms were wholly absent from oil-palm plantations. The majority of individual plants and animals in oil-palm plantations belonged to a small number of generalist species of low conservation concern. As countries strive to meet obligations to reduce carbon emissions under one international agreement (Kyoto Protocol), they may not only fail to meet their obligations under another (Convention on Biological Diversity) but may actually hasten global climate change. Reducing deforestation is likely to represent a more effective climate-change mitigation strategy than converting forest for biofuel production, and it may help nations meet their international commitments to reduce biodiversity loss.*

Keywords: biofuel plantation, compensation point, oil-palm plantation biodiversity, oil-palm plantation emission, palm-oil production impact, peatland conversion, plantation development

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Plantaciones de Biocombustible en Terrenos Boscosos: Doble Peligro para la Biodiversidad y el Clima

Resumen: *La creciente demanda de biocombustibles está promoviendo la expansión de activos agrícolas, incluyendo la palma de aceite (*Elaeis guineensis*). Las plantaciones de palma de aceite cubren más de 13 millones de ha, principalmente en el sureste de Asia, donde han reemplazado a bosques tropicales directa o indirectamente. Exploramos el impacto de la expansión de las plantaciones de palma de aceite sobre la emisión de gases de invernadero y la biodiversidad. Evaluamos los cambios en las reservas de carbono con el cambio de uso de suelo y comparamos esto con la cantidad de emisiones de carbono de combustibles fósiles que se evitarían con su reemplazo por carbono de biocombustibles. Estimamos que pasarían entre 75 y 93 años para que las emisiones de carbono ahorradas por el uso de biocombustible compensen el carbono perdido por la conversión de bosques, dependiendo de cómo fue removido el bosque. Si el hábitat original era turbera, el balance de carbono tardaría más de 600 años, Por el contrario, sembrando las plantaciones de palma en pastizales degradados llevaría a una remoción de carbono en 10 años. Estas estimaciones están asociadas con incertidumbre, pero su magnitud y proporciones relativas parecen creíbles. Realizamos un meta análisis de los estudios de fauna publicados que comparan bosques con palma de aceite. Encontramos que las plantaciones soportan comunidades de baja riqueza con pocas especies de bosque. Debido a que no se dispuso de datos de flora publicados, presentamos los resultados de nuestro muestreo de plantas en parcelas de palma de aceite y de bosque en Indonesia. Aunque la riqueza de especies de pteridofitas fue mayor en las plantaciones, contenían pocas especies de bosque. Árboles, lianas, orquídeas epífitas y palmas nativas estuvieron totalmente ausentes de las plantaciones de palma de aceite. La mayoría de plantas y animales individuales en las plantaciones de palma de aceite pertenecían a un pequeño número de especies generalistas de bajo interés para la conservación. A medida que los países pugnan por cumplir las obligaciones de reducción de emisiones de carbono en el marco de un acuerdo internacional (Protocolo de Kioto), no solo pueden fallar en cumplir sus obligaciones en el marco de otro (Convención de Diversidad Biológica) sino que incluso pueden acelerar el cambio climático. La reducción de la deforestación probablemente represente una estrategia más efectiva para la mitigación del cambio climático que la conversión de bosques para la producción de biocombustibles, y puede ayudar a que las naciones cumplan sus compromisos internacionales para la reducción de la pérdida de biodiversidad.*

Palabras Clave: biodiversidad en plantación de palma de aceite, conversión de turbera, desarrollo de plantación, emisión en plantación de palma de aceite, impacto de la producción de palma de aceite, plantación de biocombustible, punto de compensación

Introduction

Fossil fuels supply most of the energy requirements of industrialized nations, yet the greenhouse gas emissions that result threaten to seriously affect natural systems through human-induced climate change, which compromises livelihoods (Adger et al. 2003; Cotula et al. 2008), global security (CNA 2007), and biodiversity (Parmesan & Yohe 2003). Many countries have therefore set targets to reduce emissions (Royal Society 2008). Many countries have also ratified international agreements for the mitigation of human impacts on natural systems through both climate change (Kyoto Protocol) and biodiversity loss (Convention on Biological Diversity).

Biofuels derived from agricultural commodities may reduce our reliance on fossil fuels and mitigate anthropogenic carbon emissions. Nevertheless, agricultural intensification and expansion are principal drivers of habitat modification, environmental change, and biodiversity loss (Tilman et al. 2001; Geist & Lambin 2002). The demand for biofuel feedstock may drive agricultural expansion at the expense of native habitat and biodiversity (Righelato & Spracklen 2007; Koizumi & Ohga 2008).

Tropical forests contain more than half of the Earth's terrestrial species (Myers et al. 2000). Forests in Southeast Asia are among the richest in species, but are also the most threatened (Sodhi et al. 2004; Laurance 2007). Tropical forests also store around 46% of the world's living terrestrial carbon (Soepadmo 1993), and 25% of total net global carbon emissions may stem from deforestation (Skutsch et al. 2007). There is therefore an inherent contradiction in any strategy to clear tropical forest to grow crops for so-called carbon-neutral fuels.

The oil palm (*Elaeis guineensis*) is native to West Africa and has replaced soybean (*Glycine max*) as the world's most traded oilseed crop (Carter et al. 2007). Global production of palm oil has increased exponentially over the past 40 years. In 2006, 85% of the global palm-oil crop was produced in Indonesia (43%) and Malaysia (42%) (Food and Agriculture Organization 2007), countries whose combined annual tropical forest loss is around 2 million ha (Food and Agriculture Organization 2006). It is perhaps unsurprising that the main charge levied by environmental groups against the oil-palm industry relates to its contribution to deforestation (e.g., Brown & Jacobson 2005; Buckland 2005). Increasing global demand for biofuel (Coyle 2007) could promote a rapid expansion of oil-palm plantations (Koh & Wilcove 2007, 2008; Fitzherbert et al. 2008) in forest on mineral soils and in peatlands, which cover 27.1 million ha in Southeast Asia (Hooijer et al. 2006; Parish et al. 2007). Despite the attention given to both the impact of oil-palm production on biodiversity (Scharlemann & Laurance 2008) and its potential as a biofuel feedstock (Tan et al. 2007), full appreciation of the environmental costs of biofuel palm oil is lacking (Groom et al. 2008; Turner et al. 2008. Oil-palm research in context: identifying the need for biodiversity assessment. PLoS ONE DOI:10.1371/journal.pone.0001572). For example, Fargione et al. (2008) assessed the number of years required to repay the carbon debt from palm oil produced in former rainforest, but did not consider the uncertainties in their estimates of greenhouse gas emissions linked to different approaches to clearing of forest vegetation for plantations or the effects on biodiversity. The carbon balance of planting oil palms on secondary *Imperata* grassland, of which there are an estimated 8.5 million ha in Indonesia (Garrity et al. 1996), has also not been assessed.

We assessed the impacts of replacing tropical forest with oil-palm plantations on both carbon dioxide (CO_2) emissions and biodiversity. Despite the paucity of data available for such an analysis, we aimed to provide preliminary quantitative assessments with which to inform discussion of these issues and stimulate further research.

Methods

Estimating Greenhouse Gas Emissions

We used published figures to estimate the number of years an oil-palm plantation would have to produce biofuel to compensate, through avoidance of fossil-fuel emissions, for the CO_2 emissions produced by establishing the plantation in the first place. We considered plantation establishment on forest cleared by logging, forest cleared by burning, flooded peatland, and *Imperata cylindrica* grassland. For accurate assessments of changes in carbon stocks with changing land use, regional-average figures for vegetation carbon stocks in different land-use types are insufficient. Indonesia has the largest area of harvested oil palms (Food and Agriculture Organization 2007). Within Indonesia most plantations are concentrated in Sumatra and Kalimantan (Casson 2003; Fitzherbert et al. 2008). Time-averaged data on aboveground carbon stocks of forest, oil-palm plantation, and *Imperata* grassland from Jambi Province in Sumatra were therefore taken from Murdiyarso et al. (2002).

For plantation establishment on forest cleared by logging to calculate the compensation point, we divided the amount of carbon lost through forest conversion by the yearly amount of fossil-fuel carbon emission avoided through its replacement by biofuel carbon:

$$\frac{(C_f - C_{\text{op}})}{(12/44) * [\text{CO}_{2\text{eq,min-die}} - (f_{\text{cal}} * \text{CO}_{2\text{eq,bio-die-a}})] * \text{YLD}} \tag{1}$$

where C_f is the natural forest carbon stock; C_{op} is the oil-palm plantation carbon stock; $\text{CO}_{2\text{eq,min-die}}$ is the avoided CO_2 emission from mineral oil diesel based on estimated life-cycle emission; f_{cal} is the correction for difference in calorific value between palm oil and mineral oil diesel; $\text{CO}_{2\text{eq,bio-die-a}}$ is the added greenhouse gas emission from palm-oil production, transportation, mill effluent, and plantation soils. Multiplication by (12/44) converts CO_2 weight into carbon weight because the ratio between the molecular weights of C and CO_2 is $[12/(12 + 16 + 16)]$; and YLD is the yield of the oil-palm plantation (Table 1). Carbon emissions from forest cleared by logging were calculated using aboveground carbon stocks only.

Forest is often burned for plantation development, leading to emission of compounds such as methane that have greater greenhouse potency than CO_2 (Reijnders & Huijbregts 2008). To calculate the compensation point, we divided the amount of carbon lost through forest conversion and vegetation burning by the annual amount of fossil-fuel carbon emission avoided through replacement by biofuel carbon:

$$\frac{((C_f - C_{\text{op}}) + C_{\text{loss-soils}} + f_{\text{fire-agb}} * (C_f - C_{\text{op}}))}{(12/44) * (\text{CO}_{2\text{eq,min-die}} - (f_{cal} * \text{CO}_{2\text{eq,bio-die-b}})) * \text{YLD}} \tag{2}$$

where $C_{\text{loss-soils}}$ is the estimated greenhouse gas emission from mineral soils as a result of fires for land clearing; $f_{\text{fire-agb}}$ is the factor for additional emission of greenhouse gases other than CO_2 from burning of the aboveground vegetation; and $\text{CO}_{2\text{eq,bio-die-b}}$ is the added greenhouse gas emission from palm-oil production, transportation, and mill effluent (Table 1).

On peatland emission from decomposing organic matter by oxidation following drainage prior to planting is likely to exceed greenhouse gas emission from forest biomass (Germer & Sauerborn 2007). We assumed the entire stock of peat is decomposed over the life of repeated oil-palm production cycles. To calculate the compensation point, the amount of carbon lost through peatland conversion (on the basis of the average peat-soil carbon stock per hectare for Southeast Asian peatlands) was divided by the yearly amount of fossil-fuel carbon emission avoided through replacement by biofuel carbon with the following formula:

$$\frac{C_{\text{peat-seasia}} * 1/A_{\text{peat-seasia}}}{(12/44) * (\text{CO}_{2\text{eq,min-die}} - (f_{cal} * \text{CO}_{2\text{eq,bio-die-b}})) * \text{YLD}} \tag{3}$$

where $C_{\text{peat}-\text{seasia}}$ is the estimated total amount of carbon in the soils of Southeast Asian peatlands and $A_{\text{peat}-\text{seasia}}$ is

Table 1. Values used in estimating greenhouse gas (GHG) emissions.

Variable	*Value*	*Source*
C_f, natural forest carbon stock	254 Mg C/ha	Murdiyarso et al. 2002
C_{op}, oil-palm plantation carbon stock	91 Mg C/ha	Murdiyarso et al. 2002
$CO_{2\mathrm{eq,min\text{-}die}}$, avoided CO_2 emission from mineral oil diesel	3.57 Mg CO_2 equivalent/ton of mineral oil diesel used[a]	Frondel & Peters 2007
$CO_{2\mathrm{eq,bio\text{-}die\text{-}a}}$, added GHG emission from palm-oil production and transportation, mill effluent, and plantation soils	1.23 Mg CO_2 equivalent/ton of palm oil[b]	Reijnders & Huijbregts 2008
$CO_{2\mathrm{eq,bio\text{-}die\text{-}b}}$, added GHG emission from palm-oil production, transportation, and mill effluent	1.18 Mg CO_2 equivalent/ton of palm oil	Reijnders & Huijbregts 2008
$C_{\mathrm{loss\text{-}soils}}$, estimated GHG emissions from soils as a result of fires for land clearing on mineral soils	19.7 Mg C/ha	Fearnside & Laurance 2004
$f_{\mathrm{fire\text{-}agb}}$, factor for additional emission of other GHG than CO_2 from burning of the aboveground vegetation	0.15[c]	Reijnders & Huijbregts 2008
$C_{\mathrm{peat\text{-}seasia}}$, estimated total amount of carbon in soils of Southeast Asian peatlands	42 billion Mg C	Hooijer et al. 2006
$A_{\mathrm{peat\text{-}seasia}}$, total area of peatland in Southeast Asia	27.1 million ha	Hooijer et al. 2006
f_{cal}, correction for difference in calorific value palm oil/mineral oil diesel	1.13[d]	Prateepchaikul & Apichato 2003
YLD, oil palm plantation yield	3.67 Mg crude palm oil/ ha/year[e]	U.S. Department of Agriculture 2007

[a] *Based on the estimated life-cycle emission of 3 kg CO_2 equivalent/L of mineral-oil diesel, converted from liters to kilograms with a factor of 1.19 L/kg.*

[b] *Estimated GHG emission from plantation cropping, local transport, processing, and for transport to a consumer (0.98 Mg CO_2 equivalent/t of palm oil); mineral soils associated with plantation operation (0.05 Mg CO_2 equivalent/t of palm oil); and anaerobic conversion of organic waste produced by palm-oil mills (0.16–0.24 Mg CO_2 equivalent/ t of palm oil; we used 0.20 Mg CO_2 equivalent/t of palm oil). It does not include emissions from the additional input of energy necessary for the esterification process (when palm-oil diesel replaces conventional diesel).*

[c] *This factor is generally 0.10–0.20, we used 0.15.*

[d] *The quotient between the high heating values of mineral-oil diesel (44.3 MJ/kg) and palm oil (39.3 MJ/kg).*

[e] *Average yield in Indonesia during the last 10 years.*

the total area of peatland in Southeast Asia (Table 1). Emissions from conversion of aboveground peatland biomass, from fire, and from greenhouse gases other than CO_2 through peat decomposition were not taken into account.

For oil-palm plantation establishment on *Imperata* grassland, it was not necessary to develop a formula to calculate the compensation point because the carbon content of the palms surpasses the original carbon content of the grassland even before the palms have reached their maximum size (Niklas & Enquist 2004). Instead, we assessed the age at which an oil-palm plantation reaches the point at which its carbon content equals or exceeds that of the grassland.

Comparing Biodiversity: Fauna

We performed a meta-analysis to compare diversity of animal species between oil-palm plantations and forest. Literature searches located 12 studies that included species of a range of taxa in both forest and oil-palm plantations (Table 2). These were supplemented with 4 unpublished data sets acquired through the Biodiversity and Oil Palm Research Network (Brühl 2001; Scott et al. 2004; Benedick 2005; Maddox et al. 2007). For all the data sets standard sampling methods were used. No minimum sample size restriction was imposed. Species-richness estimates from forest and plantations were extracted. Primary forest data were used when both logged and primary forests were sampled. Because only 2 studies reported standardized estimates of species richness, raw species richness (total number of species recorded through the period of investigation) was used in the analysis. Where possible we also determined the number of species found in the forest site that were also found in the oil palm (i.e., shared species) and calculated community similarity index on the basis of species presence-absence information (Bray-Curtis similarity index). Where the number of individuals of each species was known, Pielou's evenness index was calculated for each site. A single publication could contribute more than one data point to the analysis, where either a single study used multiple sampling methods or where data from independent comparisons were presented. If a study used multiple nonindependent sampling sites for either habitat, the mean diversity value was used. The number of data points contributing to each meta-analysis calculation varied; the maximum number of independent variables was 7 for vertebrate taxa and 15 for invertebrates.

Table 2. Total fauna species richness for natural forests and oil-palm plantations, the number of shared species, and the associated response variables.

				Number of species (S)			Responses			
Study authors	*Country*	*Taxonomic group*	*Census method*	*forest total*	*oil-palm total*	*shared*	S *(total)*	S *(shared)*	*CS* (p/a)	J'
Invertebrates										
Room 1975	Papua New Guinea	ground foraging ants	quadrats	49	29	11	0.59	0.22	0.28	0.98
Chang et al. 1997	Malaysia	mosquitoes	human bait	6	6	6	1	1	-	-
Chung et al. 2000	Malaysia	subterranean beetles	winkler sampling	306	64	-	0.21	-	-	-
Chung et al. 2000	Malaysia	arboreal beetles	mist blowing	174	40	-	0.23	-	-	-
Chung et al. 2000	Malaysia	ground beetles	flight interception	557	75	-	0.13	-	-	-
Brühl 2001[b]	Malaysia	ants (site 1)	tuna bait	20	11	6	0.55	0.30	-	-
Brühl 2001[b]	Malaysia	ants (site 2)	tuna bait	8	15	6	1.88	0.75	-	-
Brühl 2001[b]	Malaysia	ants (site 3)	tuna bait	4	8	1	2	0.25	-	-
Liow et al. 2001	Malaysia	bees	baited transects	8	17	-	2.13	-	-	-
Benedick 2005[b]	Malaysia	butterflies	banana bait traps	26	12	1	0.46	0.04	0.05	0.72
Davis & Philips 2005	Ghana	dung beetles	pitfall traps	25	20	7	0.80	0.28	0.31	0.42
Hassall et al. 2006	Malaysia	terrestrial isopods	quadrats	8	4	0	0.50	0	0.13	-
Chey 2006	Malaysia	moths (site 1)	light traps	75	85	28	1.13	0.37	-	-
Chey 2006	Malaysia	moths (site 2)	light traps	133	73	28	0.55	0.21	-	-
Chey 2006	Malaysia	moths (site 3)	light traps	78	90	11	1.15	0.14	-	-
Koh & Wilcove 2008[c]	Malaysia	butterflies	banana bait traps	63	-	12	-	0.19	0.30	-
n							15	12	5	3
Mean response (global effect size)							0.89	0.31[c]	0.21[d]	0.70[d]
Lower 95% CL							0.60	0.19	0.10	0.42
Upper 95% CL							1.22	0.51	0.30	0.98
Vertebrates										
Danielsen & Heegaard 1995	Indonesia	birds	line transects	67	17	3	0.25	0.04	0.07	0.93
Danielsen & Heegaard 1995	Indonesia	bats	mist nets	8	1	1	0.13	0.13	0.22	-
Glor et al. 2001	Dominican Republic	lizards	glue traps	6	5	3	0.83	0.50	0.55	1.02
Scott et al. 2004[b]	Indonesia	small mammals	Sherman traps	5	3	2	0.60	0.40	0.29	0.43
Aratrakorn et al. 2006	Thailand	birds	point counts	108	41	21	0.38	0.19	0.36	-
Peh et al. 2005[c], 2006	Malaysia	birds	point counts	152	-	36	-	0.24	0.38	-
Maddox et al. 2007[b]	Indonesia	medium/large mammals	camera traps	38	4	4	0.11	0.11	0.19	-
n							6	7	7	3
Mean response (global effect size)							0.38[d]	0.23[c]	0.29[d]	0.80[d]
Lower 95% CL							0.17	0.12	0.2	0.44
Upper 95% CL							0.58	0.35	0.4	0.99

[a] *Missing values indicate insufficient data in the source publication.*

[b] *Unpublished data sets.*

[c] *No data on the total number of species in oil palm.*

[d] *Significant result.*

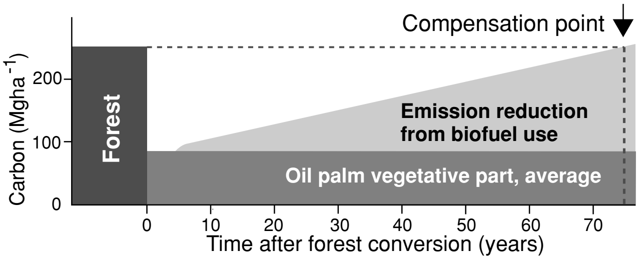

Figure 1. Carbon balance over time of 1 ha of rain forest cleared by logging and converted to palm-oil plantation for biofuel production, showing difference in carbon stocks and compensation from difference in stocks by cumulative net emission reduction when fossil fuels are substituted by palm-oil biofuel.

Following Nichols et al. (2007) we used forest biodiversity parameters to standardize the oil-palm values—forest was taken to represent intact habitat and communities—and thus to calculate the following response variables for each comparison:

(1) S_{total}, total number of species recorded in oil-palm plantations, standardized by the total number of species recorded in forest,
(2) S_{shared}, number of species shared between the forest and oil-palm sites, standardized by the total number of species in forest,
(3) CS*(p/a)*, similarity of community composition between forest and oil-palm plantations measured with the Bray-Curtis similarity index (in Primer, version 5), and
(4) J', evenness of community composition in oil-palm plantations, standardized by the evenness of community composition in forests, measured with Pielou's evenness index (Primer, version 5).

The mean response (also known as "global effect size") was calculated for each of the 4 biodiversity parameters across vertebrate and invertebrate taxa, with unweighted and with bias-corrected bootstrap 95% confidence intervals (CIs) limits (CL) derived from 999 iterations (with MetaWin, version 2; Rosenberg et al. 2000). The mean response indicated the size and direction of the difference between forest and oil-palm plantation sites. The response was considered significant if CL did not include one.

Comparing Biodiversity: Flora

To our knowledge no previous study comparing the flora of oil-palm plantations and forest has been published (Donald 2004). The data presented here are the results of sampling plants in oil palm and forest plots by H.B. in Jambi Province, Sumatra, Indonesia, in 1998. The forest comprised old-growth mixed Dipterocarp lowland rainforest without evidence of recent timber cutting, logging, or swiddening, the only human use was limited collection of nontimber products. The size of sampled forest fragments ranged from a few hectares to 900 ha. Pteridophytes were sampled in 0.16-ha plots (Beukema & Van Noordwijk 2004; Beukema et al. 2007). Total sampled area was 1.60 ha in 10 forest plots and 0.48 ha in 3 oil-palm plots located in 3 different productive plantations. Species accumulation curves were computed for both data sets with EstimateS (Colwell 2005) and sample-based rarefaction (Colwell et al. 2004). All 10 forest plots were used in the calculations. For easy comparison, Fig. 3 shows only 4 of the resulting 10 species-richness estimates for forest. Forest curves were published earlier (Beukema & Van Noordwijk 2004; Beukema et al. 2007). Because of difficulty of identification, some pteridophyte species were analyzed as one species: *Asplenium nidus* L. and *A. phyllitidis* Don; *Asplenium pellucidum* Lam. and *A. longissimum* Bl.; and *Trichomanes javanicum* Bl. and *T. singaporeanum* (Bosch) v.A.v.R. Individual species were grouped according to an independent classification of their ecological requirements and affinity with primary or late-secondary forest (Beukema & Van Noordwijk 2004; Beukema et al. 2007; Supporting Information). Nonplantation trees, native palms, lianas, and epiphytic orchids were noted as simply present or absent, regardless of species.

Results

Greenhouse Gas Emissions

Even when fully mature, oil-palm plantations contain much less carbon than old-growth forest. An estimated net amount of 163 t/ha of stored carbon is emitted to the atmosphere when rainforest is converted to oil palm, due to differences in their aboveground carbon stock.

With an average annual production of 3.7 t/ha of crude palm oil (U.S. Department of Agriculture 2007) and estimated emissions during biofuel production and transportation of 1.23 t CO_2 equivalents per ton of biofuel (Reijnders & Huijbregts 2008), we estimated that the production and use of palm-oil biofuel from land that used to be rainforest would lead to greater CO_2 release than would refining and using an energy-equivalent amount of fossil fuel for 75 years (Fig. 1). If the forest vegetation was cleared with fire, which is often the case in Indonesia (Murdiyarso et al. 2002; Germer & Sauerborn 2007), compounds that have a net greenhouse effect equal to 207 t/ha of carbon would be emitted. We estimated that recapture of this carbon would take 93 years. If the original habitat was peatland with a soil carbon stock of 1550 t/ha (Hooijer et al. 2006), we calculated that recapture of the lost carbon would take 692 years. If on the other hand the original habitat were degraded grassland with a typical carbon content of 39 t/ha (Murdiyarso et al.

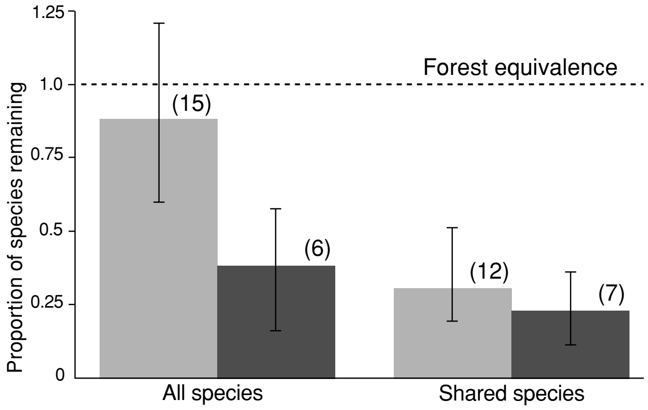

Figure 2. Impact on fauna of replacing forest with oil palms. Mean number of animal species recorded in oil palm as a proportion of those recorded in forest, with all species recorded in oil palm and only those present in both oil palm and forest ("shared species"). Data are presented as mean proportions (with bias-corrected 95% bootstrap CLs) for invertebrates (gray) and for mammals, birds, and reptiles combined (black). Meta-analysis sample sizes are provided in parentheses.

2002), oil-palm plantation establishment would lead to a net removal of CO_2 within 10 years because a 10-year-old oil-palm plantation has an aboveground carbon stock of 40 t/ha, including fruits (Niklas & Enquist 2004).

Biodiversity

Species richness of birds, lizards, and mammals was always lower in oil-palm plantations than in forest (Table 2). Across all studies, total vertebrate species richness of oil-palm plantations was less than half (38%) that of natural forest (Fig. 2). Only 23% of the vertebrate species found in forests were found in plantations. Likewise, there was only 29% similarity in community composition. The evenness response of 0.80 suggests plantations were more dominated by a few species than forest. Conversely the mean total species richness of invertebrates did not differ significantly between oil palm and forest sites (89%; Fig. 2). In some of the studies of ants, bees, and moths, total species richness was actually higher in oil palm than in the forest sites (Table 2). Nevertheless, only 31% of invertebrate species found in forests were also found in plantations, with a similarity in community composition of just 21%. The evenness response of 0.70 suggests that invertebrate communities were more dominated by a few species in oil-palm than in forest.

The flora of oil-palm plantations was impoverished compared with natural forest. Major components of the forest vegetation were completely absent from plantations, and there were no signs of regeneration: forest trees, lianas, epiphytic orchids, and indigenous palms were present in all 10 forest plots and absent from all 3 oil-palm plantations. Pteridophytes were present in all forest and oil-palm plantation plots, but their species composition, abundance, and use of substrate were different. The species richness of pteridophytes was higher in oil-palm plantations than in forest, but they held few forest species (Fig. 3). The dominant pteridophytes in oil-palm plantations were species normally seen growing on disturbed ground, along roadsides, and in early-successional vegetation after burning.

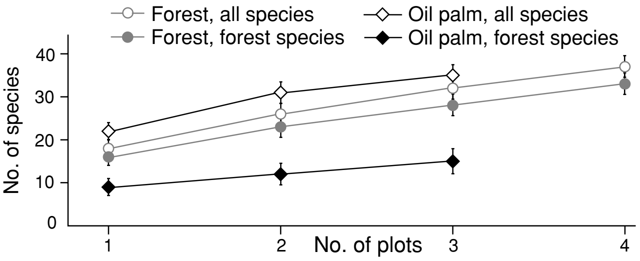

Figure 3. Impact on pteridophytes of replacing forest with oil palms. Species-accumulation curves (with SD) for pteridophytes in forests and oil-palm plantation plots (cumulative).

Discussion

Our results suggest it would take between 75 and 93 years for the carbon emissions saved through use of biofuel to compensate for the carbon lost through initial forest conversion, depending on how the forest was cleared. If the original habitat was peatland, carbon balance would take more than 600 years. Conversely, planting oil palms on *Imperata* grassland, which often takes over as the dominant habitat after deforestation, would lead to a net removal of carbon within 10 years.

Our estimates are based on published data that have inherent variation. For example, de Vries (2008) published lower estimates for the life-cycle fossil-fuel input into palm oil than we used here. Taking the lowest of his figures, $CO_{2eq,bio\text{-}die\text{-}a}$ is estimated to become 0.91 t CO_2 equivalents per ton of biofuel and $CO_{2eq,bio\text{-}die\text{-}b}$ 0.86 t CO_2 equivalents per ton of biofuel. This would reduce the carbon debt for palm oil marginally—for palm oil on mineral soils by 11 or 13 years, depending on whether or not the original forest was cleared using fire, and for palm oil from peaty soils by 96 years. Fargione et al. (2008) used lower figures for palm-oil yield, but allocated 13% of the carbon debt to by-products, used lower carbon-loss figures from aboveground biomass and made different assumptions about carbon loss from soils. Nevertheless, their estimates of compensation points for forest and peat (86 and 840 years, respectively) were very similar to ours.

Conversion of forest to oil palm resulted in significant impoverishment of the faunal community. Most forest species were lost and replaced by smaller numbers of largely nonforest species, resulting in simpler, species-poor communities dominated by a few generalist species of low conservation significance. Results of individual studies suggest that the species lost are not a random subset of the original forest fauna (Fitzherbert et al. 2008) but tend to include species with the most specialized diets, those reliant on habitat features not found in plantations (such as large trees for cavity-dwelling species), those with the smallest range sizes and those of highest conservation concern.

For example, Aratrakorn et al. (2006) found that oil-palm plantations in Thailand supported fewer bird species than forest and that these species were significantly more widespread and of lower conservation status than those in forest. Furthermore the losses of species were not random with respect to guild; all the forest woodpeckers, barbets and most of the babblers were lost, and there was a greater tendency for larger species to be lost. Maddox et al. (2007) found that 34 of the 38 medium-to-large mammals occurring within forest sites in Sumatra were absent from oil palm, including iconic species such as the Sumatran tiger (*Panthera tigris sumatrae*) and clouded leopard (*Neofelis nebulosa*). Instead, the ubiquitous wild pig (*Sus scrofa*) dominated the large-mammal fauna (Ickes 2001; Maddox et al. 2007). In Malaysia oil palm plantations lacked most bee species in the family Apidae, which are important forest pollinators (Liow et al. 2001). Beetles showed a shift in trophic structure, moving from predator-dominated communities within forests to communities with a higher proportion of fungivores and sporophages in oil palm (Chung et al. 2000). In Ghana the scarab beetle community in oil palm was dominated by invasive savanna species, which were recorded at high densities (Davis & Philips 2005), and in Sabah, ant communities were dominated by the invasive crazy ant *Anoplolepis gracilipes* (Brühl 2001).

The flora of oil-palm plantations was also severely impoverished compared with that of forest. Trees, lianas, epiphytic orchids, and indigenous palms were wholly absent from oil-palm plantations. Although the species richness of pteridophytes was higher in the plantations, they held few epiphytic forest species, which require large tree branches and the range in light and moisture levels encountered at different heights within forest. Also absent were most of the shade-loving pteridophyte species that are typical components of the understory vegetation of a mature forest. Instead, a number of nonforest pteridophyte species that normally grow on the ground were able to use the oil palms themselves as a substrate, thereby becoming even more dominant.

Our study has some important limitations. First, the analysis of greenhouse gas emissions contains uncertainties because of necessary assumptions and the limited empirical basis of some published figures. For instance, we assumed all peat is decomposed over time. Although this assumption is based on field observations of repeated deepening of drainage canals as the exposed peat layers continuously subside after being decomposed and compacted, we cannot be certain that all peat is decomposed. Nevertheless, our assessments of plantation establishment on peatland were conservative in that they did not include emissions from aboveground peatland biomass or emissions of greenhouse gases other than CO_2. We consider the magnitude of our estimates and their relative proportions reliable, although individual figures are subject to uncertainty. The uncertainties particularly arise from the paucity of studies available on the carbon stock in the soils of Southeast Asian land-use types and on the greenhouse gas emissions associated with vegetation burning, peat decomposition, and anaerobic conversion of palm-oil mill effluent (Reijnders & Huijbregts 2008).

Second, the emission analysis did not include the indirect impact of land-use change on the carbon balance of surrounding areas. For instance, the hydrology of peatlands bordering oil-palm plantations may be negatively affected by drainage taking place in the plantations. Road building and urbanization associated with agricultural expansion may also increase greenhouse gas emissions (Germer & Sauerborn 2007). Likewise, air pollution (thick haze) from forest burning can reduce photosynthesis and carbon fixation (Davies & Unam 1999). Surrounding terrestrial and aquatic ecosystems may be affected by sediments in rivers caused by soil erosion and by fertilizer and pesticide runoff from plantations. Both sediments and pollution might affect coral reefs as a potential long-term carbon sink (Wesseling et al. 1999). Again, these uncertainties are likely to make our estimates more, rather than less, conservative.

Third, our analysis of the biotic impacts of deforestation suffers from data limitations. Raw species richness is biased by differences in rates of species accumulation among habitats (Gardner et al. 2007). Where species are more easily detected, recorded species richness rises quicker. The more open vegetation in plantations might have extended the effective sampling of light traps for moths (Chey 2006). Differences in sampling effort between habitats should be standardized with methods such as rarefaction (Gotelli & Colwell 2001); however, few researchers used such techniques, and data insufficiency precluded calculation. The impact of this bias on the magnitude of the trends observed may be profound. Recorded ant species richness in oil palm was sometimes higher than in forest (Brühl 2001, Table 2), because the sampling effort in oil palm was higher. Additional sources of bias arise from between-study variation (Gurevitch & Hedges 1999). As for other meta-analyses, there is a potential publication bias of significant results (Arnqvist & Wooster 1995). Without information on species identity, we have little understanding of the influence of invasive, generalist, or transient species on the species-richness values of different habitats. The cumulative effect of all these biases is that the impact of conversion on forest species is probably underestimated.

Our findings suggest that replacing high-carbon and high-biodiversity forest or peatland with oil-palm monocultures in an effort to reduce the use of fossil fuels will accelerate both climate change and biodiversity loss. There are signs that part of the oil-palm industry is trying to minimize the impact its plantations have on biodiversity (Round Table on Sustainable Palm Oil 2007), but there is currently little effort to mitigate potential climate impacts. Other crops capable of substituting fossil fuels such as soybean (Casson 2003) and sugar cane (*Saccharum* spp.) are also rapidly expanding in some tropical countries (Food and Agriculture Organization 2007) and are likely to have similar serious impacts on both carbon (Fargione et al. 2008) and biodiversity (Donald 2004) if they are established in existing forests or peatlands.

The paucity of studies comparing biodiversity in forest and oil-palm plantations may be because most scientists find plantations biologically uninteresting and the effects of conversion predictable. Nevertheless, now that crops and cropping systems are being evaluated as possible future energy sources, such comparative studies are essential to provide the objective scientific data needed to undertake a full environmental audit. Our results on pteridophytes, for example, illustrate that species identity and ecology should be included in such studies. Changes in species composition and abundance may indicate reduced biodiversity value, and they need to be assessed. Although pteridophytes in oil-palm plantations were rather abundant and seemed to do well at first sight, our findings demonstrated that the pteridophyte flora of oil-palm plantations was very much changed and impoverished compared with that of the original rainforest.

There is a pressing need for developing and enforcing environmental standards for feedstock production and for refining practices (Groom et al. 2008). Guidance on this should be provided through environmental conventions and other international fora. The Convention on Biological Diversity has recently started to consider this matter (Convention on Biological Diversity 2007, 2008), but currently, under both the United Nations Framework Convention on Climate Change and the Kyoto Protocol, biofuels exported from developing to developed countries are considered to have zero greenhouse gas emissions when they substitute fossil fuels. To avoid perverse incentives and negative impacts, which cannot easily be reversed, all large-scale plantation and agricultural schemes should be subject to detailed environmental and socioeconomic audits before they become part of any climate-change mitigation strategy.

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Supporting Information

A list of pteridophyte species (Appendix S1) is available as part of the on-line article. The authors are responsible for the content and functionality of this material. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Adger, W. N., S. Huq, K. Brown, D. Conway, and M. Hulme. 2003. Adaptation to climate change in the developing world. Progress in Development Studies **3:**179–195.

Aratrakorn, S., S. Thunhikorn, and P. F. Donald. 2006. Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. Bird Conservation International **16:**71–82.

Arnqvist, G., and D. Wooster. 1995. Meta-analysis: synthesizing research findings in ecology and evolution. Trends in Ecology & Evolution **10:**236–240.

Benedick, S. 2005. Impacts of tropical forest fragmentation on fruit-feeding nymphalid butterflies in Sabah, Borneo. Ph.D. thesis. Institute for Tropical Biology and Conservation. Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia.

Beukema, H., and M. van Noordwijk. 2004. Terrestrial pteridophytes as indicators of a forest-like environment in rubber production systems in the lowlands of Jambi, Sumatra. Agriculture, Ecosystems and Environment **104:**63–73.

Beukema, H., F. Danielsen, G. Vincent, S. Hardiwinoto, and J. van Andel. 2007. Plant and bird diversity in rubber agroforests in the lowlands of Sumatra, Indonesia. Agroforestry Systems **70:**217–242.

Brown, E., and M. F. Jacobson. 2005. Cruel oil. Center for Science in the Public Interest, Washington, D.C.

Brühl, C. A. 2001. Leaf litter ant communities in tropical lowland rain forests in Sabah, Malaysia: effects of forest disturbance and fragmentation. Thesis. University of Würzburg, Würzburg, Germany.

Buckland, H. 2005. The oil for ape scandal. Friends of the Earth, The Ape Alliance, The Borneo Orangutan Survival Foundation, The Orangutan Foundation (U.K.), and the Sumatran Orangutan Society. Friends of the Earth Trust, London.

Carter, C., W. Finley, J. Fry, D. Jackson, and L. Willis. 2007. Palm oil markets and future supply. European Journal of Lipid Science and Technology **109:**307–314.

Casson, A. 2003. Oil palm, soybeans and critical habitat loss. World Wide Fund for Nature, Gland, Switzerland.

Chang, M. S., J. Hii, P. Buttner, and F. Mansoor. 1997. Changes in abundance and behaviour of vector mosquitoes induced by land use during the development of an oil palm plantation in Sarawak. Transactions of the Royal Society of Tropical Medicine and Hygiene **91:**382–386.

Chey, V. K. 2006. Impacts of forest conversion on biodiversity as indicated by moths. Malayan Nature Journal **57:**383–418.

Chung, A. Y. C., P. Eggleton, M. R. Speight, P. M. Hammond, and V. K. Chey. 2000. The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. Bulletin of Entomological Research **90:**475–496.

CNA Corporation. 2007. National security and the threat of climate change. CNA Corporation, Alexandria, Virginia. Available from www.securityandclimate.cna.org (accessed March 2008).

Colwell, R. K. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.0. User's guide and application. University of Connecticut, Storrs.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology **85:**2717–2727.

Convention on Biological Diversity (CBD). 2007. Recommendation XII/5 and XII/7 from 12th Meeting of The Subsidiary Body on Scientific, Technical and Technological Advice of the Convention on Biological Diversity 2007. CBD, Montreal. Available from http://www.cbd.int/ meetings/sbstta-12/ (accessed September 2008).

Convention on Biological Diversity (CBD). 2008. Recommendation IX/2 from the 9th Convention of Parties in Bonn 2008. CBD, Montreal. Available from http://www.cbd.int/decisions/?dec = IX/2 (accessed September 2008).

Cotula, L., N. Dyer, and S. Vermeulen. 2008. Fuelling exclusion? The biofuels boom and poor people's access to land. International Institute for Environment and Development, London.

Coyle, W. 2007. The future of biofuels. Economic Research Service, Washington, D.C.

Danielsen, F., and M. Heegaard. 1995. Impact of logging and plantation development on species diversity: a case study from Sumatra. Pages 73–92 in Ø. Sandbukt, editor. Management of tropical forests: towards an integrated perspective. University of Oslo, Oslo, Norway.

Davis, A. L. V., and T. K. Philips. 2005. Effect of deforestation on a southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. Environmental Entomology **34:**1081–1088.

Davies, S. J., and L. Unam. 1999. Smoke-haze from the 1997 Indonesian forest fires: effects on pollution levels, local climate, atmospheric CO_2 concentrations, and tree photosynthesis. Forest Ecology and Management **124:**137–144.

De Vries, S. C. 2008. The bio-fuel debate and fossil energy use in palm oil production: a critique of Reijnders and Huijbregts 2007. Journal of Cleaner Production DOI: 10.1016/jclepro. 2008.01.009.

Donald, P. F. 2004. Biodiversity impacts of some agricultural commodity production systems. Conservation Biology **18:**17–37.

Fargione, J., J. Hill, D. Tilman, S. Polasky, and P. Hawthorne. 2008. Land clearing and the biofuel carbon debt. Science DOI: 10.1126/science.1152747.

Fearnside, P. M., and W. F. Laurance. 2004. Tropical deforestation and greenhouse-gas emissions. Ecological Applications **14:**982–986.

Fitzherbert, E. B., M. J. Struebig, A. Morel, F. Danielsen, C. A. Brühl, P. F. Donald, and B. Phalan. 2008. How will oil palm expansion affect biodiversity? Trends in Ecology & Evolution **23:**538–545.

Food and Agriculture Organization (FAO). 2006. Global forest assessment 2005. FAO forestry paper 147. FAO, Rome.

Food and Agriculture Organization (FAO). 2007. FAOSTAT. FAO, Rome. Available from http://faostat.fao.org/ (accessed January 2008).

Frondel, M., and J. Peters. 2007. Biodiesel: a new Oildorado? Energy Policy **35:**1675–1684.

Gardner, T. A., J. Barlow, L. Parry, and C. A. Peres. 2007. Predicting the uncertain future of tropical forest species in a data vacuum. Biotropica **39:**25–30.

Garrity, D. P., M. Soekardi, M. van Noordwijk, R. de la Cruz, P. S. Pathak, H. P. M. Gunasena, N. van So, G. Huijun, and N. M. Majid. 1996. The *Imperata* grasslands of tropical Asia: area, distribution, and typology. Agroforestry Systems **36:**3–29.

Geist, H. J., and E. F. Lambin. 2002. Proximate causes and underlying driving forces of tropical deforestation. BioScience **52:**143–150.

Germer, J., and J. Sauerborn. 2007. Estimation of the impact of oil palm plantation establishment on greenhouse gas balance. Environment, Development and Sustainability DOI: 10.1007/s10668-006-9080-1.

Glor, R. E., A. S. Flecker, M. F. Benard, and A. G. Power. 2001. Lizard diversity and agricultural disturbance in a Caribbean forest landscape. Biodiversity and Conservation **10:**711–723.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **3:**379–391.

Groom, M. J., E. M. Gray, and P. A. Townsend. 2008. Biofuels and biodiversity: principles for creating better policies for biofuel production. Conservation Biology **22:**602–609.

Gurevitch, J., and L. V. Hedges. 1999. Statistical Issues in Ecological meta-analysis. Ecology **80:**1142–1149.

Hassall, M., D. T. Jones, S. Taiti, Z. Latipi, S. L. Sutton, and M. Mohammed. 2006. Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. European Journal of Soil Biology **42:**S197–S207.

Hooijer, A., M. Silvius, H. Wösten, and S. Page. 2006. PEAT-CO2, assessment of CO_2 emissions from drained peatlands in SE Asia. Delft Hydraulics, Delft, The Netherlands.

Ickes, K. 2001. Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland dipterocarp rain forest of peninsular Malaysia. Biotropica **33:**682–690.

Koh, L. P., and D. S. Wilcove. 2007. Cashing in palm oil for conservation. Nature **448:**993–994.

Koh, L. P., and D. S. Wilcove. 2008. Is oil palm agriculture really destroying tropical biodiversity? Conservation Letters DOI: 10.1111/j.1755-263x.2008.00011.x.

Koizumi, T., and K. Ohga. 2008. Biofuels policies in Asian countries: impact of the expanded biofuels programs on world agricultural markets. Journal of Agricultural and Food Industrial Organization **5:** http://www.bepress.com/jafio/vol5/iss2/art8.

Laurance, W. F. 2007. Forest destruction in tropical Asia. Current Science **93:**1544–1550.

Liow, L. H., N. S. Sodhi, and T. Elmqvist. 2001. Bee diversity along a disturbance gradient in tropical lowland forests of South East Asia. Journal of Applied Ecology **38:**180–192.

Maddox, T. M., E. Gemita, S. Wijamukti, and A. Selampassy. 2007. The conservation of tigers and other wildlife in oil palm plantations, Jambi Province, Sumatra, Indonesia. Zoological Society of London.

Murdiyarso, D., M. van Noordwijk, U. R. Wasrin, T. P. Tomich, and A. N. Gillison. 2002. Environmental benefits and sustainable landuse options in the Jambi transect, Sumatra. Journal of Vegetation Science **13:**429–438.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403:**853–858.

Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, K. Vulinec, and The Scarabaeinae Research Network. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biological Conservation **137:**1–19.

Niklas, K. J., and B. J. Enquist. 2004. Biomass allocation and growth data of seeded plants. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee. Available from http://www.daac.ornl.gov (accessed March 2008).

Parish, F., A. Sirin, D. Charman, H. Joosten, T. Minaeva, and M. Silvius, editors. 2007. Assessment of peatlands, biodiversity and climate change. Global Environment Centre, Kuala Lumpur, Malaysia, and Wetlands International, Wageningen, The Netherlands.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421:** 37–42.

Peh, K. S-H., J. de Jong, N. S. Sodhi, S. L.-H. Lim, and C. A.-M. Yap. 2005. Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed rural habitats of southern Peninsular Malaysia. Biological Conservation **123:**489–505.

Peh, K. S.-H., N. S. Sodhi, J. de Jong, C. H. Sekercioglu, C. A.-M. Yap, and S. L.-H. Lim. 2006. Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia. Diversity and Distributions **12:**572–581.

Prateepchaikul, G., and T. Apichato. 2003. Palm oil as a fuel for agricultural diesel engines: comparative testing against diesel oil. Journal of Science and Technology **25:**317–326.

Reijnders, L., and M. A. J. Huijbregts. 2008. Palm oil and the emission of carbon-based greenhouse gases. Journal of Cleaner Production **16:**477–482.

Righelato, R., and D. V. Spracklen. 2007. Carbon mitigation by biofuels or by saving and restoring forests? Science **317:**902.

Room, P. M. 1975. Diversity and organization of the ground foraging ant faunas of forest, grassland and tree crops in Papua New Guinea. Australian Journal of Zoology **23:**71–89.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin. Version 2. Statistical software for meta analysis. Sinauer Associates, Boston, Massachusetts.

Round Table on Sustainable Palm Oil (RSPO). 2007. Principles and criteria for sustainable palm oil. RSPO, Kuala Lumpur, Malaysia.

Royal Society. 2008. Sustainable biofuels: prospects and challenges. The Royal Society, London.

Scharlemann, J. P. W., and W. F. Laurance. 2008. How green are biofuels? Science **319:**43–44.

Scott, D. M., E. Gemita, and T. M. Maddox. 2004. Small cats in human modified landscapes in Sumatra. Cat News **40:**23–25.

Skutsch, M., N. Bird, E. Trines, M. Dutschke, P. Frumhoff, B. de Jong, P. van Laake, O. Masera, and D. Murdiyarso. 2007. Clearing the way for reducing emissions from tropical deforestation. Journal of Environmental Science and Policy **10:**322–334.

Sodhi, N. S., L. P. Koh, B. W. Brook, and P. K. L. Ng. 2004. Southeast Asian biodiversity: an impending disaster. Trends in Ecology & Evolution **19:**654–660.

Soepadmo, E. 1993. Tropical rain forests as carbon sinks. Chemosphere **27:**1025–1039.

Tan, K. T., K. T. Lee, A. R. Mohamed, and S. Bhatia. 2007. Palm oil: addressing issues and towards sustainable development. Renewable and Sustainable Energy Reviews DOI:10.1016/j.rser.2007.10.001.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. P. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhammer. 2001. Forecasting agriculturally driven global environmental change. Science **292:**281–284.

Turner, E. C., J. L. Snaddon, T. M. Fayle, and W. A. Foster. 2008. Oil palm research in context: identifying the need for biodiversity assessment. PLoS ONE **3**(2): e1572. DOI:10.1371/journal.pone.0001572.

U.S. Department of Agriculture (USDA). 2007. GAIN report Indonesia oilseeds PSD tables for oil palm. USDA, Washington, D.C. Available from http://www.usda.gov/wps/portal/usdahome (accessed January 2008).

Wesseling, I., A. J. Uychiaoco, P. M. Aliño, T. Aurin, and J. E. Vermaat. 1999. Damage and recovery of four Philippine corals from short-term sediment burial. Marine Ecology-Progress Series **176:**11–15.